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CONTENTS

Anti-predator Strategies. II. Grasshoppers (Orthoptera, Acrididae) Attacked by <i>Prionyx parkeri</i> and Some <i>Tachysphex</i> Wasps (Hymenoptera, Sphecinae and Larrinae): A Descriptive Study. <i>A. L. Steiner</i>	1
A Comparison of the Nest Phenologies of Three Species of <i>Pogonomyrmex</i> Harvester Ants (Hymenoptera: Formicidae). <i>William P. MacKay</i>	25
Laboratory Evaluation of Within-species, Between-Species, and Parthenogenetic Reproduction in <i>Reticulitermes flavipes</i> and <i>Reticulitermes virginicus</i> . <i>Ralph W. Howard, Eldon J. Mallette, Michael I. Haverty, and Richard V. Smythe</i>	75
Ecology and Life History of the <i>Rhytidoponera impressa</i> Group (Hymenoptera: Formicidae). I. Habitats, Nest Sites, and Foraging Behavior. <i>Philip S. Ward</i>	89
Ecology and Life History of the <i>Rhytidoponera impressa</i> Group (Hymenoptera: Formicidae). II. Colony Origin, Seasonal Cycles and Reproduction. <i>Philip S. Ward</i>	109
The Ontogeny of <i>Lyssomanes viridis</i> (Walckenaer) (Araneae: Salticidae) on <i>Magnolia grandiflora</i> L. <i>David B. Richman and Willard H. Whitcomb</i>	127
The Emigration Behavior of Two Species of the Genus <i>Pheidole</i> (Hymenoptera: Formicidae). <i>Robert Droual and Howard Topoff</i>	135
Statory Behavior in Nomadic Colonies of Army Ants: The Effect of Overfeeding. <i>Howard Topoff, Aaron Rothstein, Susan Pujdak, and Tina Dahlstrom</i>	151
Life History of <i>Antaeotricha</i> sp. (Lepidoptera: Oecophoridae: Stenomatinae) in Panama. <i>Annette Aiello</i>	163
<i>Polistes gallicus</i> in Massachusetts (Hymenoptera: Vespidae). <i>Mary Hathaway</i>	169
Notes on the Population Ecology of Cicadas (Homoptera: Cicadidae) in the Cuesta Angel Forest Ravine of Northeastern Costa Rica. <i>Allen M. Young</i>	175

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ANTI-PREDATOR STRATEGIES.

II.* GRASSHOPPERS (ORTHOPTERA, ACRIDIDAE) ATTACKED BY *PRIONYX PARKERI* AND SOME *TACHYSPHEX* WASPS (HYMENOPTERA, SPHECINAE AND LARRINAE): A DESCRIPTIVE STUDY

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INTRODUCTION

Predator and anti-predator adaptations, strategies, have been studied extensively in recent years (see for instance Curio 1976 and Edmunds 1974 for some recent reviews). Problems of predator-prey coevolution, mimicry, protective coloration (e.g., Cott's monumental work, 1940), optimal strategies, etc., have received a great deal of attention. Defense mechanisms are extremely diverse and can even involve use of a commensal species (e.g. Ross 1971). A variety of sensory channels can be used such as visual (e.g. Cott 1940; Robinson 1969), acoustical (e.g. Roeder 1965), chemical (e.g. Eisner and Meinwald 1966; Eisner 1970), mechanical, vibratory (e.g. Tautz and Markl 1975) to mention only a few examples. Predators such as mammals, birds, reptiles (e.g. Curio 1970), fish, mollusks have been extensively studied.

Among insects, solitary and social wasps have also been intensively studied but on the whole surprisingly little is known about the defensive mechanisms of their "helpless" prey. Prey capture is often very difficult to observe and even more so to study extensively in natural conditions. The few exceptions mostly deal with prey that represent a potentially formidable opponent (e.g. spider, praying

*For part I see Steiner 1968 in the Literature Cited.

Manuscript received by the editor May 11, 1981

mantis, etc.). Counter-attacks by such prey and occasional killing of the predator have even been reported (e.g., Deleurance 1941, pp. 287–288, for a praying mantis attacked by the sphecoid wasp *Stizus distinguendus*; also 1945, p. 29 for *Tachysphex costai* Dest.). Dead spider wasps have also been found in spider webs in natural conditions (pers. obs.). Non-predaceous prey can also exhibit defense reactions, however, as shown before for crickets attacked by *Liris nigra* wasps (Steiner 1968).

The anti-predator system of acridid grasshoppers is now described, analyzed, as observed both in nature and captivity (summarized in Steiner 1976). The prey are: (1) mainly adult or subadult Oedipodinae, but also a few Cyrtacanthacridinae, all attacked by the sphecoid wasp *Prionyx parkeri* Bohart and Menke, (2) to a much lesser extent smaller, earlier, instars preyed upon by *Tachysphex* wasps (details in next section). For the latter prey, defense reactions were essentially the same, except for the ones involving the wings, undeveloped at these stages. Prey hunting and stinging by *Prionyx parkeri* are described in detail in Steiner 1981 (in press).

MATERIALS AND METHODS

Field observations

Prionyx parkeri wasps were observed mainly in the grassland desert and adjacent riparian habitat of S.E. Arizona, U.S.A., at the foot of the Chiricahua Mountains, East of Willcox, during the summer of 1972.

Observations in captivity

Individually marked *Prionyx parkeri* and *Tachysphex* [mostly *tarsatus* (Say)] wasps were observed in controlled laboratory units about 60 × 50 × 50 cm (general method described in Steiner 1965): (1) at the Southwestern Research Station, Portal, Arizona, during the spring and part of the summer 1973 (= Arizona study); (2) in central Oregon, U.S.A., near Bend, using a field trailer, during the summer of 1977 (= Oregon study). The following acridid grasshoppers taken from the wasps' habitats were used in the Arizona study; (1) for *P. parkeri*, adult or last instar nymphs of: Oedipodinae, mostly *Trimerotropis pallidipennis* p. (Burm.), also *Conozoa carinata* Rehn, a few *Cibolacris parviceps* (Walker) — Cyrtacanthacridinae, a few *Psoloessa delicatula* Scudder and an occasional

Eritettix variabilis Bruner; (2) for *Tachysphex* wasps, small acridid nymphs of: Oedipodinae, mostly *Conozoa carinata* Rehn and also a few *Trimerotropis pallidipennis* p. (Burm.); Cyrtacanthacridinae, a few *Psoloessa delicatula* and an occasional *Melanoplus* sp., *Derotmema* sp., *Rehnita* sp. Rather similar but un-determined grasshoppers were used in the Oregon study, in captivity. The grasshoppers were provided either ad libitum, or in staged encounters.

Observations were mostly continuous, with "all occurrences" sampling of wasp-prey interactions. Precise quantifications were difficult or impossible because initial stages of encounters were often sudden and unpredictable. Generally speaking proof of effects of escape-defense reactions is often very difficult to establish (e.g. Edmunds 1974, p. 240). This study is basically descriptive.

Total observation times were; (1) for captive *P. parkeri* in the Arizona study about 178 h over a period of 30 observation days (\bar{X} = about 6 h-day) and in the Oregon study about 142 h for 14 observation days (\bar{X} = about 6½ h-day); (2) for captive *Tachysphex* wasps in the Arizona study about 224 h for 37 observation days (\bar{X} = about 6h-day) and in the Oregon study about 224½ h for 35 observation-day (\bar{X} = 6¼ h-day).

RESULTS: DESCRIPTION OF RESPONSES, CONDITIONS

*Common responses: escape by jumping (flying) away,
staying put = first line of defense.*

a) Field observations

Visually hunting *Prionyx (parkeri?)* wasps were observed in the short and sparse grassy vegetation, characteristic of the upper Sonoran desert grassland. Acridid grasshoppers were abundant, particularly Oedipodinae such as *Mestobregma plattei rubripenne* (Bruner) adults, also found stored in the nests of these wasps. The most common response to wasps approaching or pouncing was a very sudden, even startling, escape by jumping (Fig. 5a) and flying away (Fig. 5b). The bright flash of the colorful banded wings came in sharp contrast with the sudden disappearance from sight, after landing (crypticity: Fig. 5c). The wasps seldom followed the escaping grasshoppers in flight, but occasionally did so (Fig. 5b) and even managed to cling to them in mid air and to deliver stings before landing. Most stung grasshoppers were apparently caught by surprise or at the preparatory stages of escape. Close range and

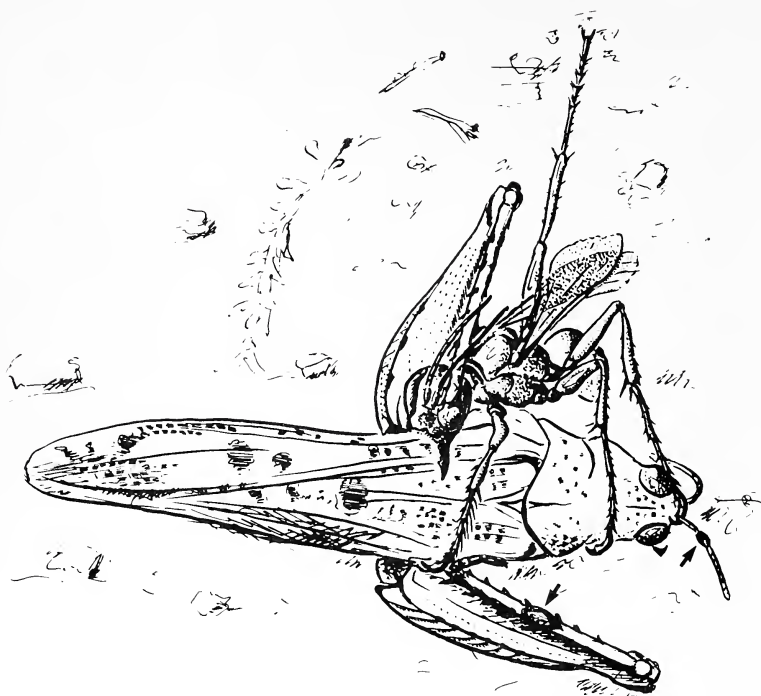


Fig. 1: Attack of an adult acridid grasshopper (Oedipodinae) by a *Prionyx parkeri* wasp. The wasp uses both the strong mandibles and long, powerful legs, to firmly hold the prey and prevent escape. The grasshopper tries (in vain) to push away the wasp with both powerful hind legs by applying strong pressure on the points where the wasp is anchored (head and one fore leg). Several drops of regurgitated repelling fluid are indicated by arrows. The wasp already assumes the appropriate posture for the first paralyzing sting, delivered in the throat of the victim.

quantitative observations were almost impossible. At times the grasshoppers stayed put instead of escaping, for no apparent reason. Attack of the wasp does not necessarily follow detection of a suitable prey, however, since hunting wasps go through periods of temporary refractoriness (Steiner 1962, 1976, 1978, 1979). This considerably complicates the study of possible effects of prey-defenses on the wasps.

b) Observations in captivity

The same responses were also recorded in captivity. Flying away

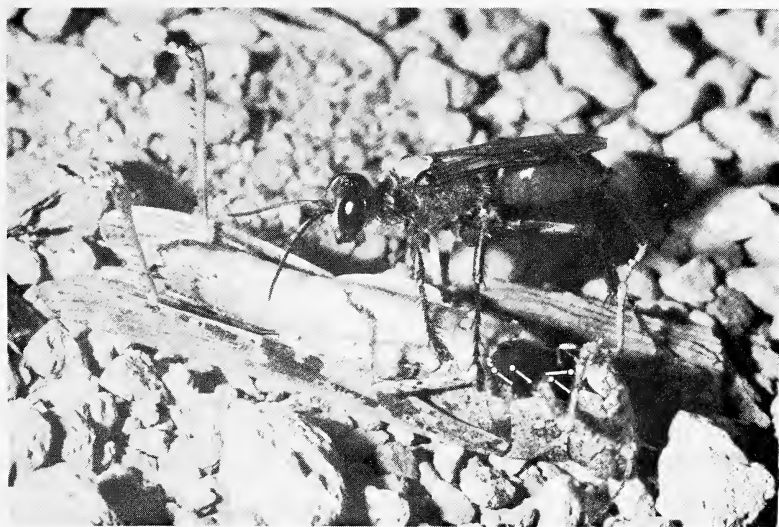


Fig. 2: Regurgitation of a repelling fluid. An acridid grasshopper (Oedipodinae), just paralyzed by a *Prionyx parkeri* wasp, lies on its back and a huge drop of fluid covers a large surface of the ventral thoracic area where all four stinging sites are located (indicated by white dots and arrows). Wasps often hesitate to dip their abdomen tip into this viscous, probably offensive, fluid. Accidental contact triggers vigorous body rubbing in an attempt to eliminate the unpleasant fluid from the body surface.

and long-range escape were impossible, however, because of space limitations.

There was no evidence of active avoidance of *Prionyx* or *Tachysphex* wasps by grasshoppers ("predator recognition"), even after repeated attacks. Escape was always in direct response to attack, imminent attack, or at least sudden movements such as a wasp running and/or pouncing. Thus predator and prey were often seen basking together. Immediately following an attack, the escape threshold was clearly lowered, however.

Mechanical defenses after contact: kicking, pushing and/or brushing away the wasp; biting; wing fluttering and flying
= second line of defense (Fig. 1)

After contact, *Prionyx* wasps attempt to anchor themselves to the struggling or escaping grasshopper. They try to gain a firm grip

using their powerful spinose legs, terminal claws, and also mandibles. These wasps tightly "embrace" the grasshopper, in an anti-parallel posture and strongly cling to them (Fig. 1). In contrast, many larrine wasps (e.g. *Liris*, *Tachysphex*) are comparatively frail, short-legged, and cannot physically overpower their prey as successfully as *Prionyx* wasps do. Their prey often struggles free, in contrast to *Prionyx* prey which seldom succeed, after the "embracing" stage, in spite of frantic efforts to kick and/or brush, push away the attacker with the powerful hind legs. *Prionyx* prey also try to deny free access of the wasp to the dorsal side by raising their long, folded, hind legs, often beyond the vertical, headwards (hind leg raising: Fig. 5e). Powerful kicks (Fig. 5e) sometimes send the wasp a few cm from the grasshopper, but this works mostly before the wasp can secure a firm grip. Pushing action with the tarsi of the powerful hind legs can also be recorded. They are very precisely directed at the points seized by the wasp as shown in Fig. 1. In the latter, drawn from a photograph, the grasshopper tries, with its right hind leg, to push away the left front leg of the wasp while it attempts, with the left hind leg, to exercise strong pressure on the head, jaws, of the attacker and presumably get the wasp to release its mandibular grip (in Fig. 5f these "points of pressure" have been circled). Wing fluttering and even flying attempts can also be observed in reponse to the grasping action of the wasp. The orthopteran also performs snapping motions with the jaws but is seldom able to bite the wasp. The very globulous abdomen of *Prionyx* wasps appears to be especially well adapted to prevent such biting. The abdomen is particularly exposed since the wasp delivers the first sting in the throat of the prey, dangerously close to the powerful jaws (Fig. 5g).

Chemical defenses: regurgitated fluid (Fig. 2)

In addition and often as a last ditch defense the grasshopper regurgitates through the mouth a large drop of dark fluid ("tobacco juice") that usually spreads rapidly over the body areas closest to the mouth, ventrally, namely the thoracic surface (Fig. 2). This surface sometimes becomes completely covered with the substance. From there it can spread to other body areas, if struggling is intense enough. On Fig. 1 one drop can be seen on the right antenna of the grasshopper and one on the tibia of the right hind leg (arrows).

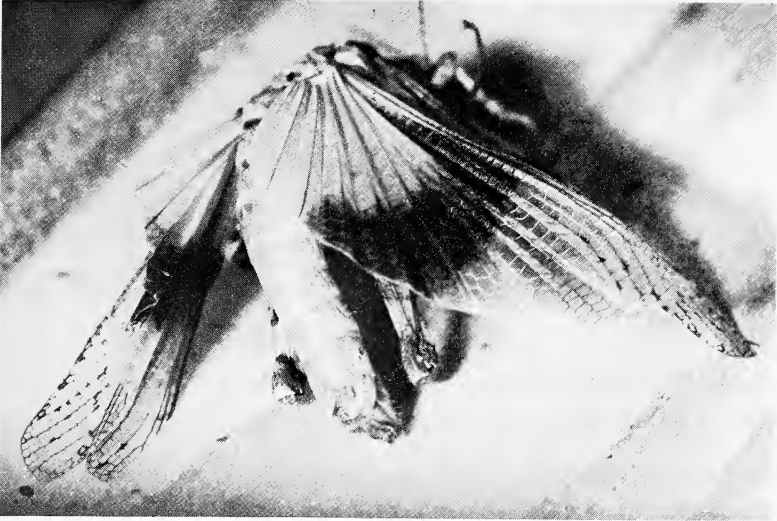


Fig. 3: Postural defense replacing escape (startle and/or death feigning display?). The attacked grasshopper froze into a hunched posture, with appendages tucked in, thus protecting the vulnerable ventral surface. The colorful wings, showing striking semi-circular dark markings, are fully extended and/or flutter convulsively. The wasp, after many vain efforts, managed to slip under the grasshopper (one leg is still visible on the right of the grasshopper head) and will attempt to reach the vulnerable ventral surface of the thorax made less accessible by the posture and interposition of appendages (obstruction behavior).

*Uncommon and odd postural defenses replacing escape:
stationary wing flashing or extension; body arching; freezing
(Fig. 3) = first line of defense.*

a) Field observations

These rare occurrences guarantee that such responses are not reducible to captivity artifacts.

The first observation was made on Sept. 4, 1972, near the end of the morning, in the Arizona grassland desert. One hunting *Prionux (parkeri?)* suddenly pounced on a motionless grasshopper. Instead of trying to escape, as usual, the latter was seen with the colorful wings open, fluttering convulsively, with a startling suddenness, thus producing a striking color flash. The hind legs were rigidly extended behind like in the flying posture (Fig. 5b). However the



Fig. 4: A *Prionyx parkeri* wasp succeeded in overturning a "frozen" oedipodine grasshopper. This makes the ventral surface of the thorax more accessible to the stings of the wasp. One small drop of repellent fluid can be seen on the abdomen of the wasp. After stinging is over, the wasp will vigorously rub its abdomen on the substrate, in an effort to eliminate this unpleasant, perhaps noxious, fluid. Note (also in Fig. 2) the dot of Testor paint on the dorsal surface of the wasp thorax, for individual identification.

whole body was strongly arched downward as in Fig. 3. For the observer, it looked as if the "frozen" grasshopper was disabled or dying. The wasp left the grasshopper alone and pursued her hunting trip. Under the impression that the prey had received a sting or two, I picked it up only to see it instantly recover without the slightest trace of paralysis. Obviously the grasshopper, later identified as an adult *Mestobregma plattei rubripenne* (Bruner), had not been stung and was not disabled at all. This species is an acceptable prey since it was also found in two nests dug up the same day, nearby. In another, similar, instance the upper wings (tegmina) opened only slightly, just enough to uncover the triangular base of the vivid red wings that remained folded. Again the wasp failed to paralyze the frozen grasshopper which later escaped just as suddenly as the first one, unharmed. The latter case might be a less intense version of the first case. Presumably all gradations could be observed.

The eliciting stimuli of such reactions could not be determined, because of the suddenness and unpredictability of such encounters. Sight of the rapidly approaching predator and/or mechanical contact are likely candidates.

b) Observations in captivity (Figs. 3 and 4)

Similar or identical responses were also observed in captivity at close range and in better conditions. Confinement seemed to even somehow favor appearance of this behavior perhaps because of restricted escape and/or greater concentration of attacks. Often the extended wings and whole body were also strongly curved downwards, sometimes even tightly pressed against the substrate (Fig. 3). The appendages and head were tucked in and more or less invisible under the protective "umbrella" of the wings. The sudden flash of the colorful wings and dark semi-circular markings, followed by the appearance of convulsive movement and finally the illusion of a disabled or dying grasshopper were, indeed, an arresting sight, at least for a human observer.

Curiously such frozen grasshoppers mostly failed to suddenly "resuscitate" and escape after it had become evident that their postural defense had failed to stop the wasp attack. Such misfiring might be a cost of this strategy because of the strong inhibitory influences apparently involved. Sometimes wing fluttering resumed as the wasp attempted to deliver the paralyzing stings. If left alone by the wasp the grasshoppers would however invariably recover without any sign of discomfort, like in the wild.

Such displays were never observed with *Tachysphex* wasps, perhaps because the much smaller grasshopper nymphs they attack have undeveloped wings . . . that cannot be used.

If the *Prionyx* wasps succeed in overcoming all these various defense mechanisms or hurdles, as they often do, they then attempt to deliver an average four successive stings, always on the same stinging sites and in a predictable order (summarized in Steiner 1976; details in Steiner 1981). The paralyzed grasshopper can then be safely and freely manipulated and stored in the nest, without any resistance, obstruction.

ANALYSIS, DISCUSSION, COMPARISONS

Discussion is concerned mainly with possible or plausible interpretations and evolutionary significance of these various defense

reactions, their degree of predator-specificity. Comparisons are made with other orthopterans, with similar and different anti-predator strategies. Effectiveness, always difficult to prove, particularly when attacks or lack thereof depend on the internal state of the predator like in the present case, will be assessed rather than analyzed mathematically.

All defenses described before (except crypticity) are secondary rather than primary defenses since they are exhibited during encounters (Edmunds 1974, pp. 1, 136). Defenses are often anti-location, anti-capture or anti-consumption devices (i.e. Alcock 1975, p. 333). Furthermore, many species have several lines of defense (integrated defense systems: Edmunds 1974, p. 243). Thus the mantid *Polyspilota aeruginosa* may run, fly, give a startle display, slash at the attacker. It can also feign death if persistently handled in a rough way. It soon recovers, however. The brightly colored abdomen might also represent flash behavior (in Edmunds 1974, p. 245). Each aspect of the defense system will now be discussed separately.

Escape by jumping, flying away

This is a classical and common case of sudden startling (flash or deimatic behavior Fig. 5b) followed by sudden disappearance into crypsis (landing; Fig. 5c) (Edmunds 1974, pp. 146–148) by using protective colors (e.g. Isely 1938). This is usually a very efficient mechanism but *Prionyx* wasps occasionally dash at flying grasshoppers (Fig. 5b), even sting them in mid air, or take them by surprise before they can escape. Pygmy mole crickets that escape by flying away are also grasped and/or stung during flight by the sphecid wasp *Tachytes mergus* (Yoshimoto, in Krombein and Kurczewski 1963, p. 147) and also by *Tachytes minutus* (Kurczewski 1966). This defense is not especially aimed at digger wasp predators.

Detection of the predator is probably visual but could also be based on hairs sensitive to airborne vibrations, as in some caterpillars such as *Barathra brassicae* (Tautz and Markl 1978).

Use of hind legs other than for jumping: kicking or obstructive behavior such as hind leg raising or interpositions, brushing away, pushing away

Hind leg autotomy used by crickets (Steiner 1968) was never observed in grasshoppers in the present study but *Prionyx* wasps

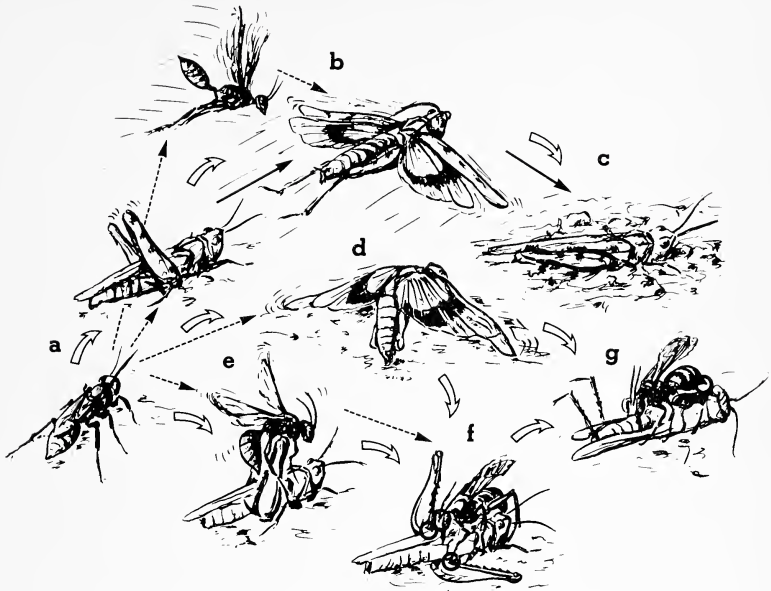


Fig. 5: Summary of oedipodine grasshopper anti-predator actions and *Prionyx*-prey interactions. a: the wasp detected a grasshopper which is at the preparatory stage of jumping (J); b: the prey flies away (F), suddenly opening very colorful wings with conspicuous semi-circular dark markings (startle display) and in some cases the wasp follows the grasshopper in flight and even stings it in midair; c: the escaping prey suddenly lands and blends with the substrate (crypsis); d: instead of escaping the grasshopper sometimes "freezes" into an odd posture somewhat remindful of an inhibited flying action; the posture and convulsive wing fluttering give the impression that the orthopteran is disabled, dying (disablement display? thanatosis?); at the same time the posture and hunching appear to emphasize the semi-circular dark markings on the wings (eyespot intimidation display, "bluff"?); furthermore in this posture, access of the vulnerable ventral side of the thorax, where stings are delivered, is reduced or impossible for the wasp (obstruction behavior); e: hind leg raising (HLR) is another obstructive behavior that makes initial posturing of the wasp difficult or impossible; kicking can also send the wasp a few cm away; f: hind legs are also used for brushing (B) and/or pushing away (P) the wasp; pressure is applied on the circled areas so as to try to force the wasp to release her mandibular and leg grip; g: as a last ditch defense the grasshopper can release a repellent fluid through the mouth, which rapidly spreads over the ventral thoracic surface where all stinging sites are located; the wasp often hesitates to dip into this pool her abdomen tip (circled); the latter is also exposed to powerful bites from the grasshopper; therefore the throat of the prey must be quickly stung to stop these mouth-based defenses. Solid and dashed arrows indicate prey and wasp movements, respectively; open arrows show possible sequences of events but these sequences can also be broken if the defenses are effective and the wasp gives up.

usually seize the wing base(s) or abdomen rather than one hind leg (Fig. 1). Hind legs of crickets, grasshoppers, sometimes phasmids, often covered with strong spines, are one of their major systems of escape and/or defense. Some wingless phasmids can jab the spines into an aggressor (Robinson 1968b). Overt defense by kicking has also been described in some large aphids (in Edmunds 1974, p. 245) and in a number of orthopterans such as crickets (Steiner 1968) and *Locusta migratoria* for instance (Parker et al. 1974). In the latter case it can be so violent that the attacker is knocked 20–30 cm away. According to Parker et al. (1974) hind leg raising often precedes kicking (threat?). It is also part of the defense postures of male *L. migratoria*, the giant weta (*Deinacrida*) of New Zealand (in Sebeok 1977, Fig. 5a, p. 342) and mormon crickets when attacked by the digger wasp *Palmodes laeviventris* (Parker and Mabee 1928, p. 9). In the latter case, as in *Prionyx* and *Tachysphex*, the wasps succeeded in stinging only with considerable difficulty. In the present study hind legs were often raised past the vertical line (Fig. 5e) and even as far forward as the level of the head, as in Fig. 1 for instance, in addition to tail or body raising. This was also observed once in response to an approaching *Tachysphex tarsatus*. Freezing into such postures made access to the dorsal area and wasp posturing very difficult, sometimes impossible (Fig. 5e) (obstructive behavior) and the efficiency of this behavior appeared even to increase as a result of repeated attacks. Interposition of legs (obstruction behavior) was also observed in mole crickets attacked by *Larra* wasps (Williams 1928).

Brushing and pushing away (Figs. 1 and 5f) are more difficult to evaluate since they are more graded and variable responses which are not easy to detect, let alone quantify, in the confusion of the attack. Plausibly these responses work best (if at all) at early stages of contact with the wasp, also if the prey is very large and vigorous or if the wasp is more likely to easily give up, for instance at early stages of hunting (Steiner 1976). It is doubtful that a firmly anchored wasp can easily be dislodged in this way.

[Remark: some orthopterans extend or raise their fore legs, vertically, as part of a threat-intimidation posture (e.g., *Neobarettia*: Cohn, in Sebeok 1977, p. 342, Fig. 5b)].

Orthopteran hind legs are often given special attention and are paralyzed first by some predatory wasps such as *Liris* and *Tachysphex* (Steiner 1962, 1976). *Prionyx* wasps can give priority to the

mouth-based defenses (biting, regurgitating), now discussed, since they effectively neutralize hind leg defenses with their powerful “embracing” legs. Correspondingly, these wasps deliver the first sting in the throat, not around the hind legs (Steiner 1976).

*Biting and retaliation (aggressive defense:
Edmunds 1974, p. 182)*

Orthopterans commonly use their powerful jaws for threat, intimidation or even active defense, retaliation, if not for predation. The predaceous North American katydid *Neobarettia* severely bites and displays the open mandibles as part of the threat-intimidation display (Cohn, in Sebeok 1977, p. 342, Fig. 5b).

In one observation in captivity (Arizona, June 24 1973, 1335 h) a wrongly positioned *Tachysphex tarsatus* (No + 1042) was clearly and severely bitten by a nymph *Trimerotropis pallidipennis* p. (Burm.) (No + 1098) during a stinging attempt. This suggests that the wasp is particularly vulnerable before proper positioning is achieved and that strong selection pressures in the direction of minimum risk must have shaped the usual stinging postures. The penalty for wrong posturing can be very heavy. Thus the above wasp was found dying in the cage the next day, June 25, most likely as a result of this violent retaliation of the prey.

Importance of mouth-based defenses is confirmed by the fact that many orthoptera-hunters deliver a special throat sting (Steiner 1962, 1976) sometimes even before any other sting (e.g. *Prionyx parkeri*). This also eliminates opposition to prey-transport and storage in the nest (and furthermore “de-activates” the prey that recovers in part from paralysis, later: Steiner 1963a). In sharp contrast, *Oxybelus uniglumis* wasps omit the throat sting when they paralyze their non-recovering fly-prey devoid of subesophageal ganglion and of potentially dangerous mouth parts (Steiner 1978, 1979). Orthoptera-hunting wasps with missing legparts or damaged antennae are often found, particularly late in the season. This might be a testimony to the efficiency of bites of their prey but also result from intra-specific fighting (see for instance Brockmann and Dawkins 1979, for *Sphex ichneumoneus*) and/or accidents during nesting. A female *Palmodus carbo* with two deep dents on the back of her abdomen was found in southern British Columbia. It is probable that this represented severe bites received from one of their large, often

predaceous, decticine grasshopper-prey rather than beak marks of some bird.

Chemical defenses: regurgitated fluid (R)

Chemical defenses are particularly widespread among insects (see for instance Eisner and Meinwald 1966; Wallace and Blum 1971, etc.) including Othopterans. Some of them have specialized glands and the substance can be ejected with considerable force (e.g. *Poecillocerus buforus*, from an opening located on the first abdominal tergite: Fishelson 1960). A froth can also be discharged through a thoracic spiracle (e.g. *Romalea microptera*: in Eisner and Meinwald 1966). Such repellents make their owner distasteful or unpalatable. The same apparently holds for fluids regurgitated from the gut through the mouth (Edmunds 1974, p. 199) by grasshoppers for instance = enteric discharges (Matthews and Matthews 1978, p. 335). Digger wasps, however, do not consume their prey usually but avoid contact with this fluid which is apparently a contact repellent. Functioning of the receptors located around the stinger could be impaired (jamming effect?) chemically and/or mechanically (Steiner 1976). Stinging remains possible, however, even with stinging sites covered with the fluid (Figs. 2 and 5b) but the wasp clearly hesitates or even gives up half way through stinging. Contact triggers vigorous, sometimes frantic, rubbing against the ground and/or hyper-grooming as in ants (Matthews and Matthews 1978, p. 335) as in hunters of regurgitating caterpillars like cutworms (e.g., *Amomphila*, *Podalonia* wasps). Body contact is clearly unpleasant if not deleterious, particularly for some small *Tachysphex* wasps (Steiner 1976).

One of the latter (*tarsatus* No + 874) had her abdomen tip covered with a thick coat of sand particles as a result of her attempts to rub off the sticky substance. The wasp was found dying the next day, June 19 (Arizona study) (the same probably happened to another *tarsatus* (No + 887) which died on June 6).

The same wasp (No + 874) was also observed the day before (June 18, 1405 h) in the process of carefully removing with the mandibles, bit by bit, a large crust of dried up fluid, from the ventral surface of the thorax and throat of a grasshopper. This was done right after "malaxation" of the fore leg bases which in some larrine wasps is a preparatory stage of egg-laying (details in Steiner 1971). Since the

egg is invariably glued right behind the fore legs, where the crust was also located, this would indicate that the regurgitated fluid could also be a serious obstacle to egg-laying or egg development. *Prionyx* wasps lay their egg at the base of one hind leg . . . where the risk of such "flooding" is clearly much reduced or even nil! Furthermore, paralyzed grasshoppers cannot remove the spilled fluid by grooming, as they normally do. Consequently "cleaning" of the soiled prey can be done only by the wasps, if at all.

This chemical defense is apparently even more effective in mole crickets against another larrine wasp: *Larra* (Williams 1928). Thus *Larra sanguinea* wasps were found with their mouthparts completely glued together by the very viscous fluid. Remarkably, some of these wasps managed to catch their mole cricket in spite of such crippling handicap! Ants are repelled by fecal material or chrysomelid beetle larvae (in Matthews and Matthews 1978, p. 343), and refuse to carry away pieces of grasshopper treated with their own repelling fluid (Eisner 1970).

In conclusion, the importance of mouth-based regurgitative defenses can be assessed by (1) the care with which these wasps try to eliminate the fluid from the prey and from their own body, (2) evolution of a specialized sting in the throat that abolishes mouth-based defenses, (3) the priority given by *Prionyx* wasps to mouth-based defenses (first sting in the throat), (4) dramatic effects, including death, observed on some wasps like small *Tachysphex*, (5) toxic effects reported in the literature, for mammals, such as topical irritation of eyes, vomiting when swallowed and severe symptoms caused by injection (Matthews and Matthews 1978, p. 335).

Such defenses are therefore particularly efficient against smaller predators like arthropods, wasps included. More experimentation is clearly needed, however.

Postural defenses, displays, replacing escape
(Figs. 3, 4 and 5d)

Such complex postures and displays will be analyzed in terms of their various components or aspects.

a) Color flash, startle response

Sudden display of colored wings, of hidden and bright structures (deimatic behavior) is common in insects, particularly in otherwise cryptically colored moths such as *Catocala scripta*, *Triphaena*

pronuba (in Edmunds 1974) and also many orthopterans. For the latter, wing opening (lifting) is for instance part of the dramatic threat-intimidation display of *Neobarettia* already mentioned (in Sebeok 1977, p. 342) or the one of *Phymateus*. Since these latter species are potentially dangerous and/or distasteful such displays are usually interpreted as warning (in Edmunds 1974, pp. 148, 154; see also for instance Frazer and Rothschild 1962). The first species bites severely while the latter has strong hind leg spines and secretes a repelling fluid if further molested. When exhibited by harmless species such as the stick insect *Metriotes diocles* (e.g. Bedford and Chinnick 1966; Robinson 1968a) or common grasshoppers it is considered as mere "bluff" based on a startle effect and/or an apparent increase in size, height, volume, etc. (intimidation behavior). Similar actions are reported from some cicadas and mantids and are particularly dramatic in the African mantid *Idolium diabolicum* (in Wickler 1968).

b) Display of dark markings or "eyespot"

Eyespots are commonly displayed by moths (see for instance Blest 1957, 1964). If even very imperfect imitations are considered effective then perhaps this also applies to the semi-circular dark markings displayed by grasshoppers (Figs. 3 and 5d). Rarity of the display is essential (in Edmunds 1974, p. 168).

c) Appearance of disabled, dying or dead insect (thanatosis) with freezing, hunching and appendages tucked in (Fig. 5d).

Inhibition of movement in itself or freezing is likely to lower the probability of detection and/or attack by predators that hunt moving live prey visually (e.g., Steiner 1962, 1976 for cricket-hunting *Liris* wasps). This probably includes many digger wasps. Thanatosis is known from a number of insects, also orthopterans (Edmunds 1974, p. 172; Robinson 1968a). The prey might also be considered unsuitable because of the unusual appearance as such (oddity effects). The latter is illustrated by "protean defenses" an unpredictable, erratic and highly diverse behavior (in Edmunds 1974, pp. 144-145; see also Chance and Russel 1959; Humphries and Driver 1971, etc.).

Furthermore, grasshoppers with wings spread, appendages tucked in and body strongly arched (Fig. 3) also seem less exposed because of reduced access to the vulnerable stinging sites, all located on the well protected ventral surface of the thorax (Steiner 1981).

Some *Prionyx* wasps experienced great difficulties in squeezing themselves under such grasshoppers (Fig. 3, one leg of the wasp visible). Sometimes also the wasps succeeded in turning over such grasshoppers, venter up (Fig. 4). Even so, stinging was difficult.

Reduced accessibility might be an accidental by-product of the "disablement" display or a more direct result of wasp-grasshopper coevolution. The apparent immunity of *Acrotylus* grasshopper nymphs to *Tachysphex pectinipes* was also attributed to restricted accessibility linked with dense and long pilosity (Ferton 1910, p. 158). Body arching has also been observed on some other orthopterans and is sometimes associated with the release or violent expulsion of repellent fluid, as in *Poeciloceris buforus* (Fishelson 1960).

d) "Intimidating" and aggressive defensive elements (Fig. 5d).

If the posture shown in Figs. 3 and 5d is also an eyespot display then it has an intimidating as well as "bluff" value.

Sideways rocking, known from some mantids (Crane 1952) and also forward-backward rocking were often observed in crickets, just before or after contact with *Liris* wasps (Steiner 1968), suggesting an intimidating function. This was also observed in *Empusa egea* in response to attacks by the sphecoid wasp *Stizus distinguendus* Handl. (Deleurance 1941, pp. 287–288), along with other aggressive responses such as wings open, striking with the raptorial fore legs. Rocking was also observed in some phasmids (Crane 1952) and roaches such as *Periplaneta fuliginosa* (Simon and Barth 1977, p. 307). Crickets also sometimes froze into odd or intimidating erect postures difficult to interpret as "death feigning" (Steiner 1962, 1968). Absence of stinging in such cases, if related at all to the display, might depend on: (1) the oddity of the posture, as Chauvin and Chauvin (1977) suggest (the vertical posture is in sharp contrast with the usual horizontal one), or (2) the possible intimidating effects associated with increased height (bluff behavior), (3) predator mimicry, namely a mantis-like appearance (see Steiner 1968, Fig. i, p. 267). [Remark: this latter possibility was considered far-fetched by one reviewer of the paper cited and consequently eliminated from the text. . . and yet Simon and Barth (1977, p. 307, Fig. 2) describe a somewhat comparable rare posture from the roach *Periplaneta fuliginosa* which they interpreted (probably rightly) as a "Mantis-threat"!]

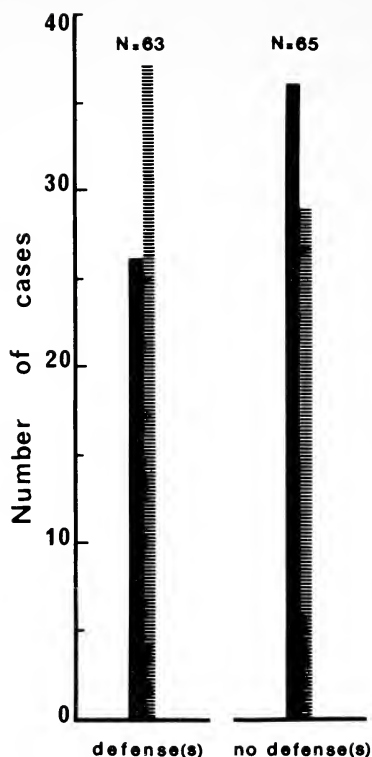


Fig. 6: Proportions of cases where negative effects on the wasp were present (hatched bars = wasp inhibited or stopped, stinging incomplete or no stinging at all) or not present (bars in solid black = complete stinging without apparent negative effects). For cases where prey defenses were recorded (left pair of bars) the proportion of negative effects is greater than no effects, whereas it is the reverse for cases where no defenses were recorded or this information was unavailable (right pair of bars). This indicates that prey defenses (all cases pooled) do have some negative effects on the wasps. It is only a trend, however, since the differences do not reach significance.

It has been suggested that some protective and intimidating displays (e.g. in saturniid and sphingid moths) could have evolved from flight movements (Blest 1957) and can be classified as (1) rhythmic, (2) static, (3) mixed and (4) cryptic. Category (1), that appears to best fit the data (Figs. 3 and 5d) would be closest to the original flight movements. Extension of hind legs, wing beats, even if convulsive, are clearly part of flying which is strongly inhibited.

Similar explanations would seem to apply to the odd cricket postures (Steiner 1968) but in the form of "frozen jumping and/or kicking" rather than "frozen flight" and reduced access to the vulnerable ventral stinging sites is also indicated. Startle displays have also been interpreted in terms of conflict between flying and freezing for some mantids (Crane 1952).

Efficiency of such defenses has been clearly demonstrated in only a few cases. Parker et al. (1974), for instance, showed that defense postures exhibited by *Locusta migratoria* had a significant negative effect on bout continuance between conspecifics. With wasp studies the problem is further complicated by wide moment-to-moment fluctuations in responsiveness of the hunting wasps (Steiner 1962, 1976, 1979). Such variables must be controlled, manipulated or eliminated to get clear answers and this was not done in the present study.

QUANTITATIVE DATA

Quantifications were too limited and inappropriate to make a statistical analysis of the effectiveness of such defenses very meaningful. Only 128 cases were known in sufficient detail to be included in the analysis. In 41.27% ($n = 26$) of the cases the defenses (lumped together) had no apparent effect and complete stinging followed and in 58.73% ($n = 37$) at least some possible effects were recorded, such as temporary, permanent, interruption or even deletion of stinging. When no defenses were observed (or unknown status) the percentages of complete vs incomplete stinging were approximately reversed as predicted: 55.38% ($n = 36$) and 44.62% ($n = 29$). These differences in proportions (Fig. 6) were not significant, however, since the calculated χ^2 was only 3.689 for a critical value of 5.991 ($p \leq 0.05$; $df = 2$; G-test of independence of rows and columns: Sokal and Rohlf 1969, p. 599). A slight advantage can have a decisive selective value in the long run, however.

CONCLUSION

Prey as harmless as herbivorous crickets and grasshoppers possess a rather complex, well integrated, system of anti-predator devices they can use against their wasp enemies. Even if some of these responses are merely obstructive, they do in fact increase the

cost of predation to the wasps by making capture more difficult, more costly, and/or less probable. Natural selection should therefore promote evolution of such anti-predator strategies which in the long run increase the fitness of the prey.

Some components of the system such as flying away and crypticity, perhaps regurgitation, are of a very generalized nature whereas other devices are more predator-specific. Thus startle displays with exposure of dark semi-circular markings are probably most efficient against small avian predators, whereas biting, mouth regurgitation, hind leg raising and obstruction behaviors are presumably more useful against smaller, more vulnerable predators such as other insects, including digger wasps. Matthews and Matthews (1978, p. 352) state that "protective adaptations in insects are intimately related to the behavior and physiology of their predators." This also applies well to wasp predators.

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SUMMARY

Harmless herbivores such as acridid grasshoppers exhibit a complex anti-predator behavior when attacked by *Prionyx* and *Tachysphex* sphecid wasps. Besides jumping and flying away with

exposure of colorful wings (flash behavior) and sudden return to crypticity upon landing, these insects show freezing, often in odd postures, with the colorful wings and dark markings ("eyespot"?) prominently exposed. Such postures also reduce access to the vulnerable ventral surface usually stung by these wasps (obstruction behavior). After contact with the wasp a second line of defense comes into effect such as kicking, brushing and pushing actions. In addition to these hind-leg based defenses, the attacked prey can also use mouth-based defenses: biting and/or regurgitating a repelling, perhaps even noxious, fluid ("tobacco juice"). Such defenses presumably lower the probability of capture or at least increase the cost to the predator and have therefore a selective value.

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A COMPARISON OF THE NEST PHENOLOGIES OF
THREE SPECIES OF *POGONOMYRMEX* HARVESTER
ANTS (HYMENOPTERA: FORMICIDAE)*

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INTRODUCTION

Ants are among the most abundant animals in most habitats (Petal 1967) and may even be the dominant insects in many ecosystems (Nielsen 1972; Nielsen and Jensen 1975). Harvester ants of the genus *Pogonomyrmex* are a major component of the energy flux through ecosystems (Golley and Gentry 1964). Ants of this genus have become increasingly important in ecological studies, including mutualism (O'Dowd and Hay 1980), competition (Mares and Rosenzweig 1978; Reichman 1979; Davidson 1980), predation (Whitford and Bryant 1979), foraging (Whitford and Ettershank 1975; Hölldobler 1976a; Whitford 1976, 1978a; Davidson 1977a, b; Taylor 1977), community structure (Davidson 1977a, b; Whitford 1978b), and impact on ecosystems (Clark and Comanor 1975; Reichman 1979). It is difficult to investigate harvester ants as seasonal processes occurring inside the nest are generally unknown and the nest populations are usually underestimated.

This investigation compares the nest phenologies of three species of *Pogonomyrmex* harvester ants: *P. montanus* MacKay, *P. subnitidus* Emery, and *P. rugosus* Emery, which occur at high, mid, and low altitudes respectively. These data form the basis for a comparison of the ecological energetics of the three species (MacKay 1981).

MATERIALS AND METHODS

The species investigated.

The altitudinal comparison is based on three species of harvester

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ants: *Pogonomyrmex montanus* MacKay, *P. subnitidus* Emery, and *P. rugosus* Emery. All three belong to the subgenus *Pogonomyrmex*. *Pogonomyrmex subnitidus* and *P. montanus* are very closely related, both belong to the *occidentalis* complex (MacKay 1980). *Pogonomyrmex rugosus* belongs to the *barbatus* complex (Cole 1968). *Pogonomyrmex montanus* is unusual for the genus in being a high mountain species occurring in pine forests in the mountains of southern California. *Pogonomyrmex subnitidus* is a mid-altitude species in the San Jacinto Mountains. *Pogonomyrmex subnitidus* is distributed throughout southern and south central California and Baja California, occurring at lower elevations throughout much of its range. *Pogonomyrmex subnitidus* is sympatric with *P. rugosus* in parts of Riverside County, but is uncommon in such areas. *Pogonomyrmex rugosus* is a low altitude species near Riverside and occurs at lower elevations throughout much of southwestern United States. It rarely occurs at higher elevations. For example, in the Joshua Tree National Monument it is present up to 1350 meters, in New Mexico it occurs at over 2100 meters.

Study areas.

Populations of all three species were studied in southern California: *P. montanus*—in a yellow pine forest community between Fawnskin and Big Pine Flat at 2100 meters elevation in the San Bernardino Mountains of San Bernardino Co., *P. subnitidus*—in the chaparral near the Vista Grande Ranger Station at 1500 meters in the San Jacinto Mountains of Riverside Co., *P. rugosus*—in the coastal sage scrub community at Box Springs at 300 meters near Riverside, Riverside Co. The three species occur in clearings within these different plant communities.

Estimation of nest populations.

Two primary methods are used in the estimation of ant nest populations: mark-recapture methods and nest excavation. Mark-recapture methods are used to compare a population before and after seasonal production. This method has been criticized as one of the assumptions is that workers mix randomly in the nest. The workers of all three species are stratified within the nests and there is strong evidence that other species are stratified as well (MacKay 1981). Also I could find no reliable way to mark the individuals such that the marks were permanent, could not be passed on to other individuals, and would not disrupt normal activities. In any case,

such a method would only estimate the numbers of foragers in a *Pogonomyrmex* nest, not the actual nest population. In addition, mark-recapture methods do not provide an estimate of the reproductives produced in a nest.

Excavation of nests destroys them for further study and requires a large expenditure of time and effort. I chose periodic nest excavation as the method of estimating production as counts of the sexuals, brood, and workers can be made.

Our experience indicates that most of the nest population is collected. *Pogonomyrmex* spp. colonies may live 15 to 20 years (Barnes and Nearney 1953), and will live at least two years after the removal of the queen (pers. obs.). Nest longevity is unknown in the three species investigated, but based on data from other species, I expect at least 5%–10% of the nests should not have queens. The high proportion of nest queens collected (84% in *P. montanus*, 77% in *P. subnitidus*, and 80% in *P. rugosus*) supports the hypothesis that most of the nest population is collected. The queens do not reside in any special "queen chamber" and are of a similar size as a worker. Therefore, it is not any easier to find the queen than it is to find any individual worker in the nest. In all cases excavation was continued at least 50 cm deeper than the position of the last ant found or the end of a burrow.

Nest excavation procedure.

The procedure was as follows: The surface dimensions of the nest were determined by removal of the top 10 cm of the nest. The hole was then extended at least 50 cm on all sides. A square ditch was dug around the perimeter of the nest to a depth of one meter in the case of *P. montanus* nests and over 1.5 meters around the nests of *P. rugosus* and *P. subnitidus*. We were able to sit in the ditches while carefully excavating the nests in 10 cm levels. As the hole became deeper, the ditches were proportionally deepened. All of the contents of the burrows, including ants, brood, guests, stored seeds, and dirt were placed in labeled half or one liter plastic containers. Later the animals were separated from the dirt, and counted. Nest excavation usually began between 06:00 and 07:00, before the ants became active. If foragers were needed for other investigations, excavation began later in the morning or early in the afternoon. Excavation and counting of a *P. montanus* nest requires 6–10 hours, of a *P. subnitidus* nest 20–30 hours and of a *P. rugosus* nest 60–90

hours. Whenever excavation was stopped to be continued on the following day, the nest was covered with a heavy vinyl cloth and 10 cm deep layer of dirt. This was necessary to keep the inhabitants, especially the males, in the nest. A total of 80 *P. montanus*, 26 *P. subnitidus*, and 20 *P. rugosus* nests were completely excavated between 1977 and 1980.

It appeared that the excavation procedure disrupted stratification of individuals within the nest only slightly. When nest chambers were exposed, many individuals emerged, but most of the population remained in the chambers, and assumed a defensive position involving opening of the mandibles and forward extension of the antennae.

The numbers of workers at each level and the position of the queen were recorded. When the nests were in production, the presence or absence of eggs was noted, but the eggs were not counted, as they were extremely small and are easily lost in the dirt. The larvae, pupae, females, males, and callows (immature, underpigmented workers) were counted when they were present in the nests. The contents of each level were summed to obtain an estimate of the entire nest population.

Seed storage in nests.

The seeds were separated from the soil by filling a 1000 ml beaker about $\frac{3}{4}$ full of soil and seeds. The contents were washed into a sieve with 0.5 mm mesh. The washing and swirling were continued until all of the seeds were removed from the soil. The material caught in the sieve was washed again until only seeds remained in the sieve. The seeds were then dried (60° C) to constant weight.

Nest structure.

In the process of nest excavation it was noted that the general form and shape of the nests were comparable in all three species. The *P. montanus* nest structure was studied by pouring a thin solution of plaster of Paris (3 tablespoons/liter of water) into one nest. The solution was dilute enough that the walls of most of the tunnel system were coated with plaster. The nest was excavated in 1–2 cm layers and the tunnel structure at each layer was measured and sketched. The resulting series of "cross sections" of the nest resulted in a composite drawing of the nest.

Nest temperature and humidity.

Temperature data were recorded from approximately weekly

readings of thermistors permanently implanted in nests of the three species. The data were supplemented with readings taken during nest excavation, following the procedure of Rogers et al. (1972). Soil temperatures taken within the excavation hole (at least 20 cm distant from ant burrows) and within the adjacent undisturbed soil at the same level were not significantly different in two cases involving *P. montanus* nests ($F = 0.00001ns$, $F = 0.13ns$). Similar comparisons were not made in the cases of *P. rugosus* and *P. subnitidus* as the soils were too compacted to allow the insertion of a thermometer in undisturbed soil to a depth of 30 or 40 cm.

Soil samples (160 grams) were collected at various depths and oven dried ($60^{\circ}C$) to constant weight to determine water content. At least three replicates of soil temperature and soil moisture content were collected at each level. It was anticipated that these parameters would determine the position of the brood within the nest. I assumed a correlation existed between the humidity within the burrows and water content of the soil as well as a uniformity of the soil structure in the first 100 cm of the nest where most of the seasonal changes in the positions of the inhabitants occurred. Sandy soils would release more water vapor to burrows than would clay soils, if both had the same level of soil moisture (Marshall and Holmes 1979). The amount of water present within the soil changes continuously under field conditions (Marshall 1959), which would also modify the relative humidity.

Food input into nest.

Food input was estimated by channeling the flow of foragers and sampling a fraction of foragers at regular intervals to determine the numbers of trips made and the amount of food brought back to the nest.

Twenty-eight nests of the three harvester ant species (13 *P. montanus*, 10 *P. subnitidus*, and 5 *P. rugosus*), were surrounded by strips of 25 gauge sheet metal. The diameters of the enclosures were approximately one meter for *P. montanus*, 1.5 meters for *P. subnitidus*, and 2 meters for *P. rugosus*. The sheet metal strips were buried to a depth such that 10 cm of the metal were exposed. Sheet metal with a total width of 20 cm was sufficient. The ants could not normally climb over the enclosure as the sheet metal was very smooth. The ants would occasionally begin to climb the enclosure at the junction of the two ends. In such cases the area was covered with Tanglefoot(R).

In some cases, especially with *P. montanus*, the ants would attempt to tunnel under the enclosure. When this occurred, the ants were removed from the site of the tunneling and placed near the nest entrance inside the enclosure. In such cases the tunneling was completely controlled by destroying the tunnel system and replacing it with soil.

The ants were allowed to enter and exit the colony through two 2 cm diameter vinyl tubes, 6 cm in length. Entrance of the ants to the colony through the "exit" tube was prevented by having a 0.5–1 cm distance between the end of the tube and the soil. In a similar manner exit via the "entrance" tube was prevented. The ants were apparently not affected by this short distance, they either simply dropped with no hesitation or rapidly climbed down from the tube to the soil. The tubes were within 15 cm of each other and were placed on the side of the nest where most of the foraging occurred. A 0.448 liter glass jar could be placed under the tube by which the ants entered the nest, thus collecting the foragers with the food items they carried. The foragers were counted and the food items collected. The foragers were released into the nest enclosure with a quantity of food (native seeds) which approximated the amount of food removed. The nests were sampled at approximately weekly intervals throughout the foraging seasons, during 1978 to 1980. All of the foragers entering *P. montanus* nests were collected, 1/5 to 1/6 of those entering *P. subnitidus* nests, and 1/60 of those entering the *P. rugosus* nests. With these proportions, one person could handle the activity of 5 nests during a single day. The forager populations were estimated by capturing all of the foragers throughout the day, as they returned to the nests.

Statistical analysis.

Unless otherwise indicated, the 5% level of significance was used in all comparisons. A single asterisk indicates statistical significance at the 5% level, double asterisks at the 1% level, triple asterisks indicate significance at the 0.1% level. Means are listed plus or minus one standard error. The percentages of the nest populations were used to make comparisons between the species possible. The data obtained were fit to least squares polynomial regressions (Snedecor and Cochran 1967). The curves were constructed from the equations.

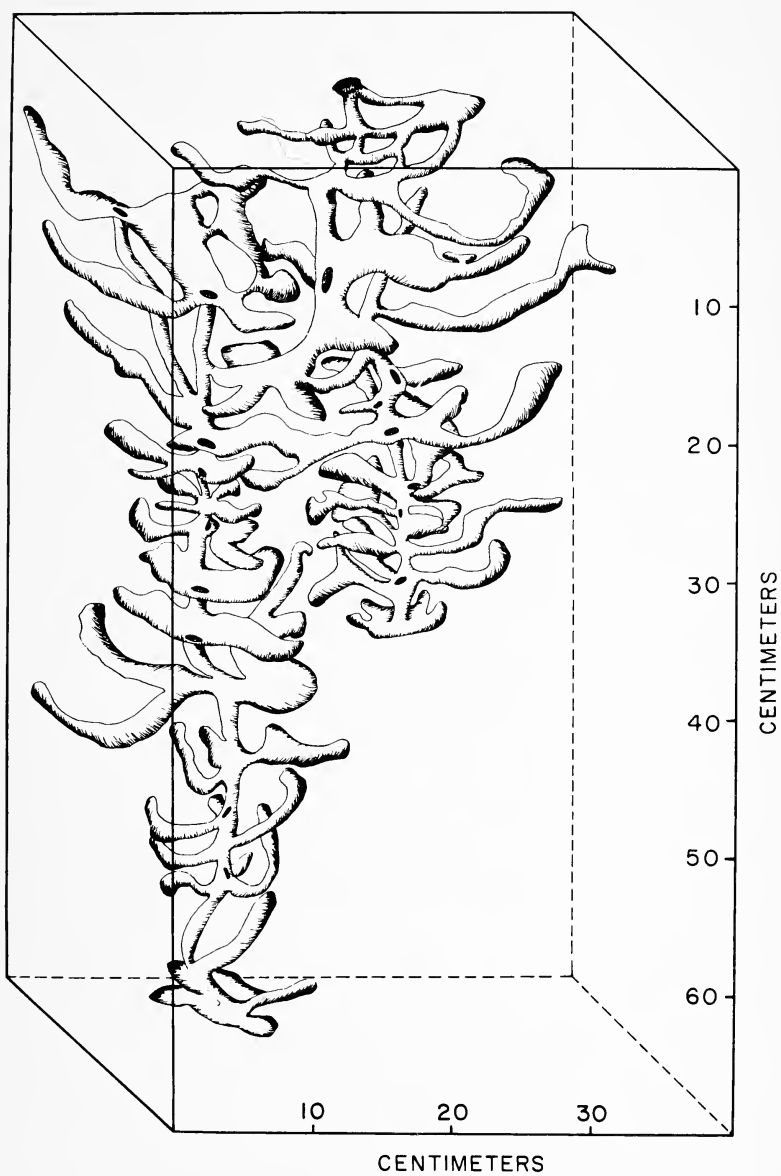


Figure 1. The structure of a typical *Pogonomyrmex montanus* nest.

RESULTS

Nest structure.

The nest of *P. montanus* has numerous burrows in the upper levels (Figure 1). Below this, there is often only a single main tunnel to the bottom of the nest. Most of the ants are found in the burrows which branch from the main tunnel. The main tunnel contains few ants and is apparently used only for movement between the side burrows. In many cases there are two separate "major tunnels", as is shown in Figure 1. In *P. subnitidus* the two major tunnels may be separated by more than 100 cm and may appear as two separate nests. One major tunnel may contain no brood and the other may contain all of the brood in the nest. The queen and brood are usually found in the major tunnel which goes to the deeper level.

The structure of the nests of *P. subnitidus* and *P. rugosus* are not shown, but are similar except that they are larger and deeper, often extending to 300 or 400 cm deep. There was no relationship between the worker populations and the nest depth (for *P. montanus* $r = 0.16ns$ (65), for *P. subnitidus* $r = 0.03ns$ (26), and for *P. rugosus* $r = 0.32ns$ (20)).

Nest microclimatology: temperature.

The seasonal changes in nest temperatures are similar for all three species (Figure 2). The nest warms rapidly in the spring and temperatures reach a maximum at the end of June or July. The soil temperature begins to drop in August and levels out during the winter months. As the species occur at different altitudes, the temperature ranges are different. The range of *P. montanus* extends from slightly below zero to 20° C, that of *P. subnitidus* from slightly above zero to 25° C, and that of *P. rugosus* from slightly below 10 to 30° C.

Only the changes at the 20 and 50 cm depths are shown in Figure 2 as the other levels are similar. The differences between the levels deeper than 40 cm were generally not significant. The only important difference between the curves of the 20 cm level and 50 cm level is that the shallow level warmed sooner in the spring and cooled sooner in the fall.

Nest microclimatology: humidities.

The seasonal changes in soil moisture are similar in the nests of all three species (Figure 3). Soil moistures are high in the winter and

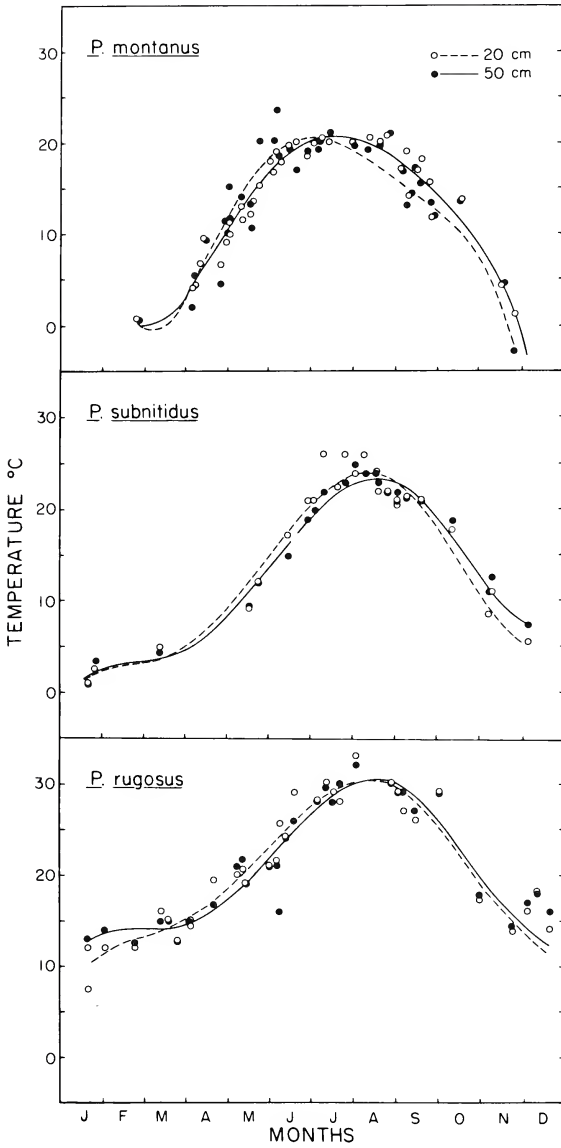


Figure 2. Seasonal changes in the mean daily nest temperatures of three species of *Pogonomyrmex* harvester ants.

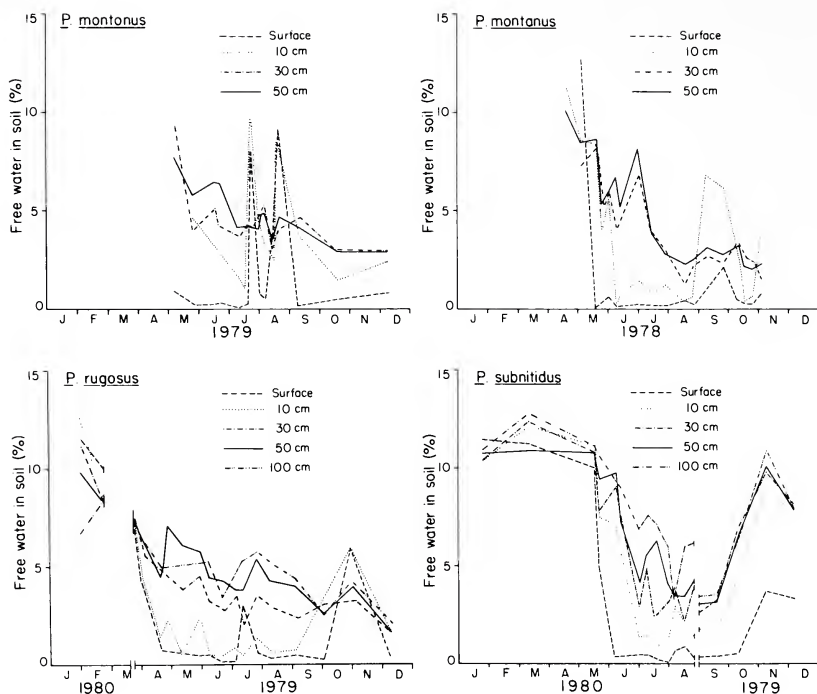


Figure 3. Seasonal changes in the nest humidities of three species of *Pogonomyrmex* harvester ants.

spring and low in the summer and fall. Throughout the winter, the soils receive relatively large amounts of rain or snow which raise the soil moistures to high levels. After this time, the surface and upper levels lose water rapidly by evaporation. The lower levels of the nest retain water throughout the entire season, although the percentage decreases. Soil moistures at levels below 30 cm are essentially the same for all three species. Summer showers rapidly increase soil moistures of the upper levels (note the peaks in the Figure 3), but have little effect on the levels below 30 cm. This water input into the soil is rapidly lost by evaporation.

The soil moisture of the lower levels is generally higher than that of the upper levels, possibly forming a relative humidity gradient. There are more fluctuations in the higher levels, both in soil

moisture and temperature. This probably accounts for much of the brood being kept in the lower nests levels.

The harvester ants apparently obtain water from several sources. Some metabolic water may be available to the ants, as it has been shown that harvester ants increase their metabolism when they are water stressed, without increasing their activity (Ettershank and Whitford 1973; Kay and Whitford 1975). Morning dew would not normally be available as foraging begins after dew has evaporated. I have seen harvester ants actively drink rain drops on the soil surface, demonstrating a curious pumping action of the gaster, but precipitation is not common in the three habitats during the summer (U.S. Weather Bureau Climatological Data). Capillary condensation occurs in the soil at relative humidities above eighty percent (Rode 1955) and may allow the ants free water. Arthropods, especially insects, are able to actively absorb water vapor from unsaturated air, although the mechanism is not understood (Edney 1974; Cloudsley-Thompson 1975). It is not known if harvester ants have the ability to actively absorb water vapor.

Seasonal changes in nest populations.

The data on nest populations obtained from the nest excavations are summarized in Appendix 1. Absolute counts could not be easily compared because the numbers of individuals present in the nests of the three species are very different. To reduce this variation between nest populations of the three species, the data are compared in the form of percentages. The seasonal changes in the brood and sexual populations are similar for all three species, when the percentage composition of each of the classes are compared (Figs. 4 & 5). In the three species, egg laying begins in late April to late May, similar to *P. owyhee*i (Willard and Crowell 1965) and *P. occidentalis* (Lavigne 1969). Development from egg to callow in the species requires five to six weeks compared to 25 days for *P. badius* (Gentry 1974) and 30 days in *P. occidentalis* (Cole 1934). It is very difficult to determine the number of larval instars in the development of ants (Wheeler and Wheeler 1976), although Marcus (1953) suggests that there are four instars in *P. marcus*i. As a consequence, all of the instars were combined into a single group. The first larvae appear about a week after the eggs are laid, first pupae about two weeks later. Callows are found in the nest about 5 or 6 weeks after the eggs were laid and

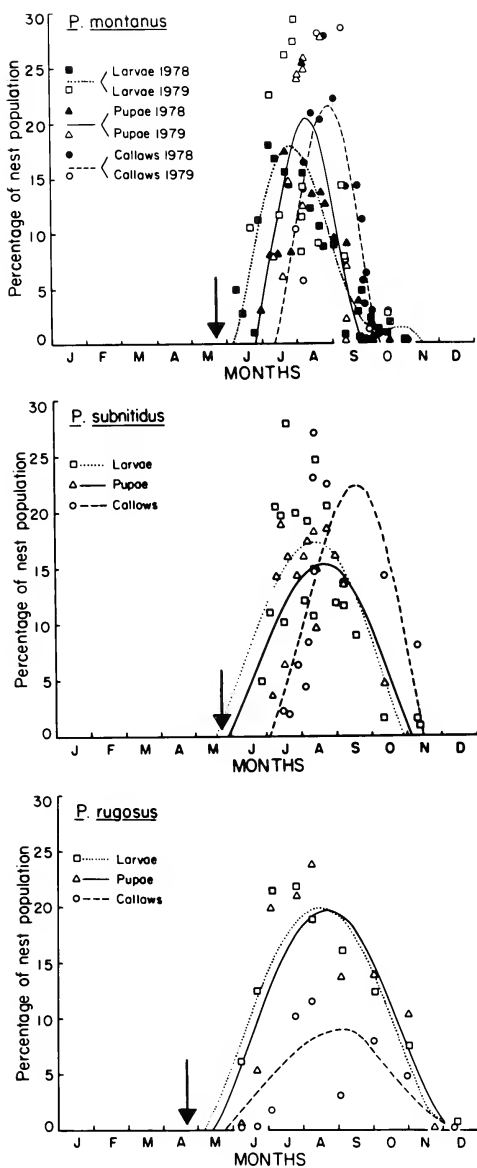


Figure 4. Seasonal changes in the brood populations of three species of *Pogonomyrmex* harvester ants. The arrows indicate the dates when eggs were first found in the nests. Nests excavated which contained only adult workers are not represented in the figure.

remain pale for about three weeks. Thus, development from the egg through the larval instars requires about three weeks, the pupal stage 2–3 weeks, and the callow stage three weeks.

Most of the eggs are laid in the spring as large amounts are found early in the season. The amounts found in later excavations decrease and eggs are rarely found after the pupae begin to appear in the nest.

The larval population reaches a maximum in late July in *P. montanus*, and mid August in *P. subnitidus* and *P. rugosus*. The pupal population reaches a maximum in mid August in *P. montanus* and late August in *P. subnitidus* and *P. rugosus*. The callow population reaches a maximum in early to mid September in all three species. The callows are easy to distinguish from adult workers in *P. montanus* as they remain pale for at least three weeks (based on laboratory observations). The callows of *P. rugosus* and *P. subnitidus* are much more difficult to distinguish from the adult workers. *Pogonomyrmex rugosus* callows darken to a color indistinguishable from mature workers within five days. *Pogonomyrmex subnitidus* mature workers are pale making it difficult to distinguish them from the callows, even if the callows remain pale for many days.

As the majority of the first individuals produced are sexuals, most of the larvae and pupae formed in the first part of the season become reproductives. Workers are also produced early in the season, especially in *P. rugosus*. All of the later brood become workers as was also found in *P. owyheeii* (Willard and Crowell 1965). The reproductives remain in the nest only until late August or early September. In *P. owyheeii* they remain in the nests until mid December (Willard and Crowell 1965).

The first winged reproductives appear in the nests in late June (*P. rugosus*) or late July (*P. montanus* and *P. subnitidus*). The mating flights are completed by the first part of September. The highest sexual populations occur in mid August. Therefore the colony begins production of reproductives early in the year and allows them to remain in the nest for extensive periods of time, even though they are consuming food. This is true to a lesser extent in *P. subnitidus*, where the reproductives appear in the nest in late July and most have left the nest by mid August (Figure 5).

There are several interesting points in Figs. 4 & 5. Although *P. rugosus* begins production earlier in the year than do the other two species, the populations of brood in the nest reach peaks later in the

year. *Pogonomyrmex rugosus* spreads reproduction out over the year to a greater extent than does *P. montanus*. *Pogonomyrmex montanus* produces relatively more sexuals than does *P. rugosus* or *P. subnitidus* and in general the production is much higher.

Mating flights.

The mating flights occur either in the morning (*P. subnitidus*) or the afternoon (*P. montanus* and *P. rugosus*). Reproductives of *P. montanus* first appeared on the nest surface on 10 August 1978. The reproductives emerged from the nest entrance, scurried over the mound for a few seconds and then returned to the nest. They may have been evaluating environmental conditions to determine when it was optimal for the mating flight. This behavior was found in all three species. A small flight occurred on 29 August 1978 between 15:30 and 16:20, a second larger flight occurred on 9 September 1978 between 13:20 and 14:10. The nests of *P. montanus* normally have a single entrance-exit hole. During the large flight on 9 September 1978 the nests had $2.7 \pm 0.3SE$ (12) exit holes per nest (range = 2 to 4). These supplemental exit holes allowed the reproductives to exit the nest more rapidly. I did not observe this behavior in the other two species. Reproductives of *P. subnitidus* were seen on the nest surface as early as 23 July 1980. The flights occurred on 6, 7, and 8 August 1980 between 8:00 and 9:30. In *P. rugosus*, reproductives first appeared on the nest surfaces on 1 August 1979. A large mating swarm was observed on 24 October 1979 between 14:00 and 15:00.

During the time the reproductives left the nest, the surfaces of the nests swarmed with workers. Apparently most or all of these workers were foragers as they were lighter in weight than the other ants in the nest (MacKay, unpubl.). The reproductives often had considerable difficulty becoming airborne, especially the females, which usually climbed up plant stems before flying.

Large mating swarms were observed in *P. rugosus* and were similar to those described by Hölldobler (1976b). The males waited on the tops of hills (over 100 m altitude above surrounding terrain) for the females. The males displayed considerable competition for females as was shown by Markl et al. (1977). As a result mating was a frenzied activity in which numerous males competed for single females by biting, pushing, and in general attempting to exclude

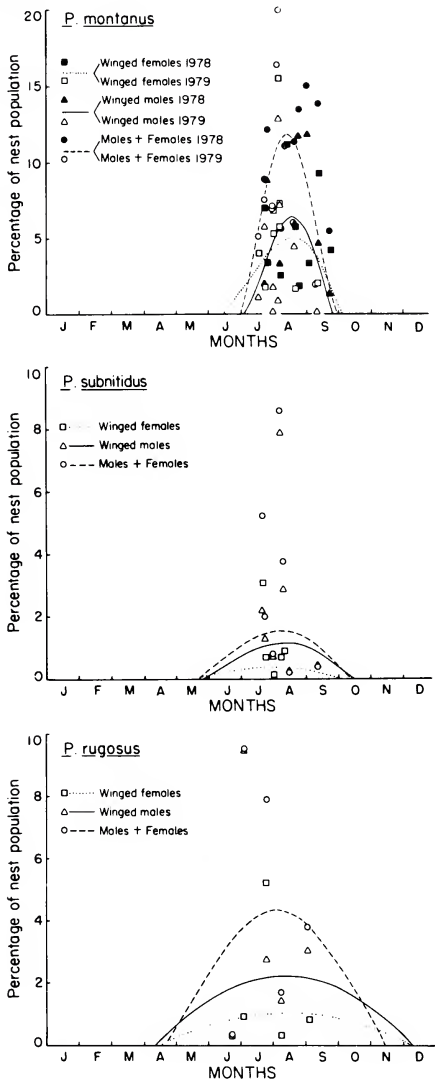


Figure 5. Seasonal changes in the populations of reproductives of three species of *Pogonomyrmex* harvester ants. Note that the percentage scale for reproductives in *P. montanus* has twice the range of the scales for reproductives in the other two species.

other males (See Figure 2 of Hölldobler 1976b and Figure 4 of Markl et al. 1977). Prior to the mating flight, male respiratory rates doubled or tripled (MacKay 1981). The individuals with higher activity levels may be able to increase their fitness by excluding other males from a female or by capturing a female quickly and moving into the copulatory position before other males arrive.

After the female has copulated for a short time, she bites the gaster of the male which is copulating with her. He usually relinquishes his position to another male. There is considerable fighting and tumbling so it is difficult to determine the numbers of times a female mates. Observations suggest that a single female mates at least 3 or 4 times. She may have mated previously with one or more of her brothers in the nest. I observed one mating within the nest of a laboratory colony of *P. montanus*. In all three species, the males attempt to mate with their sisters during emergence from the nest, although a complete copulation was never observed.

After several copulations the females leave the mating swarm either by flying or walking away. The males no longer show interest in such females, as the females apparently stop releasing a pheromone (Hölldobler 1976b). Most females then fly away from the area. A few remain and within a few minutes begin excavating nests near the mating site. As the density of such nests is very high (more than 4 per square meter) the success rate is undoubtedly low. Several times I saw females near the mating area attempt to "steal" the excavation hole of another female, but were chased away by the resident female. Such attempts are common and are occasionally successful (Markl et al. 1977).

Seasonal changes in the positions of inhabitants within the nests.

The seasonal movements in the positions of the inhabitants of the nests depicted in Figures 6, 7 and 8 are similar to those described in *P. owyhee* (Willard and Crowell 1965) and *P. occidentalis* (Lavigne 1969). The depths are not comparable between the three species as the nests of *P. rugosus* are deeper than those of *P. subnitidus* which are in turn deeper than those of *P. montanus* (Appendix 1). In most cases the time axis is expressed in months of the year with the exception of the sexuals in which only four months are shown. In all cases, the proportions represent means of all nests excavated.

Most of the nest population of *P. montanus*, including the

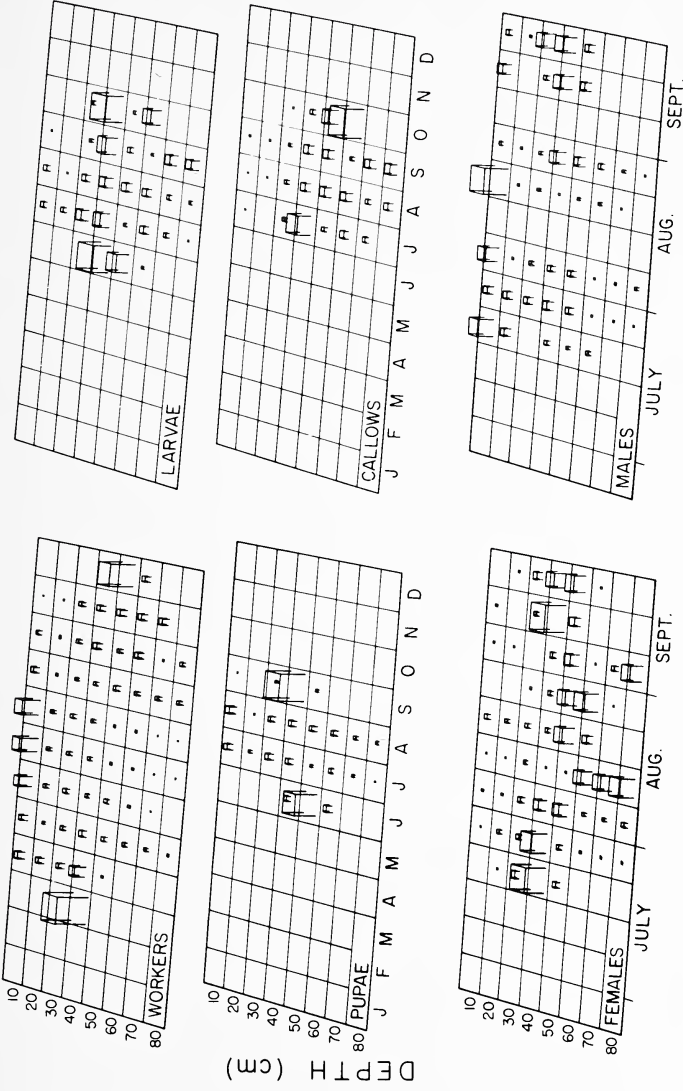
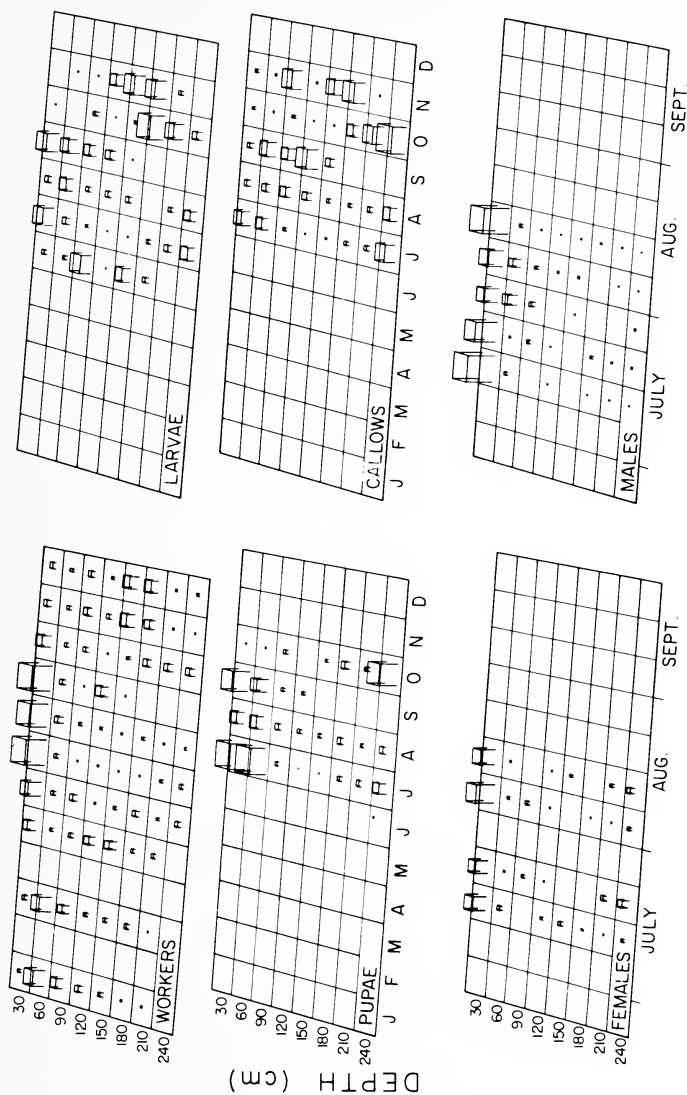


Figure 6. Seasonal movements of the populations of the various member groups in the nests of *P. montanus*. The grid has a value of zero. The value of the proportion of each element in the array is represented both by the height of the box above the grid and the linear dimensions of the box.

workers and the nest queen, overwinter near the 40 cm level of the nest (Figures 6 and 9). In the early spring the soil temperatures are low (Figure 2) and the ants are very sluggish. When the snow begins to melt, the lowest chambers of the nest fill with water. If the ants were at the lowest levels, they would probably be killed. In April and May the *P. montanus* worker population begins to spread throughout the nest. In June, July, and August, nearly 80% of the worker population moves into the upper 10 cm of the nest (Figure 6). During this time the nest temperatures are high and much of the worker population is involved in foraging, brood care, and nest construction. In September as the soil temperature begins to cool, foraging decreases and the workers begin to spread throughout the levels of the nest. In December the workers are again at the 40 or 50 cm level of the nest. The worker population in the 20 and 30 cm levels remains low and relatively constant throughout the year. There is apparently no temporal movement in the larvae or pupae, but they are present within the nest for only part of the year. In general, they are located at the 30 or 40 cm level where temperature and humidity are relatively constant throughout the season. The callows tend to occur in the deeper levels of the nest together with the brood. As most of the worker population is in the upper levels of the nest, the responsibilities of brood care are left to the callows.

It is difficult to make inferences concerning the sexuals as individuals begin to leave the nest in the middle of August. Thus, what appears to be a downward movement may simply be the result of the individuals in the upper levels leaving the nest. The females do tend to occur deeper in the nest than do the males. They may be in lower levels in the nest in order to assist in caring for the brood, as has been observed in the laboratory. It has been shown in *Formica polyctena* that workers must learn brood care during an early period of their lives or they will never care for brood (Jaisson 1975). This could occur in *Pogonomyrmex* where the female reproductives may "learn" brood care so they can later rear their own brood.

The seasonal movement in *P. subnitidus* nests is similar to that found in *P. montanus* nests (Figure 7). A high proportion of the workers remains in the upper 30 cm of the nest. In October there is a dispersion throughout the nest. By December, much of the population is at the 120 to 180 cm level, with little of the population in the lowest parts of the nest. The study area receives less snow than the

Figure 7. Seasonal movements of the populations of the various member groups in the nests of *P. subnitidus*.

area containing *P. montanus*, but the lower levels of the nest may also become flooded when the snow melts. Many of the larvae and pupae are found in the upper levels of the nest, but there is apparently a downward movement of the brood and callows in October and November. By December there is no brood in the nest. Most of the reproductives are found in the upper 30 cm of the nest (Fig. 7).

The seasonal movements in *P. rugosus* nests are similar to the other two species (Figure 8). Most of the worker population is in the upper levels of the nest throughout the spring and summer. In September and October until December, the ants become distributed throughout the nest. The larvae are dispersed throughout the nest during most of the year, but appear to be moved into the deeper levels of the nest at the beginning of the winter. The pupae are located in the upper levels of the nest but also appear to be moved into the deeper regions of the nest in the fall. The callows also demonstrate a movement into the deeper nest levels in the fall. Again, it is difficult to make inferences concerning the sexuals as they are in the nest for a short period of time, but both sexes appear to be in the upper levels.

In the winter the ants seem to be dispersed throughout the nest and do not avoid the lowest levels of the nest. There is no winter snow at Riverside and the temperatures are higher than those in the mountains (Figure 1), therefore the ants remain somewhat active throughout the year.

The seasonal patterns of distribution within the nests are similar in all three species. The reproductives (when present) and workers are most abundant in the upper levels of the nest, except in the winter. The brood are in the deeper levels where the microclimate undergoes little change. The callows are in the lower levels of the nests in all three species and apparently care for the brood. This is common in ants in general (Wilson 1971) and in *P. badius* (Gentry 1974). No callows were ever seen foraging. They do not quickly darken on exposure to sunlight.

It is commonly stated that ants keep the larvae and pupae separate within the nest to take advantage of the optimal conditions for the development of each (Wheeler 1910; Protomastro 1973). In *Pogonomyrmex*, at least *P. marcus* is reported to practice such behavior (Marcus and Marcus 1951). I have no evidence that the

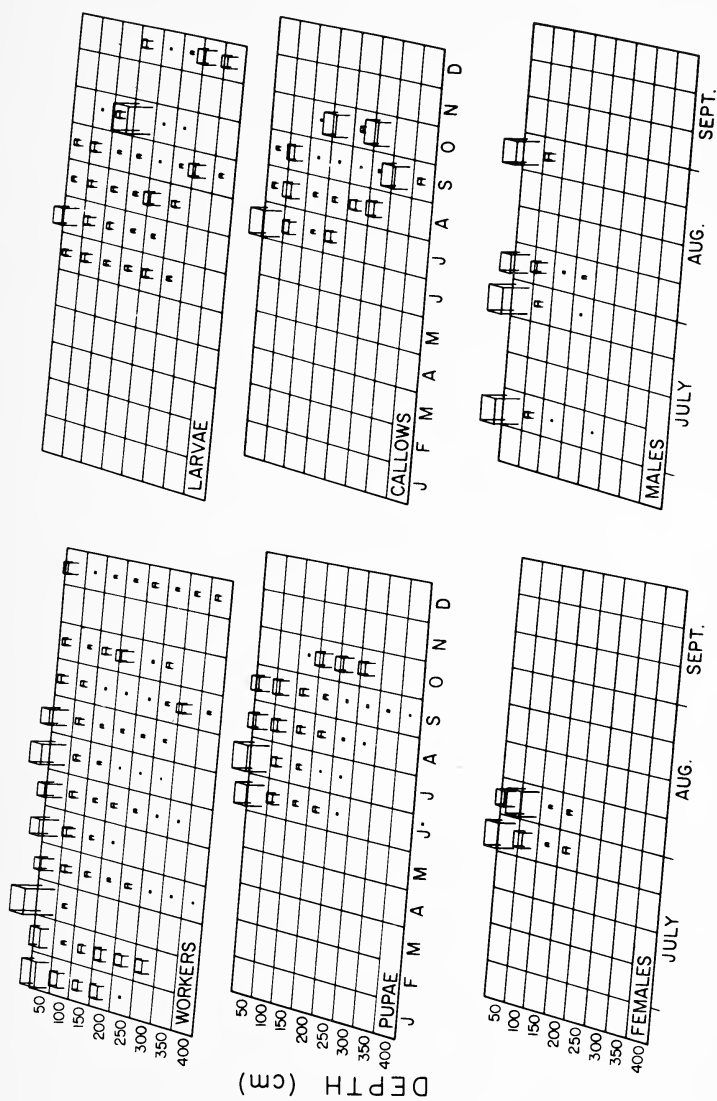


Figure 8. Seasonal movements of the populations of the various member groups in the nests of *P. rugosus*

Table 1. Three-way analysis of variance comparisons of the positions of larvae and pupae in 26 nests of *P. montanus* collected in 1978 and 1979, 3 nests of *P. subnitidus* collected in 1979, and 9 nests of *P. rugosus* collected in 1979. (As the data were expressed as percentages of the total nest population, they were subjected to an arcsin transformation before analysis.)

Source	df	MS	F
<i>P. montanus</i>			
Different nests	25	0.005	0.556 ns
Positions of larvae and pupae	1	0.007	0.778 ns
Levels in nests	7	0.315	35.000***
Nests X brood	25	0.004	0.444 ns
Nests X levels	175	0.110	12.222***
Brood X levels	7	0.028	3.111**
error	174	0.009	
<i>P. subnitidus</i>			
Different nests	2	0.000	0.000 ns
Positions of larvae and pupae	1	0.000	0.000 ns
Levels in nests	22	0.017	5.667***
Nests X brood	2	0.000	0.000 ns
Nests X levels	44	0.017	5.667***
Brood X levels	22	0.003	1.000 ns
error	43	0.003	
<i>P. rugosus</i>			
Different nests	8	0.000	0.000 ns
Positions of larvae and pupae	1	0.000	0.000 ns
Levels in nests	39	0.019	9.500***
Nests X brood	8	0.000	0.000 ns
Nests X levels	312	0.010	5.000***
Brood X levels	39	0.003	1.500 ns
error	311	0.002	

larvae and pupae are placed in separate levels of the nests in any of the three species (Table 1). There is a significant difference between the levels of the nests, which is evident in Figures 6, 7, and 8. The brood tend to be in the lower levels of the nest. Although it is commonly assumed there is segregation of the larvae and pupae, statistical analysis has not been performed in the past to support the assumption.

In one instance, a *P. montanus* nest placed a large number of brood on the soil surface near the nest entrance after a late-summer

Table 2. Analysis of variance comparisons of the positions of males and females in 17 nests of *P. montanus* collected in 1978 and 1979, 4 nests of *P. subnitidus* collected in 1980, and one *P. rugosus* nest collected in 1979. (The data were subjected to an arcsin transformation before analysis.)

Source	df	MS	F
<i>P. montanus</i>			
Different nests	16	0.007	0.538ns
Males and females	1	0.000	0.000ns
Levels in nests	7	0.232	17.846***
Nests X sexuals	16	0.005	0.385ns
Nests X levels	112	0.072	5.538***
Sexuals X levels	7	0.062	4.769***
error	111	0.013	
<i>P. subnitidus</i>			
Different nests	3	0.000	0.044ns
Males and females	1	0.002	0.231ns
Levels in nests	7	0.455	45.083***
Nests X sexuals	3	0.001	0.065ns
Nests X levels	21	0.006	0.630ns
Sexuals X levels	7	0.040	3.924**
error	20	0.010	
<i>P. rugosus</i>			
Males and females	1	0.002	1.000ns
Levels in nest	17	0.006	3.000*
error	16	0.002	

rain, possibly because the upper levels of the nest had become waterlogged. A considerable number of workers guarded the brood during this time and when disturbed, the workers immediately moved the brood back into the nest. This behavior has not been observed in the other two species.

The positions of the males and females were compared with an analysis of variance (Table 2). Although it appears from Figures 6, 7, and 8 and our impressions in the field, that females are in deeper levels of the nest than the males, there is no statistical support (Table 2). There were significant differences between the levels. Figures 6, 7, and 8 illustrate that the reproductives tend to be in the upper levels of the nests.

In *Pogonomyrmex* spp. there is evidence that little mixing of adult workers occurs within the nests (Chew 1960; Golley and

Gentry 1964; Gentry 1974). MacKay (1981) presents data on the respiratory rates and fat contents of workers taken from the different levels of the nests of the three species. In winter, spring, and fall, there are significant differences between the levels with regard to both of these parameters. If mixing of the workers did occur between the different levels of the nest, we would not have found these consistent differences between workers taken from different levels.

There is little evidence of seasonal movements of the nest queens (Figure 9). In the spring *P. occidentalis* queens ascend into the upper levels from the lower levels (Lavigne 1969). The queens may be moved into the deeper regions during the winter for greater protection. In the spring, the soil begins to warm sooner in the superficial levels. The queen may be moved to the higher warmer levels in order to increase her metabolism for initiation of egg production.

Guests.

Many species of insects and spiders were collected within the ant nests. The occurrence of most of these species is probably accidental and individuals of most species were found only in small numbers (one or two individuals per nest). Those species most commonly found include: Orthoptera—*Myrmecophila manni* Schimmer, in the nests of all three species; Coleoptera—*Echinocoleus setiger* Horn, in *P. montanus* and *P. subnitidus* nests, *Hetarius hirsutus* Martin and *H. sp.#1* with *P. montanus*, *H. morsus* Leconte and *H. sp.#2* with *P. subnitidus*, *Cremastocheilus westwoodi* Horn in the nests of *P. subnitidus*. There are at least two species of unidentified staphylinids that are common in *P. subnitidus* nests (more than 10 per nest). Hymenoptera—*Solenopsis molesta* (Say) is common in *P. montanus* and *P. subnitidus* nests, *Pheidole* spp. in *P. rugosus* nests. Of the three harvester ant species, *P. subnitidus* has the greatest number of guests and diversity of species.

Food input into nests.

All three species demonstrate similar seasonal changes in their foraging patterns, with much activity in mid-summer and no activity in the winter and early spring (Figures 10 and 11). There are important differences between the three species. Foraging in *P. rugosus* begins earlier in the spring and extends later into the fall than in the other two species. *Pogonomyrmex subnitidus* has an

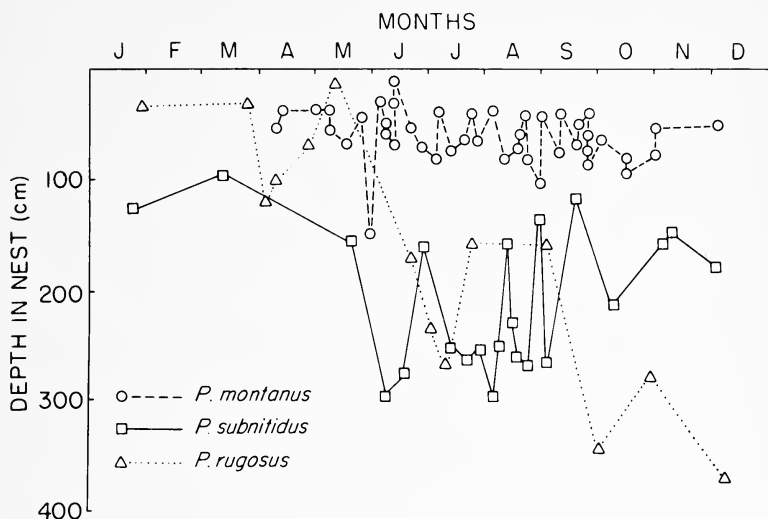


Figure 9. Seasonal changes in the positions of the nest queen in three species of *Pogonomyrmex* harvester ants.

especially short foraging period. *Pogonomyrmex montanus* begins the spring with an abrupt increase in foraging (Figure 10). The lower altitude species, *P. rugosus*, is exposed to many sunny days during the winter. During most of this time the nests of the high altitude species, *P. montanus*, are covered with snow. The nests of the mid altitude species, *P. subnitidus*, are covered by snow part of the time. In May or June foraging begins, increases throughout the summer and decreases again in the fall. This foraging pattern corresponds well with the production of workers and reproductives within the nest.

Only a small portion of the population is involved in foraging. The mean number of foragers per day (recorded during July and August, the months of peak foraging) were 378 ± 73.2 (6) for *P. montanus*, 648 ± 177.3 (4) for *P. subnitidus*, and 1427 ± 187.3 (5) for *P. rugosus*. Later excavation of the nests indicated that the population of foragers comprised 22.9%, 19.4%, and 18.4% of the total nest populations of *P. montanus*, *P. subnitidus*, and *P. rugosus*, respectively. Others have estimated that 10% of the population is involved in foraging in such species as *P. badius* (Golley and Gentry 1964), *P. californicus* (Erickson 1972) and *P.*

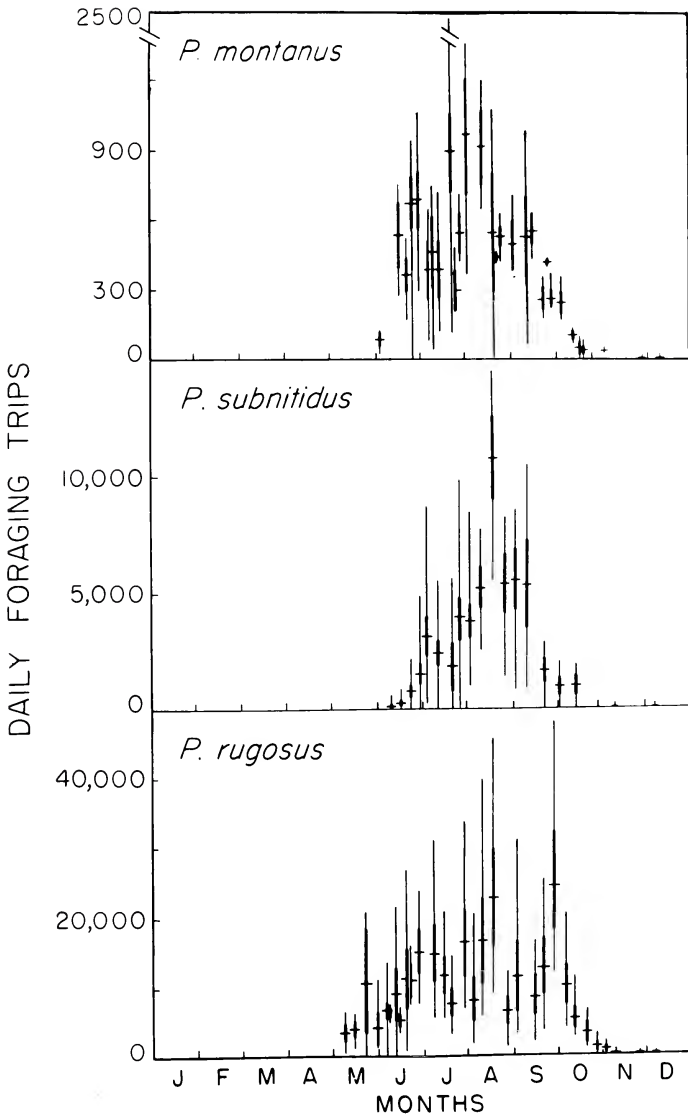


Figure 10. A comparison of the number of daily foraging trips in three species of *Pogonomyrmex* harvester ants. The horizontal lines indicate the means, the black rectangles the standard errors on each side of the mean, and the vertical lines indicate the ranges.

Table 3. Nest densities, populations and biomasses of several ant species of the genus *Pogonomyrmex*. The values are ± 1 standard error, n is presented in parenthesis.

Species	Nests/ha	# adult workers/ nest	# adult workers/ m.sq.	mg d.w. workers/ m.sq.	Locality	Authority
NORTH AMERICAN SPECIES						
<i>apache</i>		40-80			New Mexico	Cole 1954
<i>badius</i>	12-27	4000- 6000(6)	13.5	84**	South Carolina	Golley and Gentry 1964
<i>badius</i>		4736 \pm 234 (25) range = 2795-7264			South Carolina	Gentry and Stiritz 1972
<i>barbatus</i> (or <i>rugosus</i> ?)	82	12,358 10,000			Arizona	Wildermuth and Davis 1931
<i>californicus</i>	4-6	1932(1)	1*	1.4*	New Mexico	Whitford 1972
<i>californicus</i>	5.4	4536 \pm 120* (11)	2.4*	3.4*	Southern California	Erickson 1972
<i>desertorum</i>	115	400-600			New Mexico	Whitford and Bryant 1979
<i>magnacanthus</i>		100-225			Southern California	Cole 1968

Table 3 continued

Species	Nests/ha	# adult workers/ nest	# adult workers/ m.sq.	mg d.w. workers/ m.sq.	Locality	Authority
<i>montanus</i>	3-26	1665±88 (70) range= 369-3641	0.5-4.3	1.2-10.1	Southern California	MacKay Unpublished
<i>occidentalis</i>		8700(1)			Arizona	Chew 1960
<i>occidentalis</i>		3024±424 (33)			Wyoming	Lavigne 1969
<i>occidentalis</i>	3-31	2676±348* (11)	0.8-8.3*	25*	Colorado	Rogers et al. 1972
<i>rugosus</i>	21	1000-3000			New Mexico	Whitford and Eittershank 1975
<i>rugosus</i>	6.3-20.5	1895±300* (2)	1.2-3.9*	8.6-27.9*	New Mexico	Whitford et al. 1976
<i>rugosus</i>		22,000+			Arizona	Peck 1976
<i>rugosus</i>	1-25	7740±795 (20) range= 2586-14742	0.8-19.4	5.5-137.4	Southern California	MacKay Unpublished
<i>subdentatus</i>		several hundred			Northern California	Cole 1968
<i>subnitidus</i>	1-9	5934±502 (26) range= 1850-13056	0.6-5.3	1.7-15.6	Southern California	MacKay Unpublished

SOUTH AMERICAN SPECIES

<i>brevibarbis</i>	more than 500	Argentina	Kusnezov 1951
<i>carbonarius</i>	400-500	Argentina	Kusnezov 1951
<i>cunicularius</i>	few hundred	Argentina	Bruch 1916, Kusnezov 1951
<i>laticeps</i>	40-50	Argentina	Kusnezov 1951
<i>longibarbis</i>	200-300	Argentina	Kusnezov 1951
<i>marcusi</i>	450 (2)	Bolivia	Marcus and Marcus 1951
<i>mayri</i>	603±79 (8)	Colombia	Kugler, pers. comm.
<i>micans</i>	less than 300 (6)	Argentina	Bruch 1916
<i>rastratus</i>	400-500 or more	Argentina	Kusnezov 1951
<i>uruquavensis</i>	few tens	Argentina	Kusnezov 1951
<i>variabilis</i>	400-500 or more	Argentina	Kusnezov 1951
<i>vermiculatus</i>	400-500 or more	Argentina	Kusnezov 1951

* Estimations based on data from literature.

** From Brian (1965)

Table 3 continued

Species	Nests/ha	# adult workers/nest	# adult workers/m.sq	mg d w workers/m sq	Locality	Authority
<i>montanus</i>	3-26	1665±88 (70) range=369-3641	0.5-4.3	1.2-10.1	Southern California	MacKay Unpublished
<i>occidentalis</i>		8700(1) 3024±424 (33)			Arizona Wyoming	Chew 1960 Lavigne 1969
<i>occidentalis</i>	3-31	2676±348* (11)	0.8-8.3*	25*	Colorado	Rogers et al. 1972
<i>rugosus</i>	21	1000-3000			New Mexico	Whitford and Ettershank 1975
<i>rugosus</i>	6.3-20.5	1895±300* (2)	1.2-3.9*	8.6-27.9*	New Mexico	Whitford et al. 1976
<i>rugosus</i>		22,000+			Arizona	Peck 1976
<i>rugosus</i>	1-25	7740±795 (20) range=2586-14742	0.8-19.4	5.5-137.4	Southern California	MacKay Unpublished
<i>subdentatus</i>		several hundred			Northern California	Cole 1968
<i>subnitidus</i>	1-9	5934±502 (26) range=1850-13056	0.6-5.3	1.7-15.6	Southern California	MacKay Unpublished

SOUTH AMERICAN SPECIES

<i>brevibarbis</i>	more than 500		Argentina	Kusnezov 1951
<i>carbonarius</i>	400-500		Argentina	Kusnezov 1951
<i>unicularius</i>	few hundred		Argentina	Bruch 1916, Kusnezov 1951
<i>laticeps</i>	40-50		Argentina	Kusnezov 1951
<i>longibarbis</i>	200-300		Argentina	Kusnezov 1951
<i>marxii</i>	450 (2)		Bolivia	Marcus and Marcus 1951
<i>mauri</i>	603±79 (8)		Colombia	Kugler, pers comm
<i>micans</i>	less than 300 (6)		Argentina	Bruch 1916
<i>rusticatus</i>	400-500 or more		Argentina	Kusnezov 1951
<i>uriaguayensis</i>	few tens		Argentina	Kusnezov 1951
<i>variabilis</i>	400-500 or more		Argentina	Kusnezov 1951
<i>verruculatus</i>	400-500 or more		Argentina	Kusnezov 1951

* Estimations based on data from literature

** From Brian (1965)

occidentalis (Rogers et al. 1972). Chew (1960) estimated that no more than $\frac{1}{2}$ of *P. occidentalis* workers were out of the nest at any one time. In a mark recapture analysis, Whitford et al. (1976) estimated the forager population at 2786 in *P. rugosus*. This estimate is higher than the one I determined which may indicate that the nest populations of *P. rugosus* in New Mexico are larger than those in southern California. My estimates are minimal: there may have been foragers which remained within the nest. Also the experimental channeling of the forager population may have affected the natural foraging activity. The whole work force may not have been activated because of a reduction of recruitment (Hölldobler, Pers. Comm.).

A comparison of the number of foragers given above and the number of foraging trips per day (Figure 10) indicates that individual *P. montanus* foragers make two or three trips per day, *P. subnitidus* foragers about nine, and *P. rugosus* foragers make more than ten trips per day. There are considerable differences between the three species in the numbers of foraging trips made (Figure 10), which compares with the differences in the sizes of the nest populations (Table 3).

The seasonal changes in the daily amount of food brought to the nest are similar to those found in the numbers of foraging trips (Figure 11). As with the forager number, *P. rugosus* brings in food earlier in the spring and extends foraging later into the fall, compared to the other two species. *Pogonomyrmex montanus* abruptly increases the food input once foraging begins and decreases it slowly until fall. *Pogonomyrmex montanus* is the only species of the three which does not store seeds in the nests. It may have to bring in large amounts of food once the larvae begin to appear in the nest. The other two species have seed reserves and may thus avoid such an abrupt increase in foraging in the spring.

Comparisons of the food sources of the three species (Figure 12) indicate that the harvester ants utilize a wide variety of food items, although most materials are either seeds or plant parts. *Pogonomyrmex rugosus* relies almost exclusively on seeds. *Pogonomyrmex subnitidus* and especially *P. montanus* bring a much greater diversity of food items to the nest. *Pogonomyrmex montanus* relies more heavily on plant parts and insects than does *P. subnitidus*. *Pogonomyrmex subnitidus* brings in a greater proportion of feces than does *P. montanus*, although the ratio of bird to mammal feces

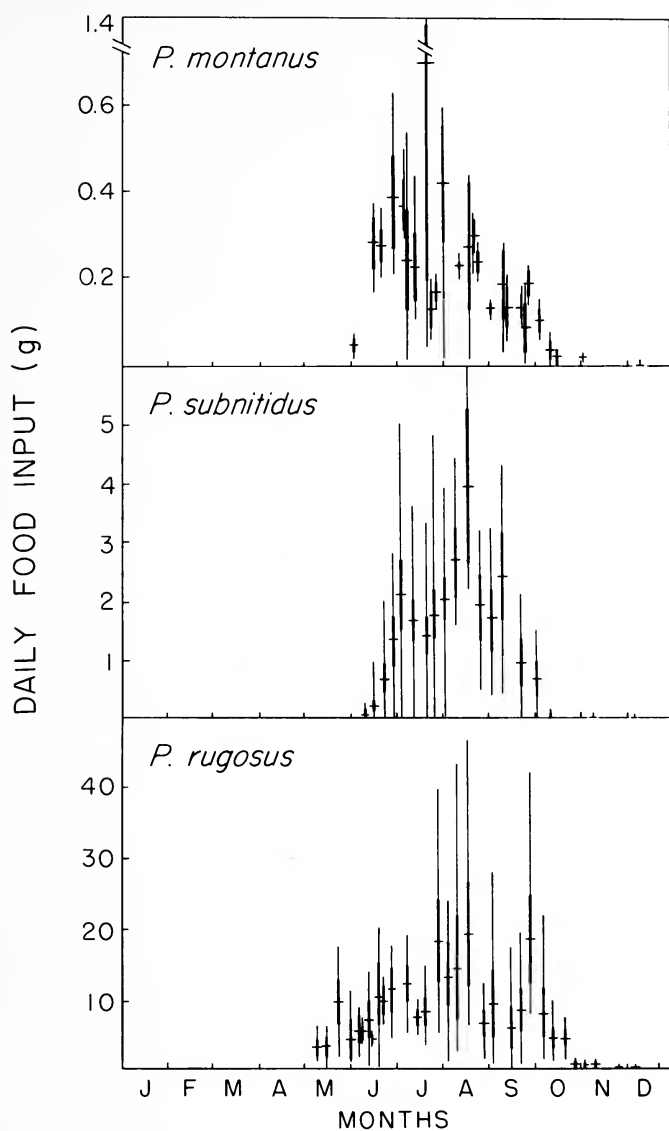


Figure 11. A comparison of the daily food input (grams) in the three species of *Pogonomyrmex* harvester ants.

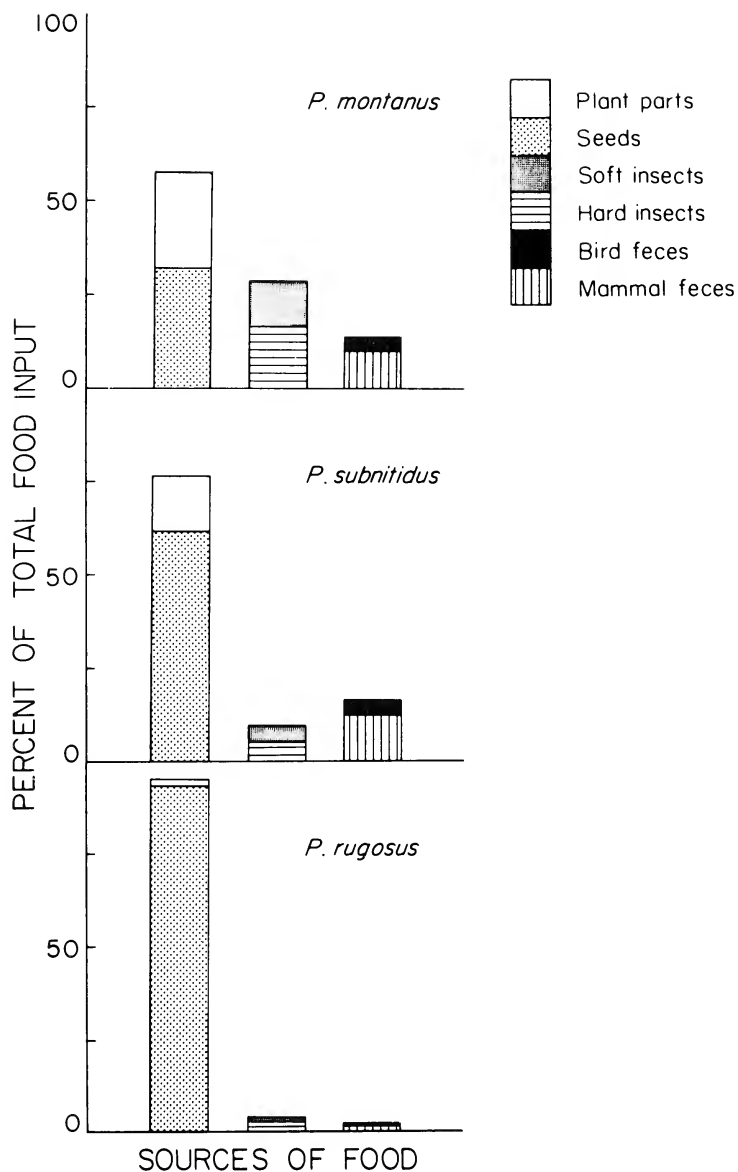


Figure 12. A comparison of the food sources in the three species of *Pogonomyrmex* harvester ants.

is similar in both species. *Pogonomyrmex rugosus* brings in more bird feces than mammal feces, *P. montanus* and *P. subnitidus* bring in more mammal feces than bird feces. A distinction was made between "hard" insects and "soft" insects. Hard insects included those heavily chitinized forms, especially the Coleoptera and certain Formicidae. Soft insects included Homoptera, most Hemiptera, most Diptera, larvae and pupae of most orders and a few non-insects such as spiders. It appears that the degree of chitinization may not be important as the proportions of hard and soft insects were similar. All three species have chitinase activity in their gasters (MacKay, unpub. data).

Plant parts consist of pieces of leaves and flowers and in the case of *P. montanus*, pine resin. Flowers of *Penstemon* spp. and *Arctostaphylos* spp. are transported to the nest and placed around the brood, possibly to increase the humidity. Later the intact flowers are discarded at the nest surface. This indicates the flowers are not placed around the brood to protect them from predators. In the case of pieces of leaves, apparently they are eaten by the ants as they do not later appear on the nest surface. There is considerable seasonal change in the food composition of *P. montanus* and *P. subnitidus* (Figure 13). The percentages of insects brought into *P. montanus* nests changes little seasonally. There is a seasonal reduction in the percentage of utilization of insects in *P. subnitidus*. There is little seasonal change in the proportion of the food sources composed of feces in the two species, although a slight reduction may occur. In both species, especially *P. montanus*, there is a seasonal decrease in the proportion of plant parts brought to the nest. In both species, there is a dramatic increase in the utilization of seeds after July. This increase is probably related to a greater availability of seeds after the flowering period of annual plants. A similar comparison was not made in the case of *P. rugosus* as non-seed materials are a very small portion of their diet (Fig. 12). In *P. rugosus*, there was a seasonal drop in the proportion of the diet composed of *Erodium cicutarium* (L.) L'Her. seeds (May 90.3%, June 91.0%, July 88.9%, August 89.7%, September 84.1%, and October 80.9%). Other seeds, especially those of *Pectocarya linearis* DC and *Festuca octoflora* Walt., made up most of the difference.

Caloric analysis of the food entering the nests of the three species indicates that a *P. montanus* colony receives an average of 166.6

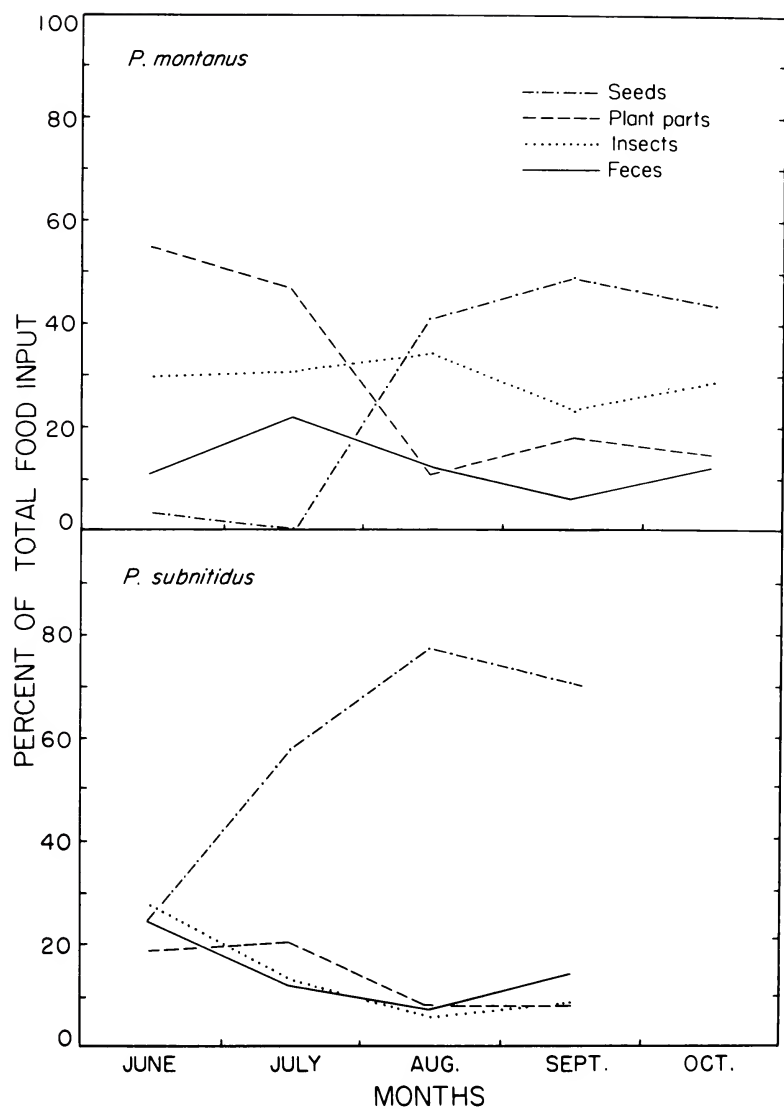


Figure 13. The seasonal changes in the food sources of *P. montanus* and *P. subnitidus*.

kcal, a *P. subnitidus* nest 1267.0 kcal, and a *P. rugosus* nest 7613.6 kcal of food during a year (MacKay 1981). Of these amounts, a *P. rugosus* colony discards seed husks and other such materials, a quantity consisting of 5004.5 kcal or 65.7% of the intake. This is indicated in the field by large discard piles of seed husks being deposited around the nests. A few seeds are discarded and germinate from the piles in the spring. Another harvester ant, *Veromessor pergandei* (Mayr) forages in the piles and removes many of the discarded seeds. *Pogonomyrmex montanus* and *P. subnitidus* discard few materials, the amounts are too small to be estimated.

Seed storage.

Seasonal changes in seed storage in *P. subnitidus* and *P. rugosus* are shown on Figure 14. *Pogonomyrmex rugosus* began both 1979 and 1980 (data for January) with 0.04–0.06 grams of seed storage per ant. The correlation of ant number vs. seed weight was very high ($r = 0.997$, $p < 0.01$). This amount dropped until May, possibly the

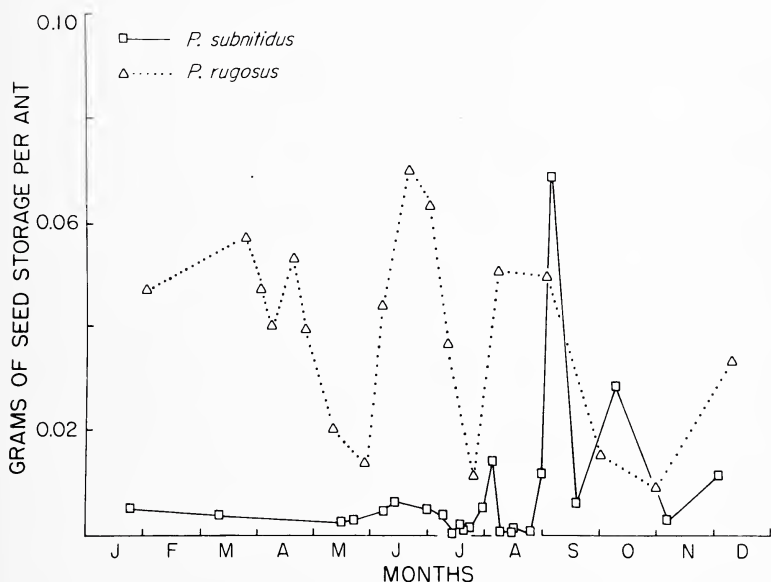


Figure 14. A comparison of the seasonal changes of seed storage in *P. rugosus* and *P. subnitidus*.

result of seed consumption by the developing larvae. I have no explanation for the other two peaks which appear. There is some evidence of a drop in seed storage in the spring in *P. subnitidus*, but it is not as great as that found in *P. rugosus*. *Pogonomyrmex subnitidus* also appears to begin the season with a constant amount of seeds, about 0.002–0.004 g/ant, much smaller quantities than *P. rugosus*. There are also many unexplained peaks in *P. subnitidus* seed storage, especially the high peak in September. *Pogonomyrmex montanus* does not store seeds in the nest. In the population at Big Pine Flats in the San Bernardino Mountains, we occasionally encountered very small caches of seeds (less than 0.0001 g/ant) which were apparently only small daily accumulations of seeds that had not been eaten at that time.

Production.

Production in the three species is summarized in Table 4. The proportion of energy invested in production varies considerably between the three species, but in all cases it is relatively low. Total production constitutes 12.2, 8.3, and 7.9 per cent of the total energy flow in *P. montanus*, *P. subnitidus*, and *P. rugosus* respectively (MacKay 1981). In all three species, a higher percentage of the total production is invested in workers than reproductives (Table 4). *Pogonomyrmex subnitidus* and *P. rugosus* both invest heavily in workers, *P. montanus* invests heavily in reproductives. The data on Table 4 suggest that the three species invest more in the production of females than in males. The costs of respiration of males are higher than of females (MacKay 1981). When respiration costs are taken into account, the colonies of each species invest about equally in the production of males and females (MacKay 1981). More numbers of males than females are produced in all three species (Table 4). Individual females are more expensive to produce than are individual males (MacKay 1981).

Most of the workers are replaced each year. *Pogonomyrmex montanus* colonies produce 1516 workers per year (Table 4), which is similar to the mean worker population of 1665 (Table 3). *Pogonomyrmex subnitidus* colonies produce 3988 workers as compared to a worker nest population of 5934; *P. rugosus* colonies produce 5298 workers per year compared to a worker nest population of 7740.

Table 4. A comparison of the investments in production in three species of *Pogonomyrmex* harvester ants.

Species	Group	Number of Individuals	Dry wt (g)	kcal	Percent Total Production
<i>montanus</i>	Workers	1516± 95	2.4	12.7	51.8
	Females	187± 30	1.2	7.8	31.8
	Males	239± 41	0.8	4.0	16.3
				24.5	
<i>subnitidus</i>	Workers	3988±438	11.6	87.4	91.5
	Females	111± 65	0.9	5.4	5.7
	Males	251± 87	0.6	2.7	2.8
				95.5	
<i>rugosus</i>	Workers	5298±763	30.3	208.2	86.6
	Females	118±100	2.7	18.9	7.9
	Males	312± 73	2.5	13.4	5.6
				240.5	

DISCUSSION

Comparison with other species in the genus *Pogonomyrmex*.

The genus *Pogonomyrmex* belongs to the tribe Myrmicini, one of the most primitive tribes in the subfamily Myrmicinae. The genus has existed at least since the Oligocene (Burnham 1978), and is distributed throughout North and South America from Canada to Patagonia, from sea level to at least 4500 meters in altitude. At the present time there are 24 valid species in North America and about 33 in Central and South America. The genus may have originated in South America and migrated northward (Kusnezov 1951) or originated in North America and migrated southward (Wheeler 1914; Creighton 1952).

Considerable work has been done on nest densities, populations, and biomasses of ants of various species of the genus *Pogonomyrmex* (Table 3). Examples of biomasses from other genera would include the following (expressed as mg dry weight/m²), *Tetramorium caespitum* at 200 (Brian et al. 1967) and 1480 (Nielsen 1974), *Lasius niger* at 60 (Odum and Pontin 1961) and 1060 (Nielsen 1974), *L. alienus* at 2090 (Nielsen 1974), *L. flavus* at 1400 (Odum and Pontin 1961) and 15,000 (Waloff and Blackith 1962), *Leptothorax acervorum* at 3000 (Brian 1956), and *Formica rufa* at 12,000

(Marikovsky 1962). In general, the biomasses of *Pogonomyrmex* are much lower than those found in other genera.

The species investigated, especially *P. subnitidus* and *P. rugosus*, are comparable to most of the North American representatives of the genus (Table 3). The South American species apparently have much smaller populations, but few nests have been excavated and most were partial excavations in which the queen was not found or after the excavation was finished, additional ants were found later. Species from arid regions tend to have larger colonies than those from mesic environments, with the exception of *P. laticeps*. The colonies of North American species live longer than South American species (Kusnezov 1951). *Pogonomyrmex montanus* is somewhat atypical for the genus in occurring at higher altitudes, but is similar to other species in several aspects. The number of nests per hectare is comparable to several other species including *P. badius*, *P. barbatus*, *P. occidentalis*, *P. owyheeii*, *P. rugosus*, and *P. subnitidus*. The nest populations of *P. montanus* are smaller than those of most of the other species, but the number of workers/m.sq. and/or the dry wt/m.sq. are comparable to *P. badius*, *P. californicus*, *P. occidentalis*, *P. owyheeii*, *P. rugosus*, and *P. subnitidus*.

With regards to the populations, the three species investigated appear to be "typical" North American *Pogonomyrmex* harvester ants. It would be very interesting to do a comparable study of "typical" South American *Pogonomyrmex* harvester ants.

Effect of altitude.

It was anticipated that altitude would have three primary effects: 1) The higher altitude species, *P. montanus*, would be subjected to lower average temperatures. 2) The higher altitude species would be subjected to shorter foraging seasons, thus reducing the yearly food input into the nest, resulting in lower production. 3. The higher altitude's shorter growing season would result in fewer available seeds from annual plants.

Although *P. montanus* is subjected to the lowest seasonal temperatures of the specific populations of the three species investigated (Figure 2), it metabolically compensates for this by having higher respiratory rates than the other species (MacKay 1981). Apparently altitude has an effect on foraging, although it was not as large as expected. The foraging season was somewhat reduced in *P. montanus* and *P. subnitidus*, when they are compared

with *P. rugosus* (Figure 10). *Pogonomyrmex montanus*, and to some extent *P. subnitidus*, are in habitats with winter snow cover. In such habitats foraging during the winter is not possible. *Pogonomyrmex rugosus* occupies a low altitude habitat where there are many warm sunny days during the winter. During these days, it does not forage, although a few workers are on the nest surface either sunning themselves or working on nest reconstruction.

The higher altitudes had shorter growing seasons, resulting in fewer annual seed producing plants. As a result *P. montanus* and *P. subnitidus* foraged on various materials but began to rely heavily on seeds later in the year (Figure 13). This was especially the case in *P. montanus*, which relied heavily on plant parts early in the year. Later when seeds became more available, they almost completely replaced plant parts in the diet (Figure 13).

Allocation of resources between worker and reproductive production.

As was expected, the highest altitude species was exposed to a shorter foraging season, but this did not result in lower production. The highest altitude species, *P. montanus*, invests a larger proportion of energy into production than do the other two species. The amount invested in reproductives is especially high (Table 4). *Pogonomyrmex subnitidus* and *P. rugosus* invested about equally in production, with investment in reproductives very low compared to *P. montanus* (Table 4).

Most *Pogonomyrmex* spp. are low altitude desert species (Cole 1968). *Pogonomyrmex montanus* appears to be in a marginal habitat for *Pogonomyrmex* spp. in that it occurs in a high altitude pine forest. The nest populations are among the smallest for the genus (Table 3) and the nests are also very shallow (Appendix 1). Both *P. montanus* and *P. subnitidus* have shorter foraging seasons and apparently are not able to exploit their optimal food source (seeds) until late in the season (Figure 13). Simulations of the effects of bad years on the nests indicate that *P. rugosus* and *P. subnitidus* are able to withstand moderately large reductions in food input whereas *P. montanus* is not (MacKay in prep.). As a result, nests may be short-lived as compared to the other two species and nest-extinction may be a common phenomenon. Apparently, as a response to such conditions, *P. montanus* invests a larger proportion of energy in the production of reproductives than do the other

two species. It might be expected that the South American species would be ecologically similar to *P. montanus* as they share many characteristics (Table 3).

Production as well as foraging and food input were spread over more of the season in *P. rugosus* than in the other two species (Figs. 4, 5, 10 & 11). This is easily explained as *P. rugosus* lives in a more moderate climate than the other two species. Actually it was expected that these processes would occur over the entire year as there are many warm sunny days at lower elevations during the winter. Yet, activities almost stop. Perhaps these processes do not continue as the nest temperatures are lower during the winter than they are in the summer (Figure 2).

The sex ratio was not constant between years (see data in Appendix 1). In *P. montanus* the female:male ratio was 0.88:1 in 1978, 1.41:1 in 1979, and 0.42:1 in 1980. In 1980 the number of males produced was three times those of the other years. An excess of females in 1979 was not found in *P. rugosus* (0.38:1) as was found in *P. montanus*. An excess of males was found in *P. subnitidus* (0.42:1) in 1980 as was found in *P. montanus*.

Nests are extremely heterogeneous in regards to sex ratio (Appendix 1). Correlations were investigated between the female:male ratio and the apparent age of the nest. Twelve *P. montanus* nests at the peak levels of production were used in the analysis. The age of a nest should be related to the numbers of adult workers present in the nest and the depth of the nest: older nests should be deeper and have a larger worker population. The product-moment correlation coefficients (Sokal and Rohlf 1969) of the sex ratio with worker population size and nest depths were both 0.17. Although the coefficients were not statistically significant, both were positive, suggesting that older nests produced greater proportions of females. The product-moment correlation coefficient comparing the sex ratio with the numbers of workers produced by the nest during the year was negative ($r = -0.38$). Although the relationship was not statistically significant, it suggested that nests involved in an increase in the worker population (i.e., younger nests) produced a smaller proportion of females. Data were presented (MacKay 1981) which indicated that food stressed nests produced a greater proportion of females; nests given extra food produced a greater proportion of males.

The factors influencing the determination of sex ratios in the Hymenoptera are currently of much interest (Herbers 1979). Experimental manipulation of food input and excavation of colonies of known age may provide information on the factors which determine the sex ratio in a harvester ant nest.

SUMMARY

This investigation compares the phenologies of foraging and reproduction in three species of *Pogonomyrmex* harvester ants along an altitudinal transect in southern California, USA. Periodic excavations of 126 nests of the three species, *P. montanus*, *P. subnitidus*, and *P. rugosus*, reveal that seasonal changes occur within the nests. The three species have similarities in the physical environment of the nest although *P. montanus*, the highest altitude species, has lower nest temperatures. Both *P. montanus* and *P. subnitidus* are snowbound during part of the season. Egg laying begins in late April or May; development to adult requires five to six weeks. The brood reach maximum numbers in late July to late August. Most of the larvae and pupae formed in the first part of the season become reproductives. Mating flights begin in late July and are completed by the first part of September. The highest reproductive populations occur in mid August.

Much of the nest population is in the upper levels of the nest during the summer and in the lower levels during the winter. During the summer, temperature and humidity gradients exist in the nests with deeper levels being cooler and moister. These gradients may account for the placement of the brood in the lower levels. There is no evidence of segregation of the larvae and pupae within the nest, which has been reported by other investigators.

All three species demonstrate similar seasonal changes in foraging patterns, with much activity in the mid summer and no activity during the winter. Only about 20% of the nest population is involved in foraging. Individual foragers make up to 9 or more foraging trips per day. The ants utilize a wide variety of food items, although most materials are either seeds or plant parts. There is a considerable seasonal change in the food composition of *P. montanus* and *P. subnitidus*.

The highest altitude species, *P. montanus*, allocates more energy to reproduction than do the mid or low altitude species. The nests

invest about equally in the production of males and females. Evidence presented suggests that the sex ratio may be ecologically determined and that there may be a yearly change in the sex ratio.

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Appendix 1. List of the populations of the excavated *Pogonomyrmex* spp. nests, including workers (W), larvae (L), pupae (P), callows (C), males (M), and females (F). The position of the queen and maximum depth of the nests are expressed in centimeters. The dates indicated are when the excavation was begun.

Date	W	L	P	C	F	M	Position of queen	Depth
<i>Pogonomyrmex montanus</i>								
21 Sept 77	793	7	514	0	0	0	50	50
23 Sept 77	1918	123	578	0	0	0	40	40

Appendix 1. cont.

Date	W	L	P	C	F	M	Position of queen	Depth
11 Apr 78	3142	0	0	0	0	0	50	50
13 Apr 78	1654	0	0	0	0	0	40	50
16 Apr 78	1874	0	0	0	0	0	*	40
3 May 78	2372	0	0	0	0	0	38	70
8 May 78	2240	0	0	0	0	0	36	60
9 May 78	3641	0	0	0	0	0	55	70
18 May 78	2277	0	0	0	0	0	65	80
25 May 78	1752	0	0	0	0	0	43	60
31 May 78	1951	0	0	0	0	0	75	75
6 June 78	491	0	0	0	0	0	32	50
8 June 78	1598	83	0	0	0	0	47	59
13 June 78	499	0	0	0	0	0	*	30
13 June 78	1841	51	0	0	0	0	10	65
23 June 78	695	7	0	0	0	0	55	60
27 June 78	1087	141	38	0	0	0	*	70
7 July 78	1488	359	160	0	0	0	39	80
12 July 78	1652	367	177	0	0	0	75	75
20 July 78	1604	426	477	0	188	54	68	68
24 July 78	1033	228	131	0	52	138	40	70
4 Aug 78	996	411	678	438	64	87	39	53
11 Aug 78	1013	290	323	496	262	0	80	82
18 Aug 78	1158	277	358	529	147	148	60	70
22 Aug 78	1057	244	359	784	48	327	40	82
30 Aug 78	1552	306	330	766	111	405	40	105
9 Sept 78	1113	14	163	254	162	83	40	75
19 Sept 78	1443	54	73	281	81	25	50	68
23 Sept 78	631	1	0	80	0	0	40	63
23 Sept 78	2271	10	2	128	1	0	70	83
24 Sept 78	2573	4	6	96	0	1	60	73
26 Sept 78	634	0	0	40	0	1	*	110
26 Sept 78	1734	5	3	117	0	0	*	84
30 Sept 78	1785	24	12	52	0	0	60	64
30 Sept 78	1024	0	0	13	0	0	59	59
30 Sept 78	652	15	1	11	0	0	**	86
7 Oct 78	1245	16	0	11	0	0	*	74
14 Oct 78	2105	20	3	63	0	0	80	92
16 Oct 78	1343	24	0	0	0	0	**	43
16 Oct 78	538	49	0	0	0	0	**	40
27 Oct 78	2812	4	0	4	1	0	50	76
7 May 79	1304	0	0	0	0	0	30	53
7 May 79	3585	0	0	0	0	0	*	61
25 May 79	2194	0	0	0	0	0	50	70
25 May 79	3141	0	0	0	0	0	40	80

Appendix I. cont.

Date	W	L	P	C	F	M	Position of queen	Depth
3 June 79	1605	0	0	0	0	0	**	40
15 June 79	1979	0	0	0	0	0	30	70
20 June 79	537	63	0	0	0	0	*	50
20 June 79	1768	0	0	0	0	0	20	60
8 July 79	599	193	67	0	0	0	50	60
16 July 79	563	84	44	0	28	8	50	50
22 July 79	2614	1318	750	0	86	290	50	60
29 July 79	947	813	710	305	198	2	40	50
29 July 79	1777	383	708	7	286	146	70	80
30 July 79	369	27	21	137	15	2	*	80
30 July 79	1111	835	693	13	149	51	60	60
3 Aug 79	1853	325	490	609	601	37	*	120
4 Aug 79	1261	483	1049	595	305	543	*	100
4 Aug 79	1625	555	1013	225	221	277	60	80
12 Aug 79 (a)	976	345	534	752	167	12	50	60
12 Aug 79 (b)	640	124	231	701	144	0	30	80
13 Aug 79 (a)	1063	619	529	495	390	11	*	50
13 Aug 79 (b)	697	244	466	660	387	85	40	70
18 Aug 79	755	234	719	729	41	113	60	70
19 Aug 79 (c)	370	4	0	107	221	4	50	70
19 Aug 79 (c)	520	108	641	322	72	262	*	50
19 Aug 79 (d)	836	168	632	1068	142	55	80	80
20 Aug 79 (d)	792	81	401	655	141	0	40	80
20 Aug 79 (e)	596	169	0	36	33	318	50	50
20 Aug 79 (e)	1079	574	839	289	54	436	50	60
7 Sept 79	1796	468	5	931	62	1	80	110
8 Sept 79	711	67	19	65	0	0	30	30
8 Sept 79	808	126	112	559	0	0	70	70
14 Oct 79	1308	35	0	0	0	0	60	60
5 Dec 79	1504	0	0	0	0	0	50	70
19 Aug 80	1039	nr	nr	780	216	309	**	nr
20 Aug 80	1388	nr	nr	501	255	343	**	nr
21 Aug 80	1346	nr	nr	144	53	274	**	nr
21 Aug 80	1687	nr	nr	351	39	634	**	nr
22 Aug 80	1800	nr	nr	185	310	516	**	nr
<i>Pogonomyrmex subnitidus</i>								
5 Nov 78	5033	47	0	0	0	0	150	210
29 Aug 79	2507	894	1212	2819	0	0	140	170
15 Sept 79	3612	867	892	4147	0	0	120	150
7 Oct 79	5442	109	321	999	0	0	220	230
3 Nov 79	3452	56	0	315	0	0	160	230
30 Nov 79	5182	0	0	0	0	0	180	240

Appendix 1. cont.

Date	W	L	P	C	F	M	Position of queen	Depth
25 Jan 80	6864	0	0	0	0	0	130	210
12 Mar 80	13056	0	0	0	0	0	100	200
16 May 80	5009	0	0	0	0	0	*	210
22 May 80	7687	0	0	0	0	0	150	150
6 June 80	4962	0	0	0	0	0	300	300
12 June 80	8679	0	0	0	0	0	*	270
30 June 80	10160	531	0	0	0	0	160	180
8 July 80	3515	470	153	0	0	0	*	260
13 July 80	2440	784	541	0	0	0	260	260
17 July 80	1784	609	579	66	0	0	*	140
19 July 80	9385	1238	767	0	368	270	*	280
22 July 80	3619	1977	1139	143	47	94	270	280
29 July 80	5215	1817	1301	570	6	66	260	260
4 Aug 80	4060	850	1127	314	52	554	*	300
7 Aug 80	4734	1816	1646	794	80	271	190	250
12 Aug 80	2420	559	953	1207	1	8	110	150
13 Aug 80	2362	750	484	1355	0	0	60	230
14 Aug 80	3877	2145	1300	1305	0	0	270	270
23 Aug 80	4168	2301	2062	2524	0	0	250	280
4 Sept 80	6901	1359	1567	1591	2	49	270	270

Pogonomyrmex rugosus

19 Nov 78	4569	0	0	0	0	0	110	200
25 Mar 79	3707	0	0	0	0	0	30	130
3 Apr 79	3778	0	0	0	0	0	120	240
8 Apr 79	14742	0	0	0	0	0	100	360
20 Apr 79	3115	0	0	0	0	0	*	270
27 Apr 79	11802	0	0	0	0	0	70	125
11 May 79	7275	0	0	0	0	0	10	160
28 May 79	10588	0	0	0	0	0	30	160
6 June 79	8033	532	37	0	0	0	*	300
20 June 79	9214	1411	594	22	0	0	170	190
2 July 79	2485	1136	1057	101	5	505	240	260
10 July 79	9374	1522	1368	21	0	0	270	280
24 July 79	3086	1753	1693	838	418	219	160	180
6 Aug 79	5648	2440	3072	1501	38	181	*	300
31 Aug 79	7219	1839	1565	365	9	342	160	270
28 Sept 79	11640	2204	2483	1440	0	0	350	360
27 Oct 79	4655	465	633	305	0	0	280	280
7 Dec 79	10538	66	0	0	0	0	370	400
1 Feb 80	7503	0	0	0	0	0	40	210
23 Feb 80	11239	0	0	0	0	0	*	300

Appendix 1. cont.

* Nest queen not found.

** Nest queen found but level not recorded.

(a) Nest received extra food in June 1979.

(b) Nest received extra food in July 1979.

(c) Nest received less food throughout 1979 season.

(d) Control nest.

(e) Nest received extra food throughout 1979 season.

See MacKay (1981) for further details.

nr= not recorded.

LABORATORY EVALUATION OF WITHIN-SPECIES,
BETWEEN-SPECIES, AND PARTHENOGENETIC
REPRODUCTION IN *RETICULITERMES FLAVIPES*
AND *RETICULITERMES VIRGINICUS*¹

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INTRODUCTION

Considerable interest currently exists regarding the reproductive strategies of social insects (Blum and Blum, 1979; Crozier, 1979). Among termites (Order Isoptera) colony foundation by alate pairs, fusion of existing colonies, splitting of existing colonies, and parthenogenesis have all been reported (Nutting, 1969). Little information is available regarding the relative importance of each of these strategies.

The genus *Reticulitermes* (Rhinotermitidae) contains six Nearctic and twelve Palearctic species, three of which have been critically examined for reproductive modes. Pickens (1932) and Weesner (1956) studied colony foundation of *R. hesperus* Banks by male + female dealate pairs, as well as by parthenogenesis. Buchli (1950) studied similar strategies for *R. lucifugus* Rossi. Clement (1979) studied interspecific hybridization of *R. santonensis* Feytaud and *R. lucifugus*. More limited studies on colony foundation by male + female dealate pairs of *R. flavipes* (Kollar) were conducted by Beard (1974).

Field studies with *R. flavipes* (Howard and Haverty, 1980) suggest that an important reproductive strategy for this species is colony splitting with subsequent production of numerous (several hundred) neotenic reproductives. However, sizeable alate flights are also a prominent feature of the biology of *Reticulitermes* spp. and

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suggest that alate-based reproductive strategies may also be important. Field studies of colony foundation by alate pairs are extremely difficult. We have accordingly chosen to investigate by laboratory studies the potential of alate based reproductive modes. We have examined incipient colony formation with males and females of the same species, males and females of different species, and pairs of conspecific females. Our results are reported here.

METHODS AND MATERIALS

Termites

Unflown alates were collected from fallen logs in the De Soto National Forest in southern Mississippi. *R. flavipes* alates were collected from mid-March to early April of 1968, 1969, and 1970 (one source colony each year) and from mid-September to early October of 1967, 1968, and 1969 (one source colony each year). *R. virginicus* alates were collected in mid-April to mid-May of 1968, 1969, and 1970 (one source colony each year). At least 500 alates/source colony were anesthetized with CO₂ (200 ml/min), sexed, placed in separate petri dishes lined with moistened filter paper, and transferred to a dark incubator at $25 \pm 1^\circ\text{C}$ for less than one week. *R. flavipes* alates to be paired with *R. virginicus* alates were held in their source wood for up to 30 days in an incubator at $15 \pm 1^\circ\text{C}$ until *R. virginicus* alates were available. All alates were allowed to lose their wings naturally before pairing.

Pairing Procedures

Each experimental unit consisted of an 8.3- × 12.7-cm piece of single strength window glass to which 2.5 mm × 1 cm strips of plexiglass had been glued to form a 6.3- × 8.9-cm rectangular cell (Howard, 1980). Washed and oven-dried sand was placed in the upper third of the cell and moistened with deionized water. Two 2- × 4-cm × 1- to 2-mm weathered strips of southern pine were gently inserted about 1 cm apart into the border of the moistened sand. Termites were placed in the cell, the cell was closed by covering the opening with four 2.5- × 7.5-cm microscopic slides, and then the cell was sealed along the edges with hot paraffin. A small opening (about 1 mm) was left to allow for air exchange.

Dealated termites were randomly selected, paired, and placed in an experimental unit. Each unit was examined daily during the first week and any termites caught in condensed moisture were freed.

Also during this period dead dealates were replaced with live ones. After the first week dead dealates were removed but not replaced. Subsequent inspections were made approximately three times a week for the following month, then two times a week for 3 months, once a week for 2 months, and once every 2 weeks thereafter until the dealates were dead or the experiment was terminated. At each inspection the number of live dealates, eggs, larvae (by stage), presoldiers, and soldiers were recorded.

Seven combinations involving the following pairings were examined: (1) *R. flavipes* male + *R. flavipes* female (spring); (2) *R. flavipes* male + *R. flavipes* female (fall); (3) *R. virginicus* male + *R. virginicus* female; (4) *R. flavipes* male + *R. virginicus* female; (5) *R. virginicus* male + *R. flavipes* female; (6) *R. flavipes* female + *R. flavipes* female; and (7) *R. virginicus* female + *R. virginicus* female. Each combination was replicated a minimum of ten times per year.

Determination of Larval Stage

Larvae from six of the seven combinations were randomly selected from at least five of the experimental units in each combination and placed in Bouin's solution. Measurements were then made of the number of antennal segments and head width. These data were used for determining the instars of live larvae through the fourth stage.

Summarization of Data

For each of the seven combinations the following two kinds of data were gathered: (1) mean number of days to the first appearance of an egg, 1st-, 2nd-, 3rd-, and 4th-stage larva, presoldier and soldier; and (2) mean caste composition of incipient colonies at selected intervals. Not all colonies were established nor observed on the same days. To make the various pairings comparable, dates of establishment and observation were converted to Julian dates. Observations were then grouped by the number of days past the data of pairing. Results of pairings replicated over 2 or 3 years were combined. To simplify data summarization, observations were grouped in 3-day intervals. Because of the different times of observation, not all of the colonies were included in each 3-day interval, giving rise to fluctuations in the number of colonies included in the summarized data.

When both dealates had died, colonies were removed from the experiment. Some of the colonies remained viable for more than 2

years. However, when the number of colonies included in any 3-day interval for any of the combinations dropped below five, we discontinued summarization of the data for that combination, since average caste compositions based on less than five colonies would have little meaning.

Examination of Symbiotic Protozoa

Fourth stage or older larvae from five of the *R. virginicus* male + *R. flavipes* female pairing and from four of the *R. flavipes* male + *R. virginicus* female pairing were examined for the presence of species-characteristic protozoa. *R. flavipes* contains mainly *Dinenympha fimbriata* Kirby, *D. gracilis* Leidy, *Pyrsonympha major* Powell, *P. vertens* Leidy, *Spirotrichonympha flagellata* (Grassi) and *Trichonympha agilis* Leidy. *R. virginicus* contains fewer species of protozoa, with the primary species being *D. fimbriata*, *P. minor*, *S. flagellata*, and *T. agilis* (Yamin, 1979).

RESULTS

Egg and Larval Development

The time to the first appearance of eggs and larval instars was rather similar for four of the seven combinations examined (*R. flavipes* male + *R. flavipes* female, spring; *R. virginicus* male + *R. virginicus* female; *R. virginicus* male + *R. flavipes* female; and *R. virginicus* female + *R. virginicus* female; see Table 1). Egg production began in these combinations about 8 to 15 days after pairing, and the first larvae were produced in about 38 to 45 days. Fourth stage larvae were present by about 75 days after pairing.

In contrast, the fall *R. flavipes* male + *R. flavipes* female combination required almost 25 days for egg production to begin and almost 60 days for the first larva to be produced. Fourth stage larvae were present by 83 days after pairing. The combination of *R. flavipes* male + *R. virginicus* female began egg production within 15 days of pairing, but only one larva was ever produced from this cross. This larva appeared normal and successfully molted twice (Table 1). Although the *R. flavipes* female + *R. flavipes* female combination was prolific in egg production, none of these eggs ever hatched.

Soldier Production

The proportion of incipient colonies producing soldiers in the

Table 1. Mean number of days until the appearance of the first egg and first individual of an instar in incipient colonies of different parentage

Parentage ¹	Egg	Instar			
		1	2	3	4
Rf♂ + Rf♀ (spring)	8.1	38.2	46.1	52.9	74.7
Rf♂ + Rf♀ (fall)	24.8	59.7	65.5	73.1	83.3
Rv♂ + Rv♀	11.5	40.2	50.5	58.6	65.1
Rf♂ + Rv♀	15.0	48.5	60.4 ²	70.6 ²	— ³
Rv♂ + Rf♀	11.7	42.2	50.5	57.0	— ³
Rf♀ + Rf♀	7.0	— ⁴	— ⁴	— ⁴	— ⁴
Rv♀ + Rv♀	14.6	45.2	57.8	64.6	— ³

¹*Reticulitermes flavipes*; *Reticulitermes virginicus*.²Values from one experimental unit only.³Not measured.⁴No larvae ever produced.

various combinations varied from 8 to 58.8 percent (Table 2). The *R. flavipes* male + *R. flavipes* female (spring) combination produced only about one-third as many colonies with soldiers as did the *R. flavipes* male + *R. flavipes* female (fall) combination. The *R. virginicus* male + *R. virginicus* female combination, however, produced approximately the same proportion of colonies with soldiers as did the *R. virginicus* female + *R. virginicus* female combination.

Temporal Colony Composition and Numbers

The relative proportions of eggs and larvae in the *R. flavipes* male + *R. flavipes* female (spring) combination (Fig. 1A), *R. virginicus*

Table 2. Soldier production in incipient colonies of different parentage

Parentage ¹	Number of colonies producing soldiers	Total number of colonies	Percent of colonies producing soldiers
Rf♂ + Rf♀ (spring)	14	69	20.3
Rf♂ + Rf♀ (fall)	20	34	58.8
Rv♂ + Rv♀	6	75	8.0
Rf♂ + Rv♀	1	85	1.2
Rv♂ + Rf♀	22	85	25.9
Rf♂ + Rf♀	0	13	0
Rv♂ + Rv♀	2	18	11.1

¹*Reticulitermes flavipes*; *Reticulitermes virginicus*.²Only one pair produced a larva.³No eggs hatched in this crossing.

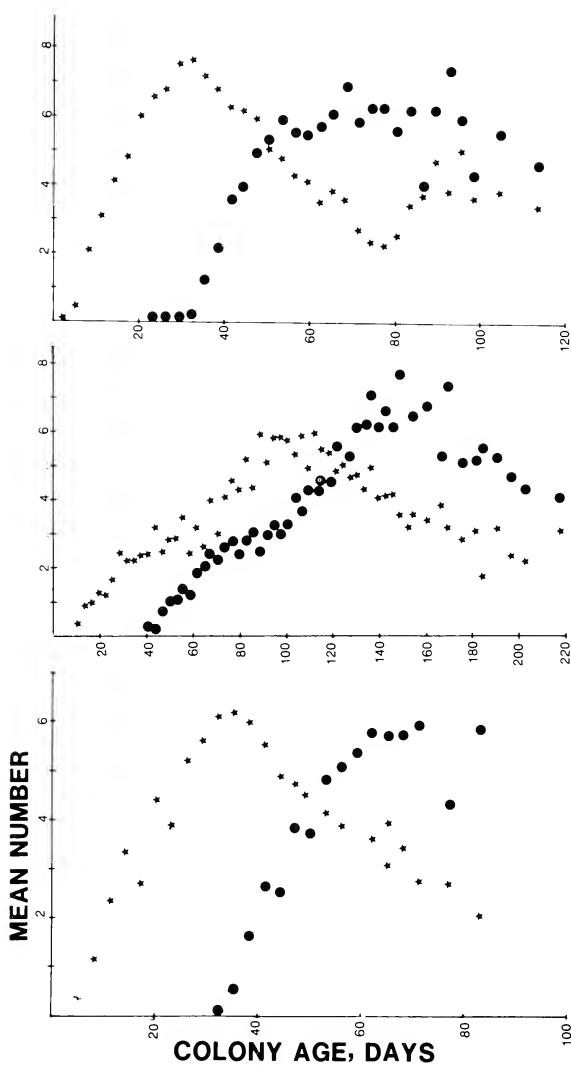


Figure 1. Mean number of eggs and larvae produced by incipient colonies headed by male and female dealates of the same species. A. *R. flavipes* (spring); B. *R. flavipes* (fall); C. *R. virginicus*. Legend: * eggs, + larvae. Each point is a mean of at least five replicates.

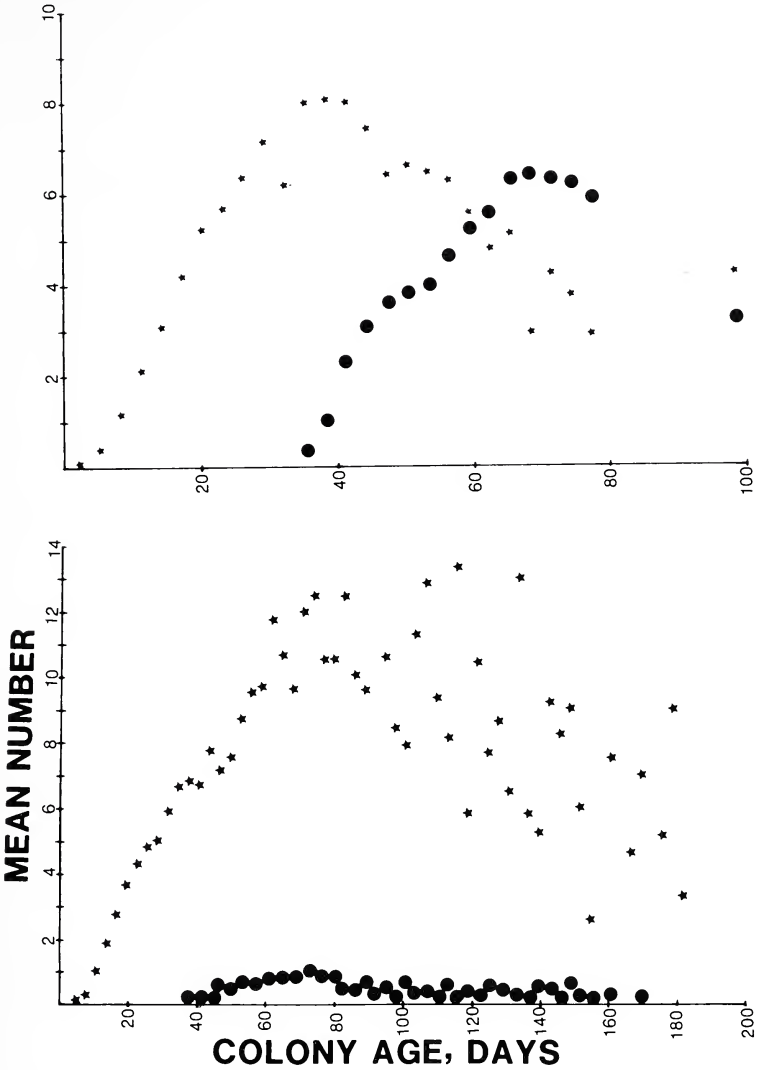


Figure 2. Mean number of eggs and larvae produced by incipient colonies headed by male and female dealates of different species. A. *R. virginicus* male + *R. flavipes* female; B. *R. flavipes* male + *R. virginicus* female. Legend: * eggs, + larvae. Each point is a mean of at least five replicates.

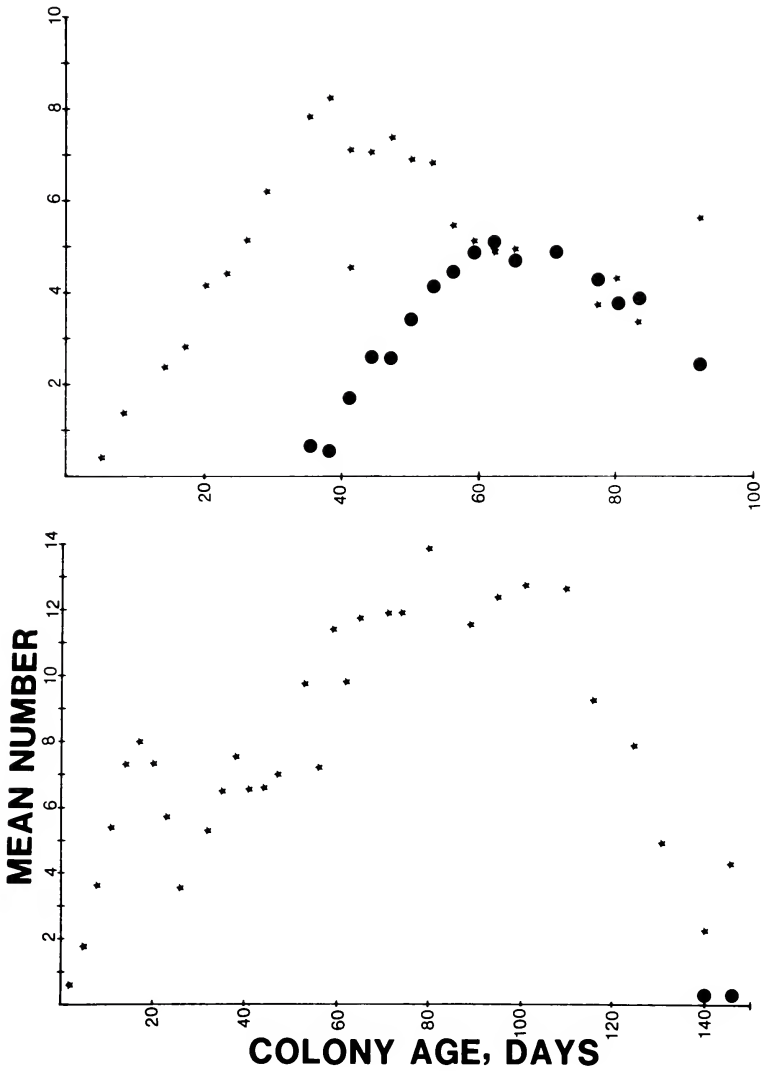


Figure 3. Mean number of eggs and larvae produced by incipient colonies headed by two female dealates of the same species. A. *R. virginicus*; B. *R. flavipes*. Legend: * eggs, + larvae. Each point is a mean of at least five replicates.

male + *R. virginicus* female combination (Fig. 1C), *R. virginicus* male + *R. flavipes* female combination (Fig. 2A), and *R. virginicus* female + *R. virginicus* female combination (Fig. 3A) were similar at all time intervals examined. A maximum mean number of six to eight eggs were present by day 40 and a maximum mean number of six to eight larvae were present by 60 to 100 days. The fall *R. flavipes* male + *R. flavipes* female combination produced similar numbers of eggs and larvae (Fig. 1B) as the above combinations, but at a slower rate.

In contrast, the *R. flavipes* male + *R. virginicus* female combination (Fig. 2B) and the *R. flavipes* female + *R. flavipes* female combination (Fig. 3B) each produced a mean of up to 15 eggs within the first 40 to 60 days, but produced essentially no larvae.

Symbiotic Protozoa in Progeny of Between-Species Pairings

R. flavipes male + *R. virginicus* female: Ten larvae beyond the third instar from four experimental units were examined for protozoa. Seven larvae contained protozoa, and of these, two contained protozoa typical of *R. flavipes*, two contained protozoa typical of *R. virginicus*, and the remaining three contained mixtures of protozoa characteristics of both termite species.

R. virginicus male + *R. flavipes* female: Seventeen larvae from five experimental units were examined for protozoa. All larvae contained protozoa. Three contained protozoa typical of *R. flavipes*, five contained protozoa typical of *R. virginicus*, and the remaining nine contained mixtures of protozoa typical of both termite species.

DISCUSSION

Successful incipient colony foundation by male and female dealates of *R. flavipes* and *R. virginicus* occurred readily in the laboratory. The young colonies were provided with abundant food, plentiful water, an absence of predators, and near optimum temperatures. Despite this, the growth rate of all colonies was slow, with no more than 20 to 30 larvae being produced within the first year. These results agree closely with published laboratory data on several other rhinotermitids. Buchli (1950) obtained ca. 30 individuals from *R. lucifugus* dealate pairs after 8 months, Weesner (1956) and Pickens (1932) obtained 15 to 20 individuals from *R. hesperus*

dealate pairs after one year, and Beard (1974) obtained ca. 53 individuals from *R. flavipes* dealate pairs after one year.

King and Spink (1974) and Akhtar (1978) working with *Coptotermes formosanus* Shiraki and *C. heimi* (Wasmann), respectively, both obtained ca. 30 individuals from dealate pairs the first year. Since each of these workers utilized different temperature and rearing methods, and still obtained similar results, the observed growth rates are probably a fair approximation of that to be expected from field colonies. Such a growth rate implies that *R. flavipes* and *R. virginicus* dealate pairs (and probably other rhinotermitids as well) are K strategists (Matthew, 1976). Incipient colonies will be successful only if the dealate pairs establish nests in sites that are sparsely occupied by other members of the same species, and which possess adequate food and defense requirements necessary for slow, long term colony growth (Oster and Wilson, 1978).

Our laboratory data suggest that at least for *R. virginicus*, it might be possible for female dealates alone to parthenogenetically establish a colony with a reproductive potential equal to that of the normal male + female dealate combination.⁶ This finding raises the question of whether all progeny resulting from the *R. virginicus* male + *R. virginicus* female combinations are sexual offspring, or whether some fraction might have been of parthenogenetic origin.

We have also found that *R. virginicus* males readily mate with *R. flavipes* females in the laboratory, producing apparently viable progeny at rates comparable to those from same-species pairings. In contrast, the pairing of *R. flavipes* males with *R. virginicus* females results in nuptial cell construction, but only a very low rate of progeny production. We infer from our data that the progeny of the *R. virginicus* male + *R. flavipes* female combinations are true interspecific hybrids rather than parthenogenetic progeny, since paired *R. flavipes* females laid many eggs, but only one of them ever hatched. Since the larvae resulting from these mixed-species mat-

⁶None of the females were dissected to verify the absence of sperm. All alates however were taken from the logs before their normal flight period, and had fully developed wings which presumably rendered them incapable of copulation within the confines of the galleries of the logs. Furthermore, no instances are known of any termite species that copulate until they have flown, shed their wings, and constructed a nuptial cell. We consider it extremely unlikely that the females used in our experiments had been inseminated.

ings contained protozoa typical of both parents, we also infer that the larvae engage in proctodeal feeding with both parents. We do not know whether such mixed-species pairing occurs in the field. The main flight periods of *R. flavipes* and *R. virginicus* are separated by about one month (late February to early April for *R. flavipes* and mid-April to mid-May for *R. virginicus*). But unpublished records from the Forestry Sciences Laboratory in Gulfport, Mississippi, indicate that *R. flavipes*, at least, may have flights every month of the year, rendering it at least theoretically possible for interspecific pairing to occur.

Despite the success of incipient colonies in the laboratory, their intrinsically slow growth rates raise serious questions regarding the importance of such pairs as a major means of population expansion. As noted in the introduction, our field studies (Howard and Haverty, 1980) suggest that *R. flavipes* frequently undergoes population expansion by colony fission with subsequent production of multiple neotenic reproductives. Since such new colonies presumably consist of several thousand individuals, their ability to survive should be markedly greater than that of dealate headed incipient colonies. It is, of course, possible that dealate individuals or pairs could be adopted by an established colony, but we know of no data to support such a position.

Clearly, considerably more work should be done to verify the findings of these studies. The success of intraspecific matings is not in question. The confounding results of the interspecific matings demand further cytological and experimental evaluation. The mechanisms of reproductive isolation should be clarified as well as the integrity of these two sympatric species.

SUMMARY

Incipient colony foundation in the laboratory by dealates of *Reticulitermes flavipes* (Kollar) and *R. virginicus* (Banks) was used to examine several possible reproductive strategies available to these sympatric subterranean termite species. Successful colony formation and progeny production occurred with pairings of *R. flavipes* males + *R. flavipes* females (from either spring or fall flights), *R. virginicus* males + *R. virginicus* females, *R. virginicus* males + *R. flavipes* females, and *R. virginicus* females + *R. virginicus* females. Few progeny resulted from pairing *R. flavipes* males + *R. virginicus*

females, or from pairing *R. flavipes* females + *R. flavipes* females. All colony growth rates were slow, producing no more than 20 to 30 individuals within the first year.

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ECOLOGY AND LIFE HISTORY OF THE
RHYTIDOPONERA IMPRESSA GROUP
(HYMENOPTERA:FORMICIDAE)

I. HABITATS, NEST SITES, AND FORAGING BEHAVIOR

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INTRODUCTION

The ponerine ants of the genus *Rhytidoponera* constitute a rich assemblage of species, widespread throughout Australia, with lesser representation in Melanesia and adjacent regions (Brown, 1958; Wilson, 1958). On the Australian mainland they have collectively occupied a broad range of habitats, and often rank among the more abundant members of an ant community. Considerable interest centers on the unusual habit, apparently widespread in the genus, of reproduction by mated "workers" in lieu of a morphologically differentiated dealate queen (Brown, 1953, 1954; Whelden, 1957, 1960; Haskins & Whelden, 1965).

The *Rhytidoponera impressa* group consists of a small, distinctive cluster of species occurring in mesic habitats (mostly rainforest and wet sclerophyll) along the east coast of Australia and in New Guinea. Until recently, the *impressa* group was thought to comprise no more than three species, all reproducing by means of distinct winged queens (Brown, 1953, 1954; Haskins & Whelden, 1965). However, recent studies of systematic relationships and colony structure in the *impressa* group have revealed the presence of at least 5 closely related species and the occurrence of reproduction by both queens and mated workers (Ward, 1978, 1980).

There is a notable paucity of detailed ecological studies on rainforest ponerines in general, and there have been no extensive field studies on *Rhytidoponera*. This paper summarizes information on habitat and nest site preferences, colony densities, and various aspects of foraging, in the *impressa* group. A second paper describes life cycle and reproductive patterns (Ward, 1981).

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METHODS

Data were gathered during a survey of the *Rhytidoponera impressa* group from approximately 100 mesic forest sites in eastern Australia and New Guinea. A detailed tabulation of these collection sites is given in Ward (1978). Field work was carried out from October, 1974 to October, 1978, with a few additional collections in May-July, 1980. Voucher specimens from these collections have been deposited in the Australian National Insect Collection (ANIC), CSIRO, Canberra.

In rainforest and wet sclerophyll forest the collection procedure was as follows: colonies of the *impressa* group were sought by examining all rotting logs, loose stones and other potential nest sites which were encountered during a more or less random (i.e. undirected) walk through a tract of suitable forest. In most localities a tally was kept of the number of "potential nest sites" (logs and stones) sampled. The "rotting log" count was confined to moist rotten logs in middle to late stages of decay, with numerous preformed cavities (corresponding roughly to the "zorapteran" and "passalid" stages of Wilson, 1959), since field observations showed that recently fallen or dessicated logs were rarely inhabited. If a single large log was dissected in two places more than 1 meter apart it was counted as two potential nest sites. Records from rotting logs include a few instances where ants also nested in soil below the log. Stones ranging in areal size from about 100 to 1500 cm² were recorded as potential nest sites if they rested completely on the ground and could be easily overturned. Fallen epiphytic fern masses on the rainforest floor were also considered potential nest sites and were examined and counted in areas where they occurred. Almost invariably, a single colony occupied only one nest site, so the terms "colony" and "nest" are used in equivalently in this paper.

When an *impressa* group colony was located, an attempt was usually made to collect the entire colony contents, i.e. all workers, reproductives, and brood. This entailed considerable excavation of rotting wood and/or soil. Where only colony fragments were believed to be collected, this was noted.

Collected colonies were returned to the lab and their contents enumerated. A few were maintained in modified Janet or Lubbock nests. The majority were frozen for electrophoresis.

Field observations of foraging behavior, colony movement, alate

dispersal, and mating behavior were also made. In addition, field observations and collections of related *Rhytidoponera* species from Australia, New Guinea, and New Caledonia provided some comparative data.

RESULTS

Habitat Preferences

The known members of the *Rhytidoponera impressa* group and their respective distributions are as follows (Ward, 1980): *chalybaea* Emery (= *cyrus* Forel), New South Wales, southern Queensland, New Zealand (introduced); *confusa* Ward, Victoria, New South Wales, southern Queensland; *enigmatica* Ward, New South Wales; *impressa* Mayr, Queensland; and *purpurea* Emery (= *splendida* Forel), northern Queensland, New Guinea.

Most species in the *impressa* group occupy a considerable range of latitude, altitude and forest types; and all species show partial sympatry with at least one other species (Table 1). In this context, a sympatric association is defined as the occurrence of two (or more) species within the dispersal range of their alates. In all cases of sympatry, non-conspecific nests were located within several hundred meters of one another, and in most instances within 50 meters. Despite the overlap between species, differences in habitat preferences are apparent.

R. confusa is essentially a species of wet sclerophyll forest and temperate rainforest. In Victoria and southern New South Wales it is principally confined to lowland wet sclerophyll, and does not occupy cool temperate rainforest of the type dominated by such trees as *Nothofagus*, *Quintinia*, and/or *Atherosperma*. At the northern limit of its range, *confusa* is restricted to temperate and subtropical rainforest at moderate to high elevations. Thus, there is an inverse relationship between elevation and latitude (Figure 1), and the regression of altitude on latitude indicates an average shift of about 70m per degree latitude.

In contrast to *confusa*, *chalybaea* is common in subtropical rainforest of northern New South Wales and southern Queensland (where *confusa* is rare or absent). At the southern limit of its distribution, *chalybaea* is confined to disturbed lowland habitats. Thus, in the Sydney region, it occurs commonly in well-watered parks and gardens, and only penetrates wet sclerophyll and

Table 1. Summary of habitats occupied by 115 *Rhytidoponera impressa* group populations sampled during the present study. Figures in parentheses refer to the number of populations occurring sympatrically with at least one other species. Vegetation categories correspond approximately to those of Specht *et al.* (1974, Tables 2.1 and 4.1). "Subtropical rainforest" is equivalent to the warm subtropical rainforest of Webb (1978), while "temperate rainforest" corresponds to Webb's (1978) submontane and cool subtropical types.

Species	No. Populations Studied	Latitudinal Range	Altitudinal Range	Wet sclerophyll forest	Temperate rainforest	Subtropical rainforest	Tropical rainforest	Littoral rainforest	Dry rainforest	Urban and suburban parkland
<i>confusa</i>	57(9)	27°-38° S	5-1000m	16(4)	30(3)	8(2)	—	2	—	1
<i>chalybaea</i>	34(9)	21°-34° S	5-1000m	4(3)	5(3)	15(1)	—	2	2	6(2)
<i>enigmatica</i>	5(5)	34° S	10-180m	4(4)	—	—	—	—	—	1(1)
<i>impressa</i>	7(1)	17°-27° S	350-1050m	—	—	5	1(1)	—	1	—
<i>purpurea</i>	12(1)	7°-18° S	30-1250m	—	—	2	9(1)	—	1	—
<i>impressa</i> group	115(25)	7°-38° S	5-1250m	24(11)	35(6)	30(3)	10(2)	4	4	8(3)

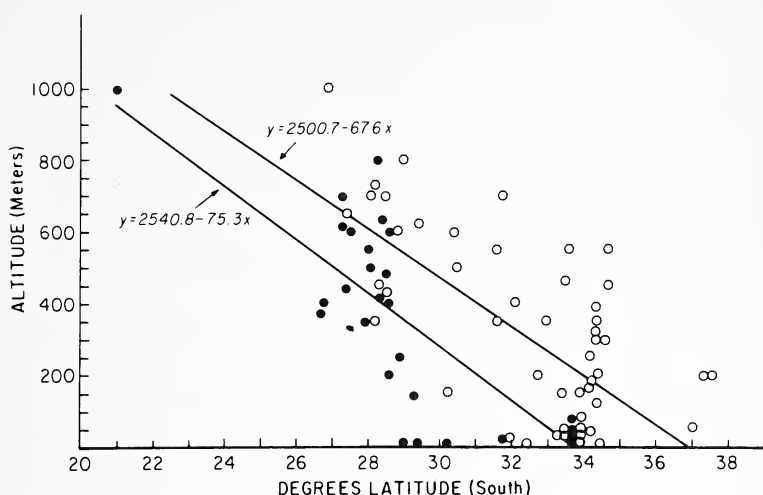


Figure 1. Altitude and latitude of 57 populations of *confusa* (open circles) and 34 populations of *chalybaea* (closed circles). Regressions of altitude on latitude for *confusa* (upper line) and *chalybaea* (lower line) are highly significant ($p < .001$).

rainforest gullies which are ecologically very disturbed, i.e. heavily encroached with introduced weeds such as *Lantana*, *Ligustrum* and *Tradescantia*.

Sympatric associations between *chalybaea* and its sibling species, *confusa*, occur in some of these disturbed gully sites, with *confusa* preferentially occupying the vegetationally less disturbed portions of the gully. These two species also occur sympatrically in stands of *undisturbed* temperate and subtropical rainforest in northern New South Wales and southern Queensland. In this region *chalybaea* tends to occupy more xeric microhabitats than *confusa*, but in one locality (an isolated patch of rainforest at Boonoo Boonoo Falls, N.S.W.) no obvious nest site or microhabitat differences were found between the two species, which nested within a few meters of one another.

R. chalybaea also shows an altitudinal shift with increasing latitude (Figure 1) and tends to occur at lower elevations than *confusa*. The general picture is one of partial ecological differentiation between these two species despite their very close morphological resemblance (cf. Ward, 1980).

Table 2. Nest site records for the *Rhytidoponera impressa* group, excluding small, incipient colonies (≤ 20 workers). Figures in parentheses represent the percentages (for each species) of colonies occupying a given type of nest site.

Species	Rotten Logs	Stones	Fallen Epiphytes	Total
<i>confusa</i>	258 (62.6)	143 (34.7)	11 (2.7)	412
<i>chalybaea</i>	145 (87.9)	19 (11.5)	1 (0.6)	165
<i>impressa</i>	13 (92.9)	1 (7.1)	0 (0.0)	14
<i>purpurea</i>	34 (100.0)	0 (0.0)	0 (0.0)	34
<i>enigmatica</i>	0 (0.0)	21 (100.0)	0 (0.0)	21
all species	450 (69.7)	184 (28.5)	12 (1.9)	646

R. enigmatica is a localized species, known only from wet sclerophyll vegetation in sandstone gullies (6 sites, including two ANIC records) and urban parkland (1 site), the latter record coming from an area where the original habitat would have been sandstone gully vegetation. The range of elevation from which it has been recorded is 10 to 180 meters. Thus, with regard to habitat preference *enigmatica* is the most stenotopic species. Most of the known populations are in sympatry with, or in close proximity to, populations of *confusa* and/or *chalybaea*.

The 7 *impressa* populations studied come from tropical rainforest (1), subtropical rainforest (5), and dry rainforest (1). These data, along with 30 other collection records in the ANIC, indicate that *impressa* is confined to Queensland rainforest at altitudes ranging from 30m to 1050m.

Based on the 12 populations studied here plus additional records from the ANIC and from Wilson (1958), *purpurea* is recorded from subtropical and tropical rainforest (and one population from dry microphyll rainforest on the Mt. Windsor Tableland) in northern Queensland (30m to 1200m), and from tropical montane rainforest (600m to 1300m) in Papua New Guinea. In north Queensland it occurs in both primary-growth and partially disturbed rainforest,

while New Guinea records indicate a predilection for second-growth montane rainforest.

Nest Site Preferences and Densities

Members of the *impressa* group are found nesting mostly in rotten logs and under stones. Nests are multi-chambered, but not highly fragmented, seldom penetrating deeper than 15–20cm into soil, or occupying more than 1m length of rotting log. Nest entrances are cryptic, without conspicuous mounds of excavated material.

Fallen epiphytes on the rainforest floor are occasionally utilized as nest sites by *confusa* and *chalybaea*. During the present study no colonies were found in living epiphytes on trees, although there are single records of a colony-founding *purpurea* queen (Brown, 1954) and a mature *purpurea* colony (Wilson, 1958) from fern epiphytes on rainforest trees.

Nest site records from the present study are summarized in Table 2 which lists, for each species, the number of colonies collected from rotten logs, under stones, and in fallen epiphytes. Excluded from this table are a small number of single records from other nest sites. Thus *confusa* was also found nesting in a *Banksia* lignotuber, in a rotting bracket fungus, directly in the soil, and (twice) in an abandoned termite mound in rainforest. A *chalybaea* colony was located under the bark sheath of an *Archontophoenix* palm, and in urban areas this species occupied less orthodox nest sites (e.g. in and under rusting metal, under concrete slabs, and in crevices along a stone wall). Three *purpurea* colonies (two in north Queensland, one in Papua New Guinea) were observed nesting in cavities in the trunks of living rainforest trees, and in New Guinea this species may be primarily an arboreal nester (Wilson, 1958; records in ANIC).

Table 2 shows that there is a clear trend towards greater specialization in the rotten log nest site in species of more tropical latitudes. The difference between *confusa* and *chalybaea* with respect to numbers of logs and stones utilized is highly significant ($\chi^2_1 = 33.0$, $p < .001$) and the difference between *chalybaea* and *purpurea* is also significant ($\chi^2_1 = 4.4$, $p < .05$). In contrast to all others, *enigmatica* (the localized species of wet sclerophyll gullies) appears to nest exclusively under stones.

In 70 populations (from 63 localities, due to some sympatry) a tally was kept of the number of "potential" nest sites (rotten logs,

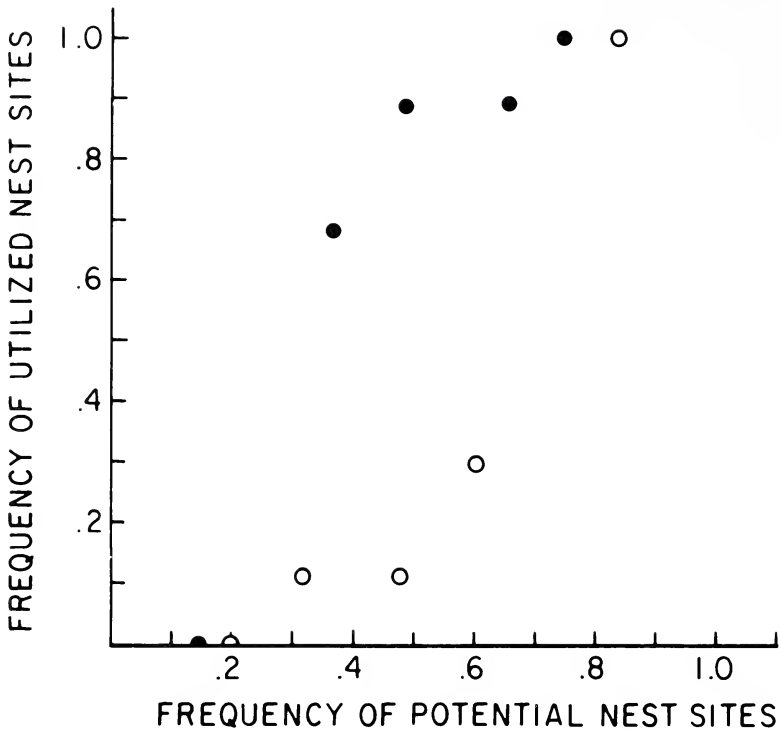


Figure 2. Within-species frequencies of utilized nest sites as a function of potential nest site frequencies, for *5 impressa* group species. Closed circles refer to log nest sites, open circles to stones.

stones, fallen epiphytes) encountered as well as the number of actual nest site occupancies (Table 3). It seems clear that nest site availability varies from species to species. For both rotten log and stone nest sites there are positive correlations ($r = 0.94$, $p < .02$, in both instances, arcsine transformed data) between the proportion of a species' colonies found in a particular nest site and the relative frequency of that nest site for the species (Figure 2). This suggests that species-specific preferences are partly a function of nest site availability. (No such correlation is found for fallen epiphytes—*confusa* shows the highest preference for this nest site despite its relative rarity in the southern rainforests; however, the numbers are in all instances rather low.)

The relative abundances of species can be crudely compared by

Table 3. Numbers of potential nest sites (pns) sampled and actual nests encountered, for 70 *impressa* group populations.

Species	No. populations		Logs	Stones	Epiphytes	Total
<i>confusa</i>	37	no. pns	1838	2984	92	4914
		no. nests	227	98	8	333
		nests/pns	.124	.033	.087	.068
<i>chalybaea</i>	22	no. pns	1164	1136	70	2370
		no. nests	141	17	1	159
		nests/pns	.121	.015	.014	.067
<i>impressa</i>	4	no. pns	260	126	7	393
		no. nests	8	1	0	9
		nests/pns	.031	.008	.000	.023
<i>purpurea</i>	5	no. pns	404	109	24	537
		no. nests	21	0	0	21
		nests/pns	.052	.000	.000	.039
<i>enigmatica</i>	2	no. pns	105	561	—	666
		no. nests	0	15		15
		nests/pns	.000	.027		.027
all species	70	no. pns	3771	4916	193	8880
		no. nests	397	131	9	537
		nests/pns	.105	.270	.047	.060

examining the proportion of potential nest sites which are occupied. (The desirable complementary data on absolute densities of potential nest sites for different geographical regions and habitats are not available). Comparing the density figures (Table 3) for *confusa* and *chalybaea*, the former occupies a significantly greater proportion of stone nest sites than *chalybaea* ($\chi^2_1 = 9.7$, $p < .01$), but no differences exist in the proportion of suitable rotten logs occupied, and the overall nest densities (considering all potential nest sites) are the same for the two species. Nest densities are considerably lower for *impressa*, *purpurea*, and *enigmatica*. *Rhytidoponera confusa* and *chalybaea* utilize a significantly greater proportion of rotten logs than *impressa* and *purpurea* (contingency χ^2 , $p < .001$, for all four comparisons), despite the greater importance of rotting logs as nest sites in the more northerly (tropical) species. This may be partly the result of greater competition for nest sites in the species-rich tropical rainforests. *R. confusa* and *chalybaea* are often common and dominant ants in temperate and subtropical rainforests, respectively, of New South Wales and southern Queensland where the

numbers of sympatric rainforest ant species are probably about one-quarter to one-half that experienced by *purpurea* in north Queensland rainforest.

It is unclear why there is a disproportionate decline in the utilization of stones as nest sites in the more tropical members of the *impressa* group (Table 3) and perhaps for tropical rainforest ants in general (cf. Wilson, 1959, p. 440). One possibility is that in subtropical and tropical rainforests on well-drained soils, stones frequently lie on subsoil below the thin organic horizon and offer an environment poorer in immediate food resources and more demanding for nest excavation than rotting logs. In temperate and some subtropical rainforests of New South Wales, soil horizons tend to be less sharply stratified and/or litter decomposition is slower, so that humic material extends below the level of loose stones.

Effects of Sympatry

Nest site densities for sympatric and allopatric populations of *confusa* and *chalybaea* are given in Table 4. Both species occupy a significantly greater proportion of log nest sites in allopatric populations (contingency χ^2 , $p < .01$ and $p < .001$, for *confusa* and *chalybaea* respectively) and *confusa* inhabits a greater proportion of stone nests sites allopatrically ($\chi^2_1 = 5.4$, $p < .05$). The lower sympatric densities of *confusa* and *chalybaea* could be a result of sympatric associations occurring in more marginal environments. However, the combined sympatric nest densities are very similar to the allopatric densities of both species. There are no significant differences between the total proportion of rotting logs occupied sympatrically and the proportion utilized allopatrically by either *confusa* ($\chi^2_1 = 0.7$) or *chalybaea* ($\chi^2_1 = 1.8$). The combined sympatric nest density under stones is the same as that for allopatric *confusa* populations. While these results could be coincidental, it seems more reasonable to conclude that sympatry has a depressant effect on relative abundance, and that competition for nest sites, food, or foraging space is important.

Other Sympatric Congeners

Other, more distantly related *Rhytidoponera* species also co-occur with members of the *impressa* group. *R. victoriae* (s.l.) is a common species (or complex of species) present in rainforest and other mesic habitats along the entire east coast of Australia. *R.*

Table 4. Number of potential nest sites sampled and the proportion occupied, for sympatric and allopatric populations of *confusa* and *chalybaea*.

Species	No. Populations	Rotten Logs		Stones	
		No. potential nest sites	Proportion occupied	No. potential nest sites	Proportion occupied
<i>confusa</i> (sympatric with <i>chalybaea</i>)	5	280	.071	650	.018
<i>confusa</i> (allopatric)	32	1558	.133	2334	.037
<i>chalybaea</i> (sympatric with <i>confusa</i>)	5	280	.043	650	.015
<i>chalybaea</i> (allopatric)	17	884	.146	486	.014

victoriae is considerably smaller than the *impressa* group species, and nests preferentially under stones.

In some north Queensland localities, *purpurea* or *impressa* coexist with one of several small *Rhytidoponera* species (e.g. *chnoopyx* and *kurandensis* nesting in logs and under stones) and with one of several larger species (*scaberimma* and related species, nesting in logs and directly in the soil). There are no rainforest *Rhytidoponera* of comparable size to the *impressa* group species that regularly coexist with the latter with the exception of *croesus* (s.l.), which nests in rotten logs and in tree trunks in rainforest and wet sclerophyll of New South Wales and southern Queensland. *R. croesus* appears to be generally uncommon, and in fact averages slightly smaller than *chalybaea*, *confusa* and *impressa* to a degree which may significantly reduce prey size overlap (see below).

Colonies of other *Rhytidoponera* species are virtually never found occupying the same nest site as an *impressa* group colony even though other medium to large ponerines such as *Amblyopone australis*, *Leptogenys hackeri* and *Prionogenys podenzanai* are occasionally found nesting in close proximity to an *impressa* group colony (e.g. under the same stone, or in adjacent cavities in a log).

Colony Movement

It appears that species in the *impressa* group are prone to move colonies from one nest site to another rather frequently. For example, in one rainforest population of *confusa* (Royal National Park, N.S.W.) eight stones under which colonies had been briefly located and otherwise left undisturbed were examined one week later: half were unoccupied. Three weeks later, only two colonies remained under the stones. While the censusing no doubt constituted a disturbance conducive to nest-movement, it demonstrates nevertheless the readiness with which colony movement is carried out.

During the course of field collections, vacated nest chambers were occasionally encountered (under stones or in rotten logs) whose previous occupants could be traced to an *impressa* group species on the basis of cocoon remains in the middens. Moreover, colony movement involving transport of brood and other workers was observed several times in *chalybaea* (and in other *Rhytidoponera* species outside the *impressa* group) (Ward, 1981).

Foraging and Food-Retrieval

Members of the *Rhytidoponera impressa* group are partly predacious on other arthropods, but also scavenge for dead insects, seeds, animal feces, etc. Capture of live prey is achieved by a short lunge forward, coincident with rapid closure of the outstretched mandibles. Prey thus captured are subdued by stinging.

In most species, foraging occurs principally on the ground, among leaf litter and rotting logs. However, *purpurea* workers were frequently observed foraging on low foliage of understorey plants, as well as on the rainforest floor, in north Queensland. In Papua New Guinea this species nests (at least partly) arboreally, but limited observations (Wau; September, 1975) suggests that it tends to forage downward from the nest entrance. Urban and suburban populations of *chalybaea*, noted for their unusual nest sites (above), usually forage on the ground and on low vegetation, in damp tree-shaded situations. On one occasion *chalybaea* workers were observed foraging in a house in an urban residential area of Sydney.

Foraging is not restricted to any particular time of the day or season, although activity decreases noticeably towards the middle of the day (and in the winter). Periods of clear warm weather after rain seem particularly conducive to high levels of foraging activity.

Field observations indicate that workers are usually lone foragers, although occasionally several individuals co-operatively transport a large food item back to the nest. Sometimes this occurs close to the nest entrance, seemingly as a result of fortuitous encounters of a heavily-laden forager with other workers. In lab colonies of *chalybaea*, single workers struggling with a large prey item in a food arena were observed to make movements of the gaster suggesting stridulation. On the other hand, chemical recruitment to food sources does occur, although this behavior is rudimentary in comparison to the mass-recruitment patterns of some higher ants. It is readily demonstrated by placing large food baits (e.g. chunks of tuna fish or large insects) close to a nest. Workers which discover the food and return to the nest with a portion of the bait can be observed dragging the tips of their gasters along the ground, and subsequent outward-bound foragers follow the same path to the food (field observations on *chalybaea* and *purpurea*). Large pieces of the bait are retrieved co-operatively by several workers; smaller portions are carried by single foragers.

When such baiting experiments are carried out, there appears to be little active defense of the food by *Rhytidoponera* workers. When baits are partially occupied by other smaller but mass-recruiting ant species, such as *Pheidole*, *Rhytidoponera* workers adopt a "grab-and-run" strategy. This is illustrated by the following observations on *purpurea* in rainforest near Cape Tribulation, north Queensland (5 June 1980).

A *purpurea* colony was located in the trunk of a living palm tree, in a cavity 60cm above ground. Workers were foraging down the palm trunk and on the adjacent rainforest floor. A small chunk of tuna fish was placed on a stone, 1.5m from the palm tree, and close to a *purpurea* forager which soon located the bait. It grasped a small piece of the tuna and returned to the nest, dragging the end of its gaster along the ground. A few minutes later, a worker (possibly the same individual) emerged from the nest entrance and returned to the bait by exactly the same trail. By this time, the remaining tuna bait was in two pieces, each attended by 2-3 workers of a *Meranoplus* sp. The *purpurea* worker carefully circled around one piece of tuna to an unoccupied corner and grabbed it, inadvertently getting a *Meranoplus* worker at the same time. The two briefly grappled, and the *purpurea* worker dropped the food and retreated several centimeters. It then approached the second piece of tuna, edged in towards another exposed corner, swiftly grabbed it (this time without a *Meranoplus* worker), and hurriedly departed for the nest by a different route.

Unrecruited workers of the *impressa* group apparently forage randomly, without laying a continuous odour trail, but upon locating food they return directly to the nest. It is unclear what method(s) of orientation are utilized. Any explanation must take into account the observation that foraging occurs nocturnally as well as diurnally (at least in *confusa* and *chalybaea*).

Food Diversity and Size

The great majority of food items collected by *impressa* group workers are small, individual objects brought in by single foragers. Eighty-one food items were returned to a single *chalybaea* nest observed over a total of 8 hours (Table 5). Of these, one item (an earthworm) was transported by four workers; the remaining food items (encompassing 56 arthropods, 17 *Ficus* seeds or pieces of fruit, and 7 pieces of miscellaneous organic material) were carried by

Table 5. List of 81 food items returned to a single nest of *Rhytidoponera chalybaea* (Sydney, N.S.W., 1–29 February, 1976; total observation time of 8.0 hours)

	Alive	Apparently dead	Total
Hymenoptera: Formicidae: <i>Paratrechina</i> sp. (worker)	1	0	1
" " <i>Iridomyrmex</i> sp. (worker)	1	0	1
" " <i>Pheidole</i> sp. 1 (minor workers)	5	1	6
" " <i>Pheidole</i> sp. 2 (minor workers)	2	0	2
" " <i>Pheidole</i> sp. 2 (major workers)	1	0	1
" " Myrmicinae (male alates)	8	0	8
Hymenoptera: Scelionidae (adult)	1	0	1
Lepidoptera: larvae	1	1	2
Lepidoptera: pupae	0	2	2
Diptera: Sciariidae (adult)	0	1	1
Diptera: larvae	2	2	4
Coleoptera: Histeridae (adult)	0	1	1
Coleoptera: Chrysomelidae (adult)	0	1	1
Coleoptera: larvae	0	2	2
Homoptera: Psyllidae (nymph)	1	0	1
Embiopoda (nymphs or adult females)	0	3	3
Insect larvae, unidentified	1	3	4
Insect parts	0	2	2
Collembola: Entomobryidae	3	2	5
Amphipoda: Gammaridae	2	1	3
Isopoda: Oniscidae	2	1	3
Diplopoda	0	2	2
Annelida: Lumbricidae	0	1	1
<i>Ficus</i> seeds	-	-	9
<i>Ficus</i> fruit (pulp)	-	-	8
Organic matter, unidentified (feces, fungi, seeds?)	-	-	7
	31	26	81

Table 6. List of 19 food items returned to a single nest of *Rhytidoponera croesus* s.l. (Royal National Park, N.S.W., 26 January, 1976) over a three-hour observation period.

Hymenoptera: Formicidae: <i>Paratrechina</i> sp. (worker)	1
" " <i>Solenopsis</i> sp. (worker)	1
" " <i>Chelaner</i> sp. (worker)	1
" " Myrmicinae (male alate)	1
Hymenoptera: Pteromalidae (adult)	1
Lepidoptera: adult microlepidopteran	1
Lepidoptera: larvae	1
Diptera: Nematocera (adults)	2
Diptera: Brachycera (adults)	2
Coleoptera: Chrysomelidae (adult)	1
Homoptera: Coccoidea (nymph)	1
Homoptera: Cicadellidae (nymph)	1
Insect larva, unidentified	1
Unidentified insect legs	2
Acarina (small mite)	1
Mammalian (?) excrement, with veg. matter and insect parts	1
	19

single workers. Thirty-one (55%) of the 56 arthropod items were alive when retrieved from their captors (near the nest entrance). Some of the remaining items may have been killed or paralyzed during capture; others were clearly scavenged as dead material.

It is of some interest to note that 19 (34%) of the 56 arthropod items consisted of other ant species (including alates). Some of these ants, particularly alates, may have been injured or dying when collected. On the other hand, predation on healthy, active worker ants was observed first-hand in the field: *chalybaea* workers from the Sydney University population were seen preying at the soil entrances of *Pheidole* nests, grabbing workers as they emerged.

For comparison with another similar-sized, rainforest species of *Rhytidoponera* outside the *impressa* group, Table 6 lists the food items returned to a *Rhytidoponera croesus* nest over a three-hour observation period. The mean head widths for workers of *croesus* and *chalybaea* are 1.25 ± 0.03 s.d. ($n=8$) and $1.36 \text{ mm} \pm 0.08$ s.d. ($n=80$), respectively. Although there is considerable similarity in food items taken by the two species as measured by ordinal taxonomic categories, an analysis of food size (Figure 3) reveals that the mean food item length of *croesus* (2.5 mm) is significantly less than that of *chalybaea* (3.5 mm) (t-test, $p < .02$). However, the food

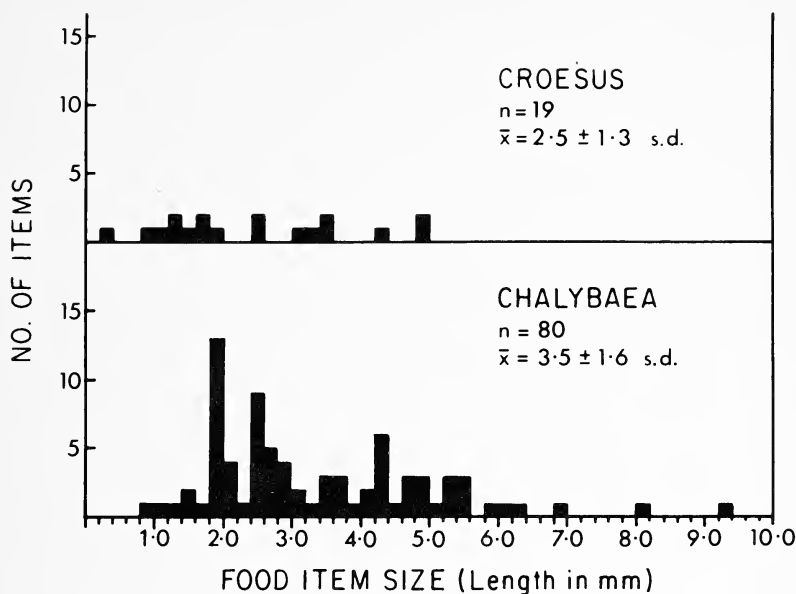


Figure 3. Frequency distributions of the lengths of food items taken from 80 *chalybaea* foragers and 19 *croesus* foragers (see Tables 5 and 6). Each distribution is based on workers from one colony only.

size distributions are based on limited single-nest samples, and there is likely to be significant temporal and spatial heterogeneity within, as well as between, species.

Additional studies on food item diversity and overlap in *Rhytidoponera* are desirable. Such studies are feasible for ants which are primarily lone-foraging predators and scavengers, because of the discrete, visible nature of most foraged items. However, difficulties remain in assessing the importance of honeydew and other liquid foods, which may be carried in the crop as well as between the mandibles.

Two species in the *impressa* group were recorded collecting honeydew from homopterans. Workers of *chalybaea* were seen tending coccids on a fresh shoot emerging from the trunk of a camphor laurel tree (*Cinnamomum camphora*), in the Sydney region. *R. purpurea* workers were observed tending aphids on ginger plants (*Alpinia caerulea*) in several places at Lake Eacham, Qld.

In one of the latter instances, observations were made intermittently over a period of 2 days, during which time a force of about 15 workers was regularly maintained on the plant. These workers gave outward-facing aggressive displays (mandibles barred) when the plant was disturbed. A small contingency of workers was also clustered among leaf litter at the base of the plant, apparently controlling access to the plant and aphids. Defense of "tending rights" may be important since other aggressive, aphid-tending ants such as *Pheidole* were present in the same locality. The colony of the *purpurea* workers was located in a rotten log 5m distant. Workers returning to the colony from the ginger plant showed high fidelity to a particular route which involved following the ground for half the distance and then proceeding along a decumbent liana (one of many) which led back to the log.

Thus, despite the "lone forager" status of most *impressa* group workers, short-term recruitment, co-operative food retrieval, and (in at least one species) persistent, long-range trails, may be used. Excepting persistent trails, species in the *impressa* group appear to show a level of individual foraging and recruitment similar to that described for the myrmicine ant, *Novomessor* (Hölldobler, *et al.*, 1978).

The species in the *impressa* group with the most sophisticated foraging and recruitment behavior (*purpurea*) is the only member whose colonies are entirely monogynous and queenright. It is tempting to speculate that widespread polygyny and worker reproduction in other *Rhytidoponera* species may have constrained ergonomic improvements because of a reduction in the efficacy of colony-level selection (cf. Oster & Wilson, 1978).

SUMMARY

The five known species of the *Rhytidoponera impressa* group collectively inhabit a variety of mesic forest habitats (from wet sclerophyll to tropical rainforest) along the east coast of Australia, with one species (*purpurea*) also occurring in montane rainforest of New Guinea. *R. chalybaea* has invaded mesic anthropogenic habitats (parks and gardens) in the Sydney region. All species show partial sympatry with at least one other species.

Most colonies are located in rotten logs or under stones. There are significant differences between species in the frequencies with

which different nest sites are utilized, and these preferences are correlated with the availability of potential nest sites. The more tropical species (*impressa* and *purpurea*) show a stronger preference for rotten logs, but occur at lower nest densities, than inhabitants of temperate and subtropical rainforest (*confusa* and *chalybaea*). Where *confusa* and *chalybaea* occur sympatrically, they have significantly lower nest densities than allopatrically.

Workers of the *impressa* group are generally lone-foraging predators and scavengers, but co-operative food retrieval and recruitment to food sources occur to a limited degree. The majority of food items are small arthropods: other ant species may be a significant component of the diet. Foraging usually occurs among leaf litter and logs on the ground but at least two species (*chalybaea* and *purpurea*) also forage on low foliage and tend homopterans.

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ECOLOGY AND LIFE HISTORY OF THE
RHYTIDOPONERA IMPRESSA GROUP
(HYMENOPTERA:FORMICIDAE)
II. COLONY ORIGIN, SEASONAL CYCLES,
AND REPRODUCTION

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INTRODUCTION

This paper is concerned with colony foundation and with seasonal cycles in brood composition and alate production in the *Rhytidoponera impressa* group, a species complex of ponerine ants restricted to rainforest and other mesic habitats in eastern Australia and New Guinea.

Life cycle information is most complete for *confusa* and *chalybaea*, and most of what follows refers to those species. Relevant data on the other three members of the *impressa* group (*enigmatica*, *impressa*, and *purpurea*) are given where available. When pertinent to the discussion, some observations on related *Rhytidoponera* species outside the *impressa* group are also included.

METHODS

Collection methods are described in Ward (1981). Most of the data are based on field observations and collections. Where appropriate, suspected reproductive females were dissected to ascertain the condition of the ovaries and spermatheca.

RESULTS

Colony origin

In the *Rhytidoponera impressa* group there are two methods by which colonies can originate:

- (i) from lone, colony-founding winged females (queens), in the manner characteristic of many ants; or

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- (ii) as a result of colony fission or budding (hesmosis), in which one or more mated "workers", accompanied by uninseminated nest-mates, leave the parent colony to found a new daughter nest.

As the foregoing remarks imply, there are two kinds of reproductive females: queens and ergatoid (worker-like) gynes, the latter indistinguishable morphologically from unmated workers. This is the first record of reproductive workers in the *impressa* group (they are common and well-documented in some other *Rhytidoponera*) where previous reports suggested that the only functional reproductives were winged queens (cf. Brown, 1953, 1954; Haskins & Whelden, 1965). Mated queens and ergatoid gynes never coexist in the same nest, but they often occur in different nests in the same population (in *confusa*, *chalybaea* and *impressa*). This rather remarkable dimorphism of female reproductives in the *impressa* group and the resulting differences in colony structure and genetic relatedness will be examined in more detail elsewhere (Ward, in prep.).

There is little information on the frequency of colony fission in worker-reproductive colonies or on the size of newly-budded daughter colonies. Occasionally small isolated clusters of workers and brood are seen in the field, under stones or in rotten log cavities. Table 1 summarizes the composition of four such clusters in the *impressa* group, and two from other *Rhytidoponera* species (*tasmaniensis* and *fulgens*). Similar observations were made by Haskins & Whelden (1965) on *R. metallica*. Note that in the two cases where workers were dissected (Table 1), only one individual in each cluster was found to be inseminated. In no instance in the *impressa* group (or in any other *Rhytidoponera* species) was a single isolated worker, with brood, located in the field, in contrast to the frequent occurrence of single colony-founding queens (see below).

The process of colony fission is observationally difficult to distinguish from the movement of a colony from one nest site to another, and the two events may be inter-related. Table 2 summarizes observations made on colony movement in *chalybaea* and in three other *Rhytidoponera* species (outside the *impressa* group). In only one instance (*maniae*) was a single colony observed splitting into two nests, but the same event may have been occurring during the other observations, if some workers remained at the original nest site.

Table 1. Composition of small, isolated clusters of workers and brood (incipient worker-reproductive colonies?) in *Rhytidoponera confusa*, *chalybaea*, *tasmaniensis*, and *fulgens*.

Species	Locality	Date	No. workers	Brood
<i>confusa</i>	Royal Natl. Park, N.S.W.	5.xi.1974	5	eggs, larvae
"	Pearl Beach, N.S.W.	9.iv.1977	25*	9 eggs, 8 larvae
"	Seal Rocks, N.S.W.	14.vi.1977	13	several larvae
<i>chalybaea</i>	Whian Whian State Forest, N.S.W.	14.v.1977	9	several larvae
<i>tasmaniensis</i>	nr. Wonboyn Lake, N.S.W.	25.x.1975	6	none seen
<i>fulgens</i>	Mt. Koghis, New Caledonia	18.ii.1977	4*	several larvae, one worker cocoon

*workers dissected, one inseminated.

In view of the apparent scarcity of very small isolated clusters of workers and brood (of the size documented in Table 1, i.e. 5–25 workers), it seems likely that colony fission in the *impressa* group often produces daughter colonies larger in size. (Mature worker-reproductive colonies, i.e. those with alates, contain, on average, about 150 workers.) More field observations on budding are needed; the small amount of information accumulated thus far suggests that nocturnal observations might be rewarding. It is also possible that some worker-reproductive colonies develop from former queen-right colonies in which the queen has died.

The origin and development of queen-founded colonies in the *impressa* group has been more extensively documented. Incipient queen-right colonies have been observed repeatedly in the field (Table 3). Mated queens apparently disperse for some distance, undergo dealation, and search for a suitable nest site (under stones, rotting logs, etc.). Having located shelter, the queen excavates a small cavity, lays several eggs, and rears a small brood of workers, the first of these appearing within about 6 months (3–4 months in lab colonies). Unlike the claustral colony foundation typical of higher ants, queens forage outside the nest for food, and feed their larvae partly on insect prey.

The available field information on incipient, queenright colonies suggests that they are usually founded in the spring and early

Table 2. Field observations on colony movement and worker transport in *Rhytidoponera*.

Species	Date	Locality	Time (EDT)	Weather	Observations
<i>chalybaea</i>	13.i.1976	NSW: Sydney University	6.00 p.m.	cloudy, after raining much of the day	several workers transporting others to nest entrance (crack in sidewalk); all came from the same direction
<i>chalybaea</i>	28.ii.1976	NSW: Sydney University	6.30 p.m.	sunny period after raining most of the day	several instances of worker transport (and one of larval transport) from top of a stone ledge to a nest entrance on the side
<i>chalybaea</i>	6.iii.1977	NSW: Balgowlah, nr. Sydney	6.15-6.45 p.m.	mild, clear	workers carrying eggs, larvae, cocoons and other workers from one nest entrance at the base of a palm tree to another about a third of the way around the circumference, a distance of less than 1 meter
<i>victoriae</i>	28.xi.1976	NSW: Jct. of Kanagra Crk. & Coxs River	9.45-10.30 a.m.	overcast, mild	colony moving from one stone to another 1 meter distant; workers carrying egg clusters, larvae, cocoons, and other workers
<i>metallica</i>	10.i.1976	NSW: Gordon, nr. Sydney	2.30-3.30 p.m.	cloudy, following rainy period	workers transporting other workers (and in one instance a male) from one nest entrance (in soil) to another, 3 meters distant; worker transport still occurring the following day at 10.00 a.m.
<i>maniae</i>	1.xi.1975	NSW: 15 km N Coombah	c.9.00 a.m.	cloudy	workers carrying brood and other workers to one of two new nest sites, 0.6 and 2.5 meters, respectively, from old nest site, the directions at right angles to one another; all nests directly in soil

Table 3. Field data on 43 incipient, queenright colonies (with ≤ 20 workers). All *Rhytidoponera confusa* except the following accessions: 2006 (*chalybaea*), 2620 (*chalybaea*) and 2580 (*impressa*).

Accession no.	Population code no.	Date	Dealate Female(s)	Workers	Brood*			Probable year of origin
					Eggs	Larvae	Cocoons	
373	16	21.xi.74	1	5	0	+	0	1973
402	1	26.xi.74	1	2	0	+	+	1973
479	12	22.xii.74	1	14	+	+	+	1973
270	16	23.x.74	1	0	0	0	0	1974
273	16	23.x.74	1	0	0	0	0	1974
330	38	9.xi.74	1	0	0	0	0	1974
370	16	14.xi.74	1	0	+	0	0	1974
426	3	29.xi.74	1	0	+	0	0	1974
451	16	12.xii.74	1	0	+	0	0	1974
454	15	15.xii.74	1	0	-	-	-	1974
457	17	19.xii.74	1	0	+	+	0	1974
461	17	19.xii.74	1	0	+	+	0	1974
462	17	19.xii.74	1	0	+	+	0	1974
465	17	19.xii.74	1	0	-	-	-	1974
483	12	22.xii.74	1	0	-	-	-	1974
551	28	9.i.75	1	0	0	+	0	1974
552	28	9.i.75	1	0	+	+	+	1974
553	28	9.i.75	1	0	+	+	+	1974
554	28	9.i.75	1	0	0	+	0	1974
571	16	22.i.75	1	?	-	-	-	1974
580	13	22.i.75	1	0	0	+	+	1974
800	38	10.v.75	1	0	+	0	0	1974 or 1975
803	38	10.v.75	1	3	0	+	+	1974

Table 3 (continued).

Accession no.	Population code no.	Date	Dealate Female(s)	Workers	Brood*			Probable year of origin
					Eggs	Larvae	Cocoons	
808	38	10.v.75	1	?	-	-	-	1974
881	2	24.v.75	1	7	0	+	+	1974
970	34	13.vii.75	1	20	0	+	0	1974
1323	38	5.x.75	1	2	+	+	0	1974
1366	8	9.x.75	1	0	+	0	0	1975
1548	16	7.xii.75	1	0	+	0	0	1975
2020	25	5.xi.76	1	4	+	+	+	1975
1971	33	18.ix.76	1	0	0	+	0	1976
1988	30	2.x.76	1	?	-	-	-	1976
1996	30	3.x.76	2	0	0	0	0	1976
2006	57	4.x.76	1	0	0	0	0	1976
2022	25	5.xi.76	1	0	0	0	0	1976
2433	22	17.iv.77	1	0	0	0	0	1976 or 1977
2444	21	30.iv.77	2	0	0	0	0	1976 or 1977
2547	49	16.v.77	1	0	0	+	0	1976 or 1977
2472	39	11.v.77	1	12	+	+	0	1976
2580	93	9.vi.77	1	7	0	+	0	1976
2620	88	11.vi.77	1	17	0	+	0	1976
2849	30	8.x.77	1	0	+	0	0	1977
2850	30	9.x.77	1	0	+	0	0	1977

* brood: +, present; 0, absent; -, no information

Table 4. Composition of 322 *confusa* colonies, with respect to numbers of cocoons and alates, and month of collection. Large standard deviations are due to variation in colony size, and to the fact that not all nests produce alates in a given season.

Month	Sample Size (#colonies)	# worker cocoons mean \pm S.D.	# alate cocoons mean \pm S.D.	# alates mean \pm S.D.
Sept.	13	0.0 \pm 0.0	0.0 \pm 0.0	10.8 \pm 13.9
Oct.	47	0.2 \pm 0.5	0.0 \pm 0.0	5.3 \pm 12.7
Nov.	42	3.6 \pm 6.5	0.0 \pm 0.0	0.2 \pm 1.5
Dec.	13	16.3 \pm 27.7	5.7 \pm 14.6	0.1 \pm 0.3
Jan.	24	43.0 \pm 55.3	16.9 \pm 38.0	0.0 \pm 0.0
Feb.	10	62.8 \pm 40.1	15.9 \pm 15.7	1.0 \pm 2.8
Mar.	15	20.5 \pm 25.2	3.9 \pm 5.2	6.9 \pm 8.3
Apr.	26	27.5 \pm 32.5	1.8 \pm 4.4	23.1 \pm 29.9
May	41	0.4 \pm 1.2	0.0 \pm 0.0	12.7 \pm 21.4
June	50	0.1 \pm 0.3	0.0 \pm 0.0	25.5 \pm 39.0
July	32	0.0 \pm 0.0	0.0 \pm 0.0	25.0 \pm 29.7
Aug.	9	0.0 \pm 0.0	0.0 \pm 0.0	21.9 \pm 34.1

summer, and that development proceeds rather slowly. Of the 17 dealate females collected with eggs or no brood at all, 13 came from spring and early summer months (October–December) and only 4 from the fall (April–May) (Table 3). These findings are consistent with the observation that virgin alates usually remain in the nests throughout the winter, and fly in the spring. Nevertheless the occurrence of a few incipient colonies in apparently early stages of development in April and May requires some explanation: it seems likely that either development was hindered in these colonies or that occasional fall mating flights occur.

Colony foundation in the spring and early summer appears to be the pattern followed in *purpurea*: Brown (1954) noted many colony-founding dealate females of this species in October and November on the Atherton Tableland, north Queensland.

Forty-one of the 43 incipient colonies listed in Table 3 contained only a single queen. The two instances of primary pleometrosis (colony foundation by more than one queen) both involved colonies in a very early stage of development, without brood. One of these pairs (acc. no. 1996) was brought into the lab, and colony development was monitored. The two queens cohabited peacefully from 3 October, 1976 until the end of December, at which time the colony contained 12 eggs, 8 larvae and 8 worker cocoons. The first worker emerged 2 January, 1977; four days later (after a second

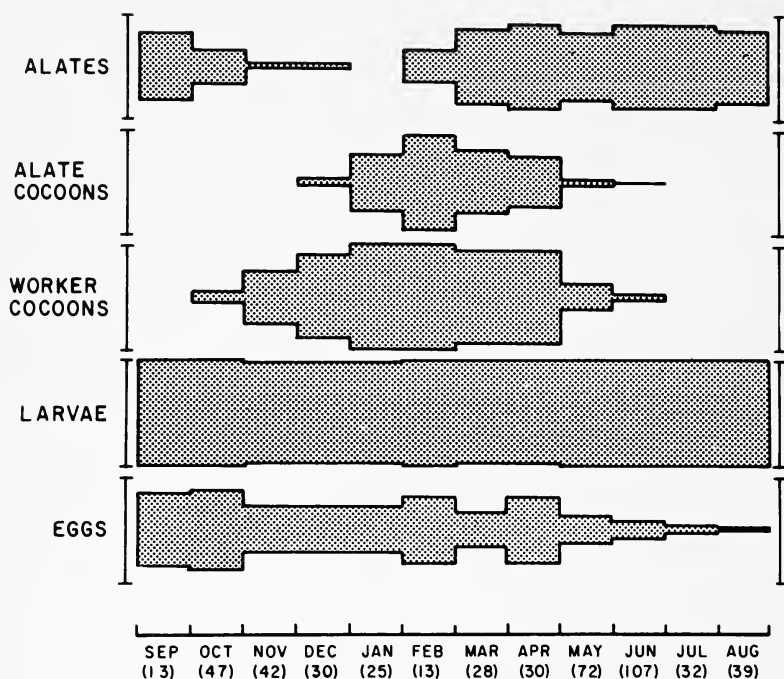


Figure 1. Seasonal changes in brood and alate composition in colonies of *confusa* and *chalybaea*, as measured by the proportion of colonies with various life stages. Maximum width (shown at either side of figure) indicates that 100% of colonies contain the particular stage. Because there were no obvious differences between species or between years, data covering both species over 3½ seasons have been combined. Figures in parentheses refer to the number of colonies sampled in each month. Total sample size: 479 colonies.

worker had eclosed) one queen was found ousted from the nest and almost dead. The colony (with one remaining queen) continued to develop until artificially terminated 15 months later. Subsequent spermathecal dissections and electrophoretic analysis using allozyme markers confirmed that both females were inseminated, and that both had contributed worker offspring to the incipient colony.

Seasonal cycle in mature colonies

There are consistent seasonal patterns in the occurrence of brood and alates in mature colonies of the *impressa* group. These seasonal patterns are essentially the same for both queenright and worker-reproductive colonies, except that alates in the latter are pre-

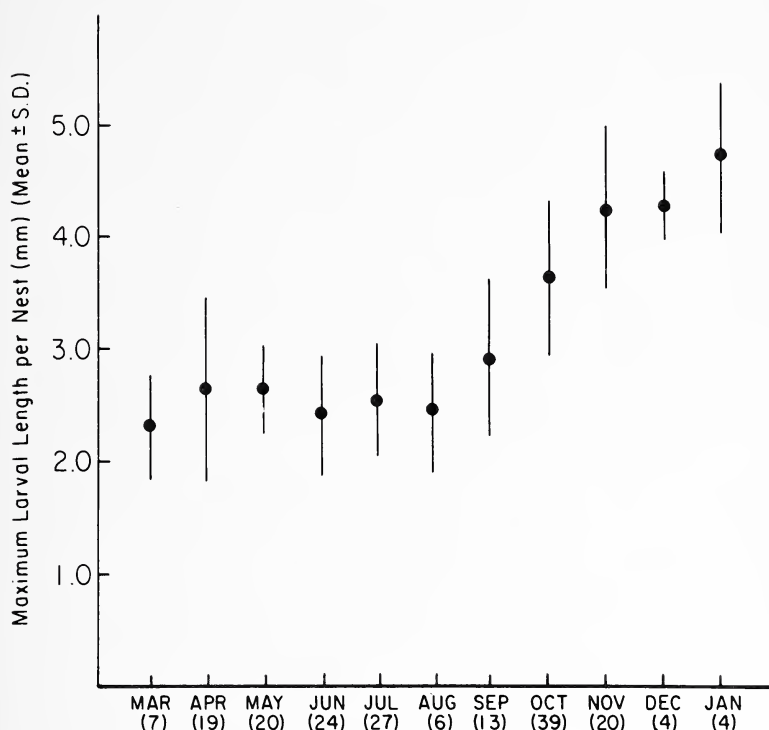


Figure 2. Maximum larval length per nest (measured in millimeters, with larva in natural resting position), in relation to time of year, for 183 nests of *confusa*. One larva (the largest) was measured in each nest. Figures in parentheses indicate the number of nests sampled. No data available for February.

dominantly male only. Figure 1 summarizes the seasonal changes for *confusa* and *chalybaea*, in terms of the proportion of colonies containing various stages of brood or alates, for each month. Data on absolute numbers of worker cocoons, alate cocoons, and alates are given in Table 4 for 322 *confusa* colonies (similar patterns are shown by *chalybaea*, but numbers average higher).

In *confusa* and *chalybaea* there appear to be two peaks of egg production—one in the spring (September–October) and another in the late fall (February–April). Larvae are continually present; those overwintering are small to medium-sized and show little growth until the spring, when development proceeds rapidly (Figure 2). Worker cocoons first appear in October–November, and not until

approximately two months later do the first alate cocoons appear (December–January). Adult workers emerge from January until June, while alates eclose over a shorter time period (February–April). Most, or all, of the alates overwinter in the nest, and are released in the spring, possibly in several bursts, since some nests have been found with alates as late as November (and one nest with a single male in early December).

Several points of interest emerge from the foregoing:

(1) There is only one crop of adults produced each year, and alate production is restricted to a limited period of the total time that new offspring are produced. At any given time, the standing crop of new cocoons consists on average of no more than about 30% alates (Table 5). These facts may be relevant to a consideration of control of the sex ratio of investment.

(2) No cocoons are overwintered, and there is a period of 6 months (July–December) when no new individuals are added to the workforce. At first glance, this would seem detrimental to the increased foraging requirements during rapid larval growth in the spring and early summer. However, because of a time lag between worker eclosion and foraging (callow workers remain in the nest) it may in fact produce an effective increase in the foraging force when it is most needed.

(3) In the absence of data on sex- and caste-specific growth rates, it is difficult to know whether alates arise from the overwintering larvae (hence, from eggs laid the previous season) or from eggs laid in the spring. However one piece of evidence suggests the latter: the discrepancy between the appearances of the first worker and first alate cocoons (two summer months) seems to be too great to be explained by assuming that equivalent-sized overwintering larvae require that extra period of time (and quantity of food) to develop into reproductives. Rather, it would seem more likely that the reproductives develop from spring-laid eggs or alternatively from smaller overwintering larvae.

Not all nests of *confusa* and *chalybaea* contain alates in a given season, alate production being associated with larger colony sizes (Table 5). Nevertheless, there is considerable overlap in colony size between nests with and without alates, partly due to the fact that worker-reproductive colonies produce alates at a smaller size (and probably younger age) than queenright colonies (Ward, 1978). It seems likely that a variety of genetic, environmental, and develop-

Table 5. Mean colony size (number of workers) for nests with alates and for those without alates at the time of year (February–September) when winged reproductives are normally present.

Species	Mean no. workers (\pm S.D.)	
	Alates present	Alates absent
<i>confusa</i>	203.1 \pm 179.9 (n=132)	83.9 \pm 65.7 (n=41)
<i>chalybaea</i>	270.7 \pm 206.2 (n=68)	146.7 \pm 122.4 (n=41)

mental (ergonomic) factors influence the production of alates.

The available information on *impressa* and *purpurea* indicates a seasonal brood cycle similar to that of *confusa* and *chalybaea*. Nests of the two former species collected in the winter in Queensland generally had small larvae (sometimes eggs), alates, and few or no cocoons (sample of 8 *impressa* colonies, 16 *purpurea* colonies). A lowland population of *purpurea* from near Cape Tribulation, north Queensland, was exceptional in overwintering with mature larvae, as well as worker cocoons and adult alates. Nothing is known of the brood cycle in New Guinea populations of *purpurea* which inhabit much less seasonal environments.

Thus, in Australia at least, four species in the *impressa* group produce one brood of sexuals a year, most or all of which are overwintered in the nest and released in the spring. This occurs *despite* contrasting climatic regimes at the north-south extremes of range (summer rainy season in the north, and winter rains in the south) (cf. Brown, 1954).

Collections of *enigmatica* suggest a similar brood cycle (i.e. small, overwintering larvae; cocoons present only in summer), with one important distinction: alates are usually absent from nests in the winter. Of 13 nests collected in the early winter (April 30–July 1) only one contained alates (all males); on the other hand, four out of five nests collected in the summer (January 12–March 7) contained alate pupae (also all males). The differences are significant ($p < .02$, two-tailed Fisher's exact test), and suggest that alates fly principally in the fall. If this is so, there would appear to be considerable temporal isolation between *enigmatica* and its two sympatric congeners (*chalybaea* and *confusa*).

Mating Flights

Two pieces of indirect evidence suggest that reproductives of *confusa* and *chalybaea* normally mate in the spring:

- (i) the proportion of nests containing alates is more or less constant throughout the late summer, fall and winter, dropping rapidly in the spring; and
- (ii) there is a flush of colony-founding females in the early to mid-summer. To the extent that *impressa* and *purpurea* share the same seasonal cycle, it may be supposed that their nuptial flights also occur in the spring.

Alates of *confusa* and *chalybaea* were observed actively dispersing or swarming on several occasions in rainforest and urban parkland in the Sydney region. All observations but one (out of 15) were made in the spring (September 15–November 10), and the only large-scale mating swarms were seen at this time. Most observations involved congregations of males around nest entrances. On six occasions, isolated male or female alates were observed away from the nest, apparently in a dispersing phase. Spring mating flights were observed for 3 consecutive years (1976–78) in the *chalybaea* population occurring on the University of Sydney campus. Because of the scarcity of information on this important stage of the life cycle, the 1976 mating swarm is described in detail.

This flight took place on 4 October 1976, a mild overcast day with brief periods of sunshine and light rain. At the time observations were begun (10:15 a.m. EST) large numbers of *chalybaea* alates, mostly males, were observed flying in parts of the University campus. Alates were distinctly concentrated into clusters in tree-shaded areas. Three of these concentrations were examined in detail (Sites A, B and C in Figure 3).

Site A. This cluster was centered about a *chalybaea* nest entrance between two slabs of sandstone which formed part of a stone wall. Between 10:45 and 11:45 a.m. there were several hundred males within 2 meters of the nest entrance. No alate females were seen. Although males spent most of the time on the ground chasing other individuals, the congregation appeared to be formed by males flying into the site. There were large numbers of workers milling around the nest entrance and most behaved aggressively towards the males, but this did not deter the latter from making repeated attempts to mate with workers (and with other males). Three apparently successful male-worker matings were observed; in each instance the pair was already in copulation when discovered, in a position similar to that described by Hölldobler & Haskins (1977) for *R. metallica*. The worker dragged the male on the ground for about 30

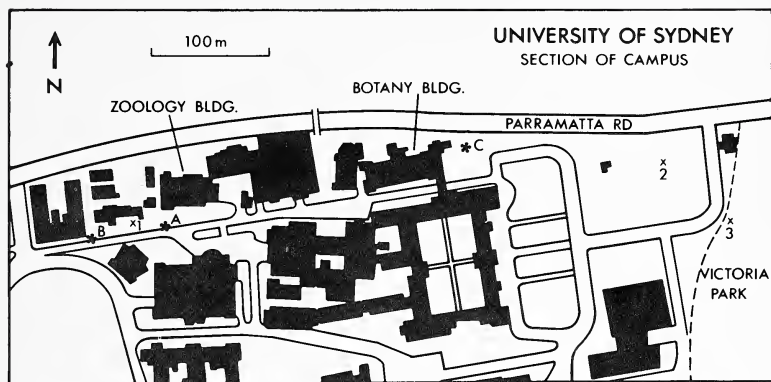


Figure 3. Section of University of Sydney campus where *chalybaea* nuptial flights were observed. A, B, and C represent sites of large clusters of alates, described in text. Lesser numbers of alates were observed at locations 1–3, and elsewhere.

seconds, after which separation occurred. Wings were vibrated rapidly during attempts by males to mount workers. A mating attempt by one male often attracted others, resulting in a buzzing, frolicking ball of males. Males were also observed to enter (and leave) the nest, and may perhaps have mated with workers within the nest. Several instances were noted of workers forcibly evicting males from the nest, dragging them to a distance of 1 meter from the nest entrance. Workers were still foraging during these events: two which were observed returning with a dead honey-bee, and another with a seed, were unmolested by males.

Sites B and C. Similar observations were made at these sites (Figure 3), with large numbers (> 100) of alates and workers clustered in the vicinity of nest entrances, along sandstone walls. A few alate females were also seen among these swarms. Despite persistent attempts by males, no successful worker-male or queen-male matings were recorded. There was a noticeable decline in swarming activity by early afternoon.

Male alates were observed in smaller numbers at several other places on campus, particularly at Sites 1, 2, and 3 (Figure 3). A single, inseminated dealate female was encountered at Site 3 in mid-afternoon, apparently searching for a nest site. During the day, samples of alates were collected from each observation site. Out of a total of 293 alates, 279 (95.2%) were males, and 14 (4.8%) were females.

Later in the evening (10:45 p.m.), lesser numbers of alate males were present, but inactive, on the ground at various locations. Over the next 3 weeks small congregations of males were seen around nest entrances, but never in such numbers or frenzied activity as during the large-scale swarm of 4 October.

The Sydney University population of *chalybaea* consists principally of worker-reproductive colonies, so the preponderance of males among alates is not surprising. The 1976 mating swarms apparently involved insemination of both workers and queens. Only one mated queen was found, however, and it remains unclear if queens mate predominantly in the vicinity of nest entrances or in separate rendezvous sites.

Given the limited number of successful matings observed, it is conceivable that the mating swarm had already passed a peak of activity at the time that observations began (10:15 a.m.). This is also suggested by the absence of workers in a sex pheromone-releasing posture (as described by Hölldobler and Haskins (1977) for *R. metallica*). Such "calling" workers were observed in lab colonies of *chalybaea*, where the behavior occurred both inside and outside the artificial nest. The posture adopted was similar to that described for *metallica* (i.e., head and mesosoma lowered, gaster raised and arched, with tergites exposed). In addition, workers repeatedly rubbed the sides of the gaster with their hind tibiae, presumably facilitating release of pygidial (=tergal) gland pheromone. Such rubbing movements have been reported in *Amblyopone pallipes* queens (Haskins, 1979) but not previously in *Rhytidoponera*.

A mated worker from one of the copulating pairs observed at Site A was isolated in a modified Janet (plaster-of-Paris) nest in the lab and fed on honey and *Drosophila*. On 11 November the first egg was seen, and by 21 December there were 2 eggs, 1 larva and 1 worker cocoon. Just before the colony was terminated, in March, 1977, this mated worker had produced three worker offspring (the first had appeared on 19 January 1977). This is perhaps the first record among the Formicidae of colony-foundation by a lone worker. However, as mentioned previously, there is no evidence that single workers found colonies in the field and it appears that they are always accompanied by an entourage of uninseminated workers.

The inseminated dealate female, also collected on 4 October 1976, was kept under similar lab conditions for five months. The first worker appeared on 7 January 1977. At time of termination

(March, 1977) the colony consisted of 1 queen, 1 worker, 1 worker cocoon, 1 larva and several eggs.

The following spring, in the morning and early afternoon of 1 October 1977 another large mating swarm of *chalybaea* occurred on the University of Sydney campus. As before, this consisted mostly of male alates, concentrated into more or less discrete clusters around several nest entrances. Large clusters were situated at Sites A and C (Figure 3), at exactly the same places observed in 1976. No matings were directly observed, but a timid worker which was being mobbed by males was later found to be inseminated. Workers were generally very aggressive towards males, but the latter persisted in attempts to mate. Once again, samples of alates were collected from various sites, of which 97.0% (195) were males and 3.0% (6) were females. These figures are not significantly different from those of 1976.

On October 12, 1978 small swarms (20–30 individuals) of *Rhytidoponera chalybaea* males were observed at Site C and at several other locations on campus (but not Site A). At 10:15 a.m. males were mostly at nest entrances, apparently in the process of emerging. One alate female was observed; this individual emerged from a nest entrance, and flew off into open sky, ascending rapidly. Similar behavior was observed in males. By 11:30 a.m. many males appeared to be flying into the area, congregations had formed outside nest entrances, and males made repeated attempts to mate with workers.

On the afternoon of the same day two *chalybaea* queens (one alate, one partially dealate) were seen floundering on the sidewalk in a heavily built-up section of downtown Sydney. Both were uninseminated. This suggests that alate females may disperse a considerable distance before mating.

Colony Structure and Life Cycle

In most populations of *confusa*, *chalybaea*, and *impressa*, queen-right and worker-reproductive colonies coexist, in intermediate proportions. Despite the likely disparity between mating sites of winged queens and workers, genetic data from electrophoretic studies (Ward, 1978, 1980) reveal no indication of extensive inbreeding or assortative mating with respect to colony type. This is consistent with the observation that brood development and alate production proceed at similar rates in the two colony types, and that

release of alates in worker-reproductive colonies occurs synchronously with (or at least in the same season as) queenright colonies.

As for the remaining species in the *impressa* group, only queenright nests are known in *purpurea* and this species shows a brood development pattern similar to the three others. By contrast, distinct winged queens are unknown in *enigmatica* (all recorded colonies worker-reproductive), and this species diverges from its closely related congeners by releasing most alates in the fall, although males were found overwintering in one nest. The limited information indicates a possible relaxation of synchrony in the release of ergatoid-seeking male alates, a pattern which would be predicted with the loss of the winged queen caste, especially if the sexual calling behaviour of ergatoid gynes is temporally dispersed. This trend is continued in some other *Rhytidoponera* species outside the *impressa* group, in which functional queens are rare or absent, and flights of alates (males) are reported to be highly non-specific with respect to season (Brown, 1958; Haskins & Whelden, 1965; Haskins, 1979). However, since most of the data come from lab colonies of one species (*metallica*) additional field observations are desirable.

Scattered collections of colonies from different times of the year may give a misleading impression of patterns of alate production. In at least two species of the *impressa* group, alates can be found in some nests from February to November. Although this superficially suggests aseasonal production of alates, a detailed examination of brood development demonstrated that only one crop of alates is produced each year and that alates are released over a limited time period. Additional field studies are necessary to determine whether brood development in *Rhytidoponera* species without queenright colonies is less constrained by the need for synchronous alate release. For comparison with the *impressa* group, such studies would be most appropriately directed towards other species of east Australian mesic forests, in order to minimize climatic and other environmental differences.

SUMMARY

In the *Rhytidoponera impressa* group there are two kinds of colonies, which are distinguished by the type of reproductive female present: queenright colonies with a single dealate queen, and

worker-reproductive colonies in which one or more mated "workers" occur in lieu of a queen. It appears that worker-reproductive colonies normally reproduce by colony fission or budding, although information on this process is fragmentary. Queenright colonies are founded by lone queens. Colony-founding queens are most frequently encountered in the spring and early summer; such queens leave the brood chamber to forage for food.

In mature colonies of *confusa* and *chalybaea*, the development of brood and production of alates is highly seasonal (and essentially similar for both queenright and worker-reproductive colonies). One crop of workers and alates is produced each year, the former eclosing from cocoons between January and June, the latter between February and April. Most or all alates overwinter in the nest (along with small to medium-sized larvae), and are released in the spring (September–November). Similar seasonal patterns are shown by *impressa*, *purpurea* (in Australia), and *enigmatica*, except that colonies of *enigmatica* generally do not retain alates over the winter.

In the population of *chalybaea* on the University of Sydney campus, mating flights took place in early October for 3 consecutive years. During these flights, flying males became concentrated into clusters around nest entrances where they attempted to mate with workers, with males, and with the occasional alate female. Several worker-male but no queen-male matings were observed in these nest-associated swarms. Like males, queens appear to disperse some distance before mating, and possibly utilize mating sites other than nest entrances.

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THE ONTOGENY OF *LYSSOMANES VIRIDIS*
(WALCKENAER) (ARANEAE: SALTICIDAE)
ON *MAGNOLIA GRANDIFLORA* L.¹

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INTRODUCTION

Lyssomanes viridis (Walckenaer) is a translucent green spider found in the southeastern United States from North Carolina to Florida and Texas (Kaston 1978). It has sometimes been placed in a separate family, Lyssomanidae, but the most recent taxonomic study (Galiano 1976) includes it in the Salticidae. This species commonly lives on the tree *Magnolia grandiflora* L. in mesic situations, on palmettoes in various habitats, and on *Lyonia* sp. and other shrubs in the sand pine scrub of central Florida. No complete life cycle has been published for any *Lyssomanes* species. Crane (1950) did present descriptions of the early stages, including second postembryo (her first instar) and first instar (her second instar) of *L. bradypilus* Crane. The current paper is the result of a total of two and one half years of collection and observation of a natural population of *L. viridis* for the purpose of learning about the ontogeny of this spider in the wild.

METHODS

Eggs, immatures, and adults of *L. viridis* were collected on the undersides of leaves by turning the leaves and catching the spiders in vials in a stand of *Magnolia grandiflora* at Tall Timbers Research Station, Leon County, Florida (Figure 1). These were collected monthly from August 1971 to February 1973 and usually twice a month from June 1977 through June 1978. The population densities were measured by counting the number of spiders collected per 1000 leaves from September 1977 through the death of the adults and the

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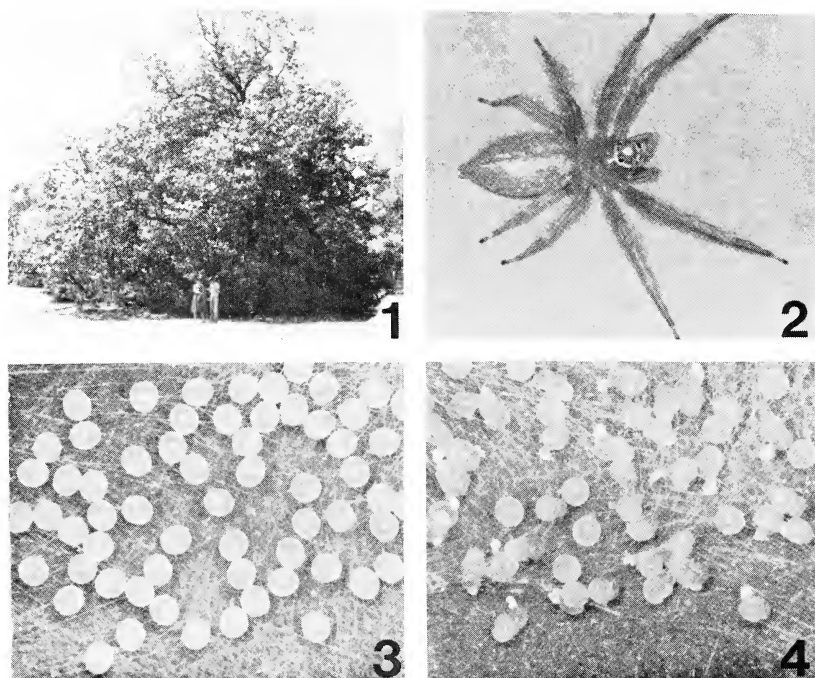


Figure 1. Magnolia stand at Tall Timbers Research Station, Leon County, Florida. Figure 2. Gravid female of *Lyssomanes viridis* (Walckenaer). Figure 3. Eggs of *Lyssomanes viridis* on underside of magnolia leaf. Figure 4. First postembryos of *Lyssomanes viridis* on magnolia leaf.

rise of immatures in June 1978. Leaves were counted arbitrarily as the stand was circled. Collections were made from 0 to 2 m above ground level on both the outside edge and within the stand. All spiders with prey were preserved separately and identifications of the prey obtained from various specialists. Carapace widths were measured using a dissecting microscope equipped with an ocular micrometer for 20 specimens per sample, if available. The number of instars was calculated by using a method of simple regression of carapace widths developed by Hagstrum (1971). It was assumed that salticids exhibit a similar mean relationship between logarithms of carapace width and stadium ($\log y = 0.0871x - 0.2692$ where $x = \text{stadium}$ and $y = \text{carapace width}$) as Lycosids, Loxoscelids, Clubionids, Oxyopids, and Ctenizids. Egg masses collected on the magnolia trees were allowed to hatch and the time spent in the first

and second postembryonic stages was measured in the laboratory; however, these were not raised through the various instars.

Weather information for Tall Timbers was obtained from the research station. Rainfall during August 1971 to February 1973 averaged 11.4 cm (SD = 7.6 cm) with 33.7 cm falling in June 1972 (hurricane Agnes) and only 1.6 cm falling in September 1972. Rainfall during July 1977 through June 1978 averaged 10.9 cm (SD = 4.3 cm) per month with a maximum of 16.9 cm in August 1977 and a minimum of 3.7 cm in October 1977. Relative humidity almost always reached 100% at some time during the day except for a few days during the winters.

RESULTS AND DISCUSSION

We found that mating took place in May and that the males disappeared by mid-June. Some females lingered on at least until August. Gravid females (Figure 2) laid 25–70 eggs (mean 42.7, SD=11.6, no.=24) at a height of 33–131 cm (mean 87.9, SD=28.0, no.=12) on the magnolia stand from May 31 to July 6. Second clutches may have been produced only occasionally as females usually guarded the eggs until first instar and females laid second clutches only twice (infertile) in the laboratory (not included in egg counts). The bright green eggs (Figure 3) were ca. 1 mm in diameter and were loosely covered by silk (there was no distinct cocoon). The first postembryonic stage (Figure 4—chorion molted) lasted 32–35.5 hours (no. of egg masses = 4) and the second postembryonic stage (legs free of vitelline membrane) lasted 7 days (no. of egg masses = 5). The carapace widths (Figure 5) indicated that there were probably 7 instars including adult female after second postembryo, based on Hagstrum's (1971 Figure 1) data for laboratory reared Lycosidae, Loxoscelidae, Clubionidae and Oxyopidae and for field collected Ctenizidae. Males may have one less instar than females. The immature stage individuals lasted from June to the next May when most matured (Figure 5). Spiderling first instars occurred from June to July, most individuals reaching second instar by the first of August. The majority reached third to fourth instar in September and passed through the winter as third to fifth instars. The female's sixth, or penultimate, instar started to be evident in March. Courtship was observed by Richman (in press).

Immature spiders, especially early instars, fed primarily on

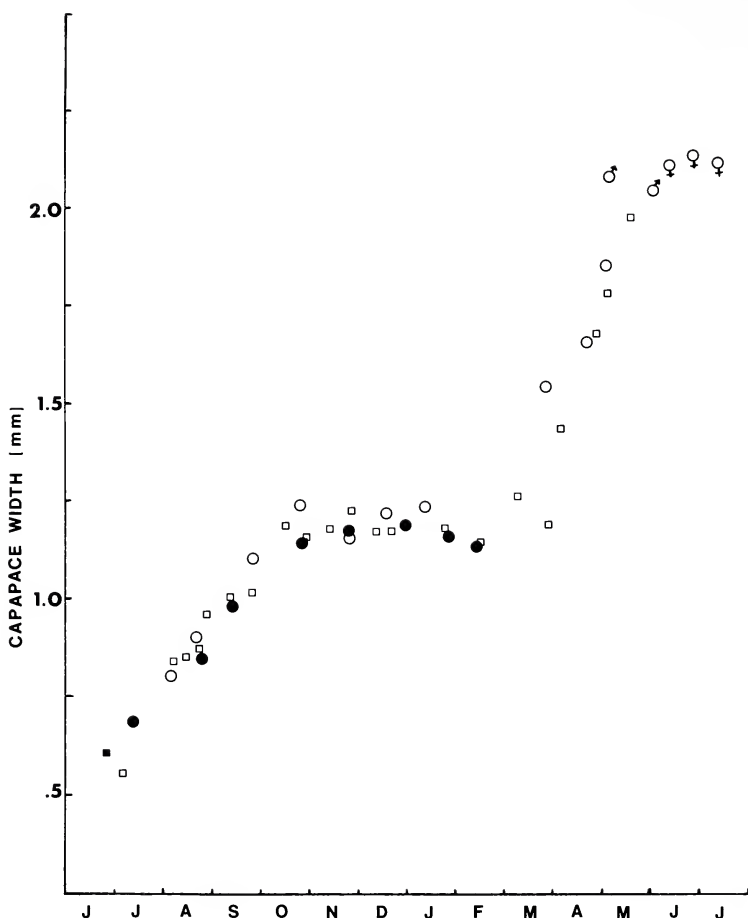


Figure 5. Mean carapace width of immature and adult *Lyssomanes viridis* (Walckenaer) at Tall Timbers, Leon County, Florida 1971-1973 and 1977-1978. Open circles = 1971-1972, closed circles = 1972-1973, open squares = 1977-1978, closed square (1) = 1978 broods. Sex symbols indicate males and females for 1971-1972 and 1977-1978.

midges of the family Chironomidae. Adults and large immatures tended to take larger prey, such as syrphid and dolichopodid flies. Of 12 prey records, immatures were found with 3 chironomids, (one identified as *Orthocladini* by A. R. Saponis), 1 chaoborid fly, 1 syrphid fly (genus *Toxomerus* identified by H. V. Weems), 1

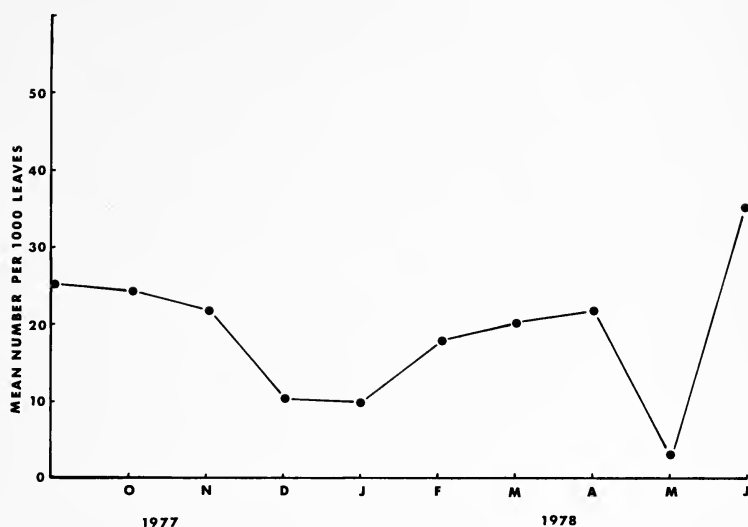


Figure 6. Population densities of *Lyssomanes viridis* (Walckenaer) in magnolia stand at Tall Timbers fall 1977 to spring 1978. Data points are means between surveys made both inside and outside the stand, during the last half of each month.

encyrtid wasp and 1 aphid (genus *Macrosiphon* identified by H. A. Denmark). Adult males were collected with an unknown dipteran and a salticid spider of the genus *Hentzia*. Adult females were collected with a dolichopodid fly, an unknown dipteran and a psocid.

The population density (Figure 6) dropped during the winter, but rose in the spring nearly to that of the previous fall, probably reflecting inactivity during the winter, rather than a significant mortality. The population drop during May is probably a result of the death of adults. Adults were only found during the spring and early summer.

Some adult spiders were found in the nest of a mud dauber of the genus *Trypoxylon* by G. B. Edwards at Newnan's Lake, Alachua County, Florida. A large *Trypoxylon* was observed during June at Tall Timbers and a fresh nest was found on the underside of a magnolia leaf. The nest in this case was filled with Araneidae. One adult female *L. viridis* was collected and found to have a large mirmithid nematode in its abdomen. No egg parasites were seen.

Complete life histories have been published for several salticids,

notably *Philaeus chrysops* Poda (Bonnet 1933), three species of *Corythalia* (Crane 1948) and *Phidippus johnsoni* Peckham and Peckham (Jackson 1978). Female *P. chrysops* generally had seven molts (six instars) before maturity, and this was also true of the three species of *Corythalia* observed by Crane (1948). Jackson (1978) reported 6-9 molts for *P. johnsoni*. Thus, the life cycle of *L. viridis* seems to compare well with those of other salticids.

SUMMARY

A population of the salticid spider *Lyssomanes viridis* (Walckenaer) was sampled for two and one half years on a stand of *Magnolia grandiflora* L. trees in North Florida. Mating took place in May and adult males disappeared by mid-June. Females laid 25-70 eggs per clutch mostly during June. These hatched from June to July and the immatures overwintered in middle instars. After temperatures increased in the spring the spiders rapidly developed to adults. Simple linear regression of the carapace widths indicated that this species has a total of seven instars from the end of second postembryo through adult female. Males may have one fewer instar. *L. viridis* feeds primarily on Diptera in this habitat.

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THE EMIGRATION BEHAVIOR OF TWO SPECIES OF THE GENUS *PHEIDOLE* (FORMICIDAE: MYRMICINAE).

BY ROBERT DROUAL¹ AND HOWARD TOPOFF²

INTRODUCTION

Colony emigrations are common among ants (Wilson 1971) and occur for a diversity of reasons. However, except for the legionary ants, in which colony emigrations are an inherent part of the foraging ecology (Wilson 1971), and species which inhabit delicate and easily disturbed nests (Hölldobler and Wilson 1977, Möglich 1979), emigrations are thought to occur infrequently. Here we present evidence that two species of the genus *Pheidole*, *P. desertorum* Wheeler and *P. hyatti* Emery, emigrate frequently under environmentally stable conditions. We further advance the hypothesis that the surplus nests resulting from these emigrations, reduce the secondary losses which occur as a consequence of the panic-alarm defense these species employ against army ants of the genus *Neivamyrmex*, by serving as temporary shelters and centers for colony reorganization.

METHODS

This investigation was conducted during the months of June, July and August, 1980, at two different study sites. One site was an oak-juniper woodland located on the grounds of the Southwestern Research Station of the American Museum of Natural History near Portal, Arizona (elev. 1646 m). The other site was a desert-grassland located 8 km N.W. of Rodeo, Hidalgo Co., New Mexico (elev. 1250 m). In both habitats a winter (Dec., Jan., Feb. and March) and a summer (July, June and August) rainy season occur. On the oak-juniper woodland site colonies of both *P. desertorum* and *P. hyatti* were located and marked; on the desert-grassland site only colonies of *P. desertorum* were located and marked.

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Table 1. Emigration characteristics of *P. hyatti*.

Colony	Days Observed	Number of Emigrations	Returns to a Former Nest	Distance Between First and Last Observed Nests (m)
H-Jn14-1	66	6	3	4.2
H-Jn14-2	66	16	11	1.1
H-Jn14-3	66	8	2	5.4
H-Jn15-1	23	1	0	1.5
H-Jn15-2	63	7	3	0.0
H-Jn17-1	63	0	0	—
H-Jn17-2	63	6	2	0.8
H-Jn18-1	62	10	5	3.2
H-Jn18-2	55	7	2	6.8
H-Jn19-1	61	7	4	0.0
H-Jn19-2	57	4	1	0.0
H-Jn19-3	61	6	2	1.5
H-Jn19-4	60	5	2	0.0
H-Jn19-5	61	7	5	2.0
H-Jn21-1	59	3	0	2.6
H-Jn21-2	58	6	4	1.9
H-Jn21-3	57	4	2	0.0
H-Jn21-4	57	6	3	3.0
H-Jn23-1	53	2	0	0.8
H-Jn24-1	56	7	1	0.8
H-Jn26-1	51	5	1	2.5
H-Jn26-2	16	2	0	1.1
H-Jn27-1	46	8	2	0.4
H-Jn28-1	52	4	2	2.4
Total		137	57	

Colony designations were based on the species (*D* - *desertorum*, *H* - *hyatti*), the date when the colony was found (Jn - June, Jl - July, A - August) and the order in which it was found on that date. For example, H-Jn18-2 is the second *P. hyatti* colony found on June 18.

Activity for both species began at approximately 2000 hr (MST) and ceased 0500 hr. To determine emigration frequency all colonies were inspected at least once daily between 2000 and 2400 hr. In order to avoid disturbing the colony any prolonged observations were made using red light. About two-thirds of the emigrations for each species were documented indirectly when a colony occupying a nest one night was found at another nest the following night. A colony was assumed to be occupying a nest if 10 foragers were

Table 2. Emigration characteristics of *P. desertorum*.

Colony	Days Observed	Number of Emigrations	Returns to a Former Nest	Distance Between First and Last Observed Nests (m)
D-Jn10-1a*	70	4	2	0.5
D-Jn11-1a	63	7	3	4.8
D-Jn11-2a	68	0	0	—
D-Jn12-1a	60	4	1	15.6
D-Jn12-2a	68	1	0	2.5
D-Jn12-3a	68	2	1	0.0
D-Jn12-4a	64	6	3	3.0
D-Jn12-5a	21	1	0	4.2
D-Jn13-1a	57	2	1	0.0
D-Jn14-1a	61	3	2	0.0
D-Jn15-1a	65	6	3	6.6
D-Jn15-2a	62	3	1	0.0
D-Jn16-1b	64	4	3	0.0
D-Jn17-1b	57	4	2	0.0
D-Jn17-2b	63	5	3	2.4
D-Jn18-1a	49	3	1	3.1
D-Jn20-1b	57	8	6	0.0
D-Jn25-1a	55	7	4	1.5
D-Jn28-1a	50	5	3	3.7
D-Jl 1-1a	42	7	3	2.4
D-Jl 13-1b	37	2	1	0.0
D-Jl 13-2b	37	3	1	1.2
D-Jl 15-1b	33	4	1	0.0
D-Jl 30-1b	20	6	3	0.0
D-Jl 30-2a	19	2	1	0.0
D-A 1-1a	18	2	0	4.0
Total		101	49	

*a: desert-grassland; b: oak-juniper woodland.

observed leaving the nest during a 1 min period. If this criterion was not met, or if there was some other reason to doubt the location of the colony, a small peanut butter bait was used to locate the colony. To avoid confusion when using this indirect method, an attempt was made to locate and mark any neighboring conspecific colonies. The remainder of the emigrations were observed directly when an emigration was discovered in progress. The nests were marked and the distance between the old and the new nests measured.

With the statistical tests employed in this paper probabilities of .05 or less were accepted as significant.

RESULTS

Colonies of both *P. desertorum* and *P. hyatti* showed considerable variation in their frequencies of emigration (see Tables 1 and 2). One colony of each species (D-Jn11-2 and H-Jn17-1) did not emigrate at all, while one *P. desertorum* colony (D-Jn20-1) emigrated 8 times, and one *P. hyatti* colony (H-Jn14-2) emigrated 16 times. Despite this variability, both species showed a clear tendency to emigrate frequently: over one-half of the *P. desertorum* colonies emigrated at least 4 times, and over one half of the *P. hyatti* colonies emigrated at least 6 times. To statistically compare the emigration frequency of the two species, the percentage days for which an emigration was documented was calculated for each colony, and the percentages for each species were compared using the Wilcoxon two-sample test (Sokal and Rohlf 1969). No significant difference was found in the emigration frequency between the two species ($.1 > P > .05$).

This similarity between species in emigration frequency can also be seen if the frequency of time interval between emigrations is compared. Figures 1 and 2 show the frequency of emigration interval for *P. hyatti* and *P. desertorum*, respectively. Both distributions are strongly skewed to the right with a surprisingly high number of emigrations occurring 1 to 2 days after the previous emigration. No significant difference was found in the frequency distribution between the two species (Wilcoxon two-sample test: $.4 > P > .2$).

The daily occurrence of emigrations among all colonies is shown in the form of frequency histograms in Figs. 3, 4 and 5. The upper line in the graphs outlines the number of colonies which were included in the sample size each night. Excluded from the sample were colonies which were raided by army ants, or were still suffering from the effects of an army ant raid (see Discussion). Superimposed over the graphs is a bar diagram showing the daily rainfall.

A positive correlation was found to exist between emigration frequency and daily rainfall in all three cases (Spearman rank correlation coefficient: *P. hyatti* : $r_s = .28$, $N = 66$; *P. desertorum* in oak-juniper woodland : $r_s = .25$, $N = 64$; *P. desertorum* in desert-grassland : $r_s = .32$, $N = 70$). The effect of rainfall on emigration frequency is most clearly seen in *P. desertorum* in the desert-grassland habitat (Fig. 5). During the 29 days before the first heavy

rainfall on July 9 only three emigrations occurred, but within 9 days after this rainfall 29 emigrations occurred. During this 9 day period 13 of the 15 colonies being observed on this site emigrated at least once.

The emigration distance for both species was variable. Mean emigration distance for *P. hyatti* was 1.8 ± 1.0 m (N=137; range 0.3 — 4.9) and mean emigration distance for *P. desertorum* was 2.5 ± 1.4 m (N=102; range 0.4 — 6.9). The larger emigration distance of *P. desertorum* over that of *P. hyatti* correlates with the larger size of this species (mean length of *P. hyatti* minor = 2.64 ± 0.04 mm, N=50; mean length of *P. desertorum* minor = 3.14 ± 0.03 mm, N=57).

Despite the high emigration frequency of both species, colonies of neither species tended to move far from the nests at which they were first discovered. Tables 1 and 2 show the number of times each colony returned to a former nest, and the distance between the first and last nests. As can be seen, 49% of *P. desertorum*'s emigrations, and 42% of *P. hyatti*'s emigrations were to former nest sites, and 11 *P. desertorum* colonies and 5 *P. hyatti* colonies at the end of the study were at the nest at which they were first discovered. This crisscrossing pattern of emigrations is illustrated for three colonies of each species in Figs. 6 and 7. The relative location of the nests reveal a clumped rather than a linear arrangement which would be expected if the colony were emigrating out of an area. The dates of nest movements for each colony show that the variability of emigration interval within each colony was considerable. This can be readily seen by examining the ranges of emigration intervals for the colonies shown in Figs. 6 and 7: for the *P. hyatti* colonies the ranges are, H-Jn14-2: 1-17 days; H-Jn14-3: 3-18 days; H-Jn18-1: 1-8 days; for the *P. desertorum* colonies the ranges are D-Jn25-1: 1-19 days; D-Jn12-4: 1-21 days; D-J130-1: 1-4 days.

Because *P. desertorum* and *P. hyatti* emigrated so frequently about 33% of the emigrations of both species were discovered in progress. These emigrations were readily noticed as hundreds to thousands of workers, most carrying brood, formed a column connecting the old nest to the new nest. The width of this column for *P. hyatti* was about 3 cm, while for *P. desertorum* the column tended to be wider (on one occasion reaching a width of 15 cm). Laboratory experiments have revealed that *P. hyatti*'s emigrations

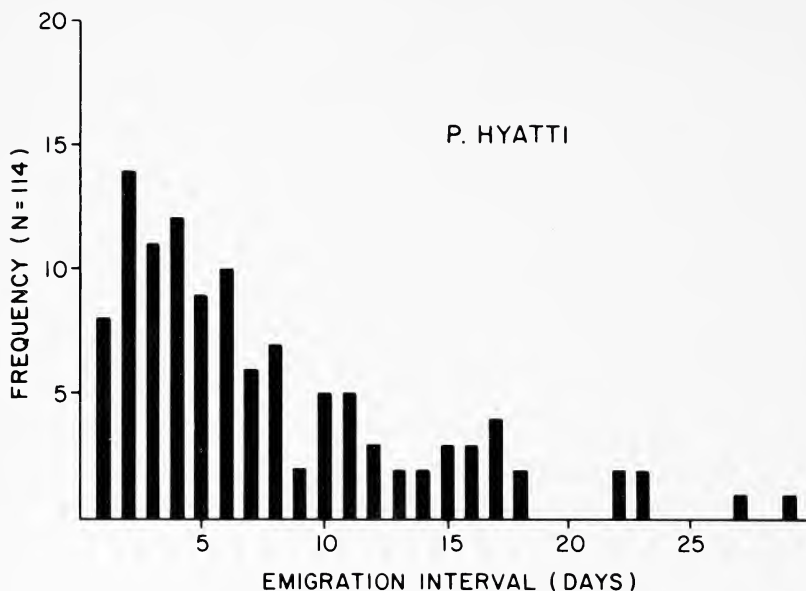


Figure 1. Frequency of the time interval between emigrations for *Pheidole hyatti*.

are totally organized by a substance secreted by the poison gland (Droual et al., in prep.). The queen of both species moved independently in the emigrations although she was usually surrounded by a retinue consisting mostly of minor workers (workers of the genus *Pheidole* are dimorphic) who tugged her by the mandibles or antennae if she hesitated en route to the new nest. During June and the early part of July alates were frequently seen in the column also moving independently. However, on one occasion, during a *P. desertorum* emigration, workers were observed carrying some of the males.

A number of phenomena related to these species' high emigration frequencies were observed. One colony of each species (D-Jn20-1 and H-Jn19-2) performed what we call an aborted emigration. In these cases the colony was observed emigrating to a new nest but on the following night was found to be back at its old nest. One *P. desertorum* colony (D-Jn-25-1) appeared to perform two emigrations in one night. On August 17 the colony was observed emigrating from nest 2 to nest 1 (see Fig. 6). However on the following night the colony was found at nest 3. On a number of occasions an

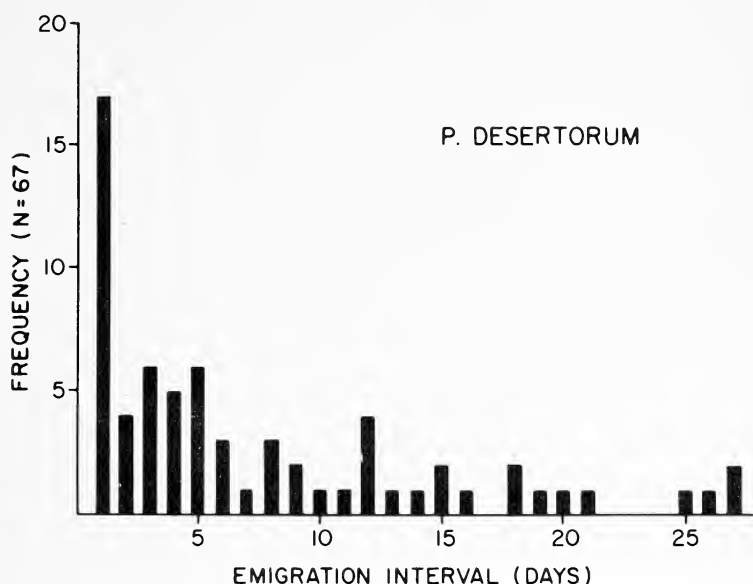


Figure 2. Frequency of the time interval between emigrations for *Pheidole desertorum*.

emigration could be predicted in advance by the colony's excavation activity at another site. For example, before colony D-Jn12-2 emigrated to its second nest site on 8/17, workers from the colony were observed excavating at the site on 8/4, 8/5, 8/7 and 8/10-8/17. However two colonies of both *P. desertorum* and *P. hyatti* were observed excavating at sites to which they did not emigrate even though they emigrated later to other nests.

DISCUSSION

In this paper we have shown that *P. desertorum* and *P. hyatti* emigrate frequently and that the emigration frequencies of the two species are similar. This similarity in emigration frequency becomes even more marked when it is taken into account that most of *P. desertorum*'s emigrations in the desert-grassland occurred after the first rainfall. The sharp increase in emigration activity after the rain can possibly be explained by the affect of the rainfall upon the soil. Before the rains began the soil was very hard and compact, but after

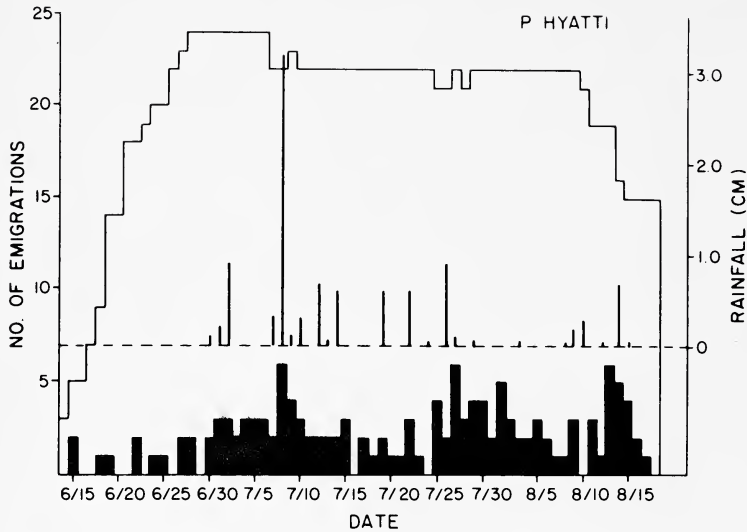


Figure 3. Daily occurrence of emigrations for *Pheidole hyatti*. Black bars indicate the number of colonies which emigrated each night. Upper line outlines the number colonies included in the sample each night. Right ordinate indicates rainfall for the superimposed bar diagram showing daily rainfall.

the first heavy rainfall the soil loosened considerably. This undoubtedly made the excavation of new nests by the desert-grassland dwelling colonies much easier. The same reasoning can be applied to explain the positive correlation between emigration frequency and daily rainfall in both habitats. However, in the oak-juniper woodland, the greater amount of vegetation, the rockier soil and the generally moister conditions probably account for the relatively higher emigration activity before the beginning of the rainy season in this habitat.

The need to perform a colony emigration is a contingency almost all species of ants can be expected to face (Wilson 1971). However some species emigrate more than others. Among the legionary ants, particularly the Ecitoninae and Dorylinae, colony emigrations are an integral part of the foraging ecology (Wilson 1971). Opportunistic nesters such as *Tapinoma melanocephalum*, *T. sessile*, *Paratrechina bourbonica* and *P. longicornis* occupy ready-made nests such as the tufts of dead grass and hollow plant stems which

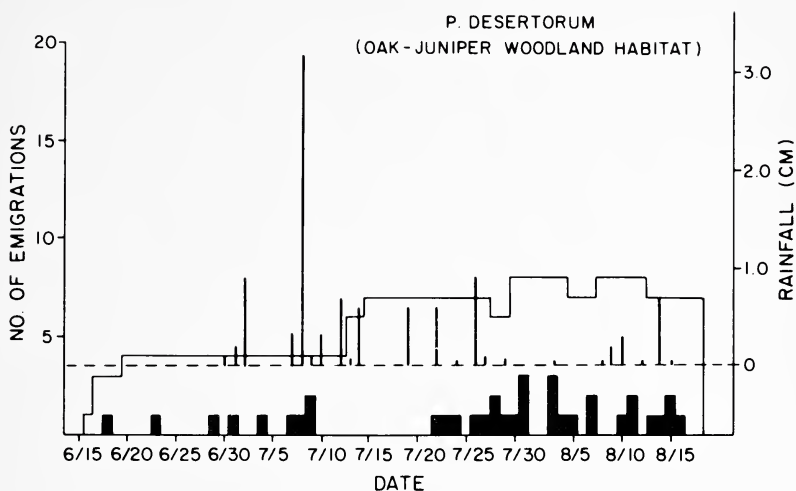


Figure 4. Daily occurrence of emigrations for *Pheidole desertorum* in oak-juniper woodland (See Fig. 3).

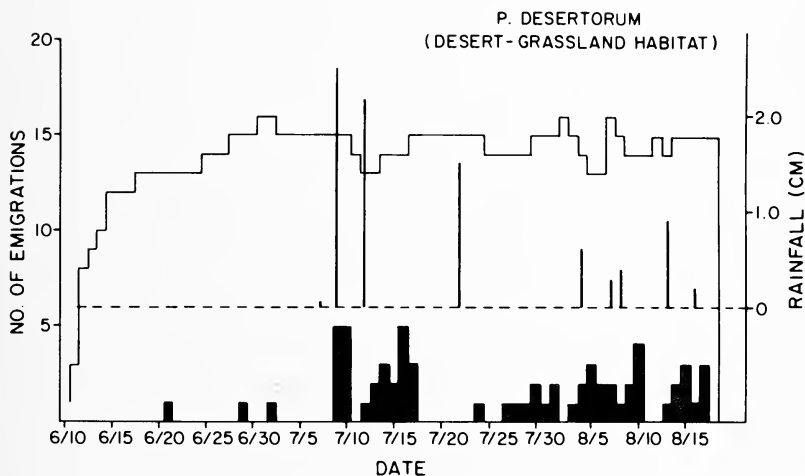
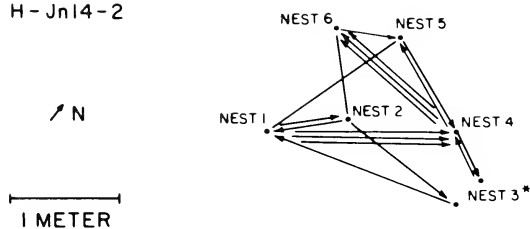


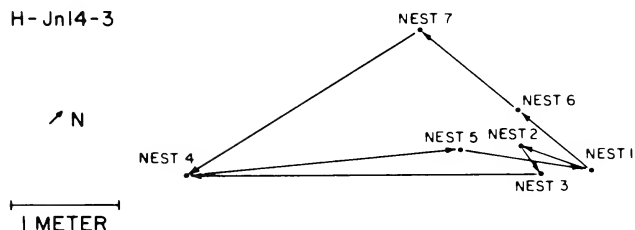
Figure 5. Daily occurrence of emigrations for *Pheidole desertorum* in desert-grassland (see Fig. 3).

H-Jn14-2



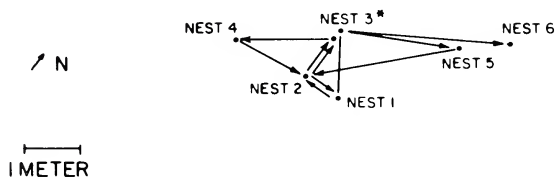
NEST MOVEMENT	DATE
1-2	6/15
2-3	7/2
3-1	7/7
1-4	7/9
4-3	7/15
3-4	7/18
4-5	7/22
5-1	7/27
1-4	7/30
4-6	7/31
6-5	8/3
5-4	8/5
4-6	8/6
6-2	8/11
2-1	8/13
1-4	8/15
4-6	8/17

H-Jn14-3



NEST MOVEMENT	DATE
1-2	6/18
2-3	6/22
3-4	7/10
4-5	7/20
5-1	7/27
1-6	8/1
6-7	8/11
7-4	8/14

H-Jn18-1



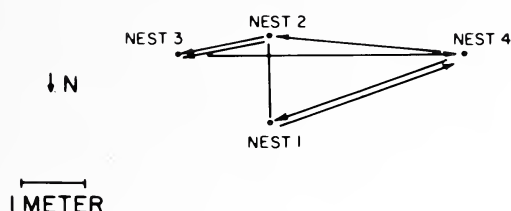
NEST MOVEMENT	DATE
1-2	7/1
2-3	7/5
3-4	7/11
4-2	7/17
2-3	7/21
3-5	7/29
5-2	8/4
2-1	8/5
1-3	8/8
3-6	8/13

Figure 6. Patterns of emigrations for three colonies of *Pheidole hyatti*. Dates of nest movements are shown on the right. *This nest had two entrances.

are short-lived. When these nests are disturbed, the colonies quickly organize emigrations to other such nests (Hölldobler and Wilson 1977). *Leptothorax acervorum* in oak-juniper woodland, construct delicate nests under stones which can be easily dislodged by large vertebrates, and are prone to emigrate when their nest is disturbed (Möglich 1979).

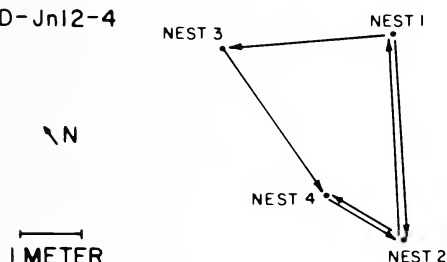
Most species build or choose nest sites which are longer-lived and less easily disturbed and are thought to emigrate infrequently. Among these species emigrations can be due to a local factor such as

D-Jn 25-1



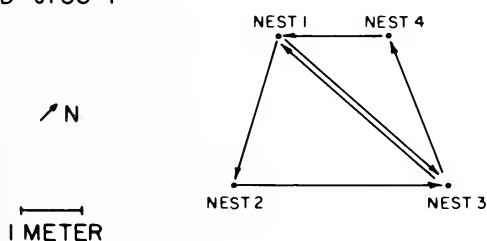
NEST MOVEMENT	DATE
1-2	7/12
2-3	7/15
3-4	7/16
4-1	8/5
1-4	8/6
4-2	8/15
2-3	8/17

D-Jn12-4



NEST MOVEMENT	DATE
1-2	7/10
2-1	7/31
1-3	8/1
3-4	8/4
4-2	8/5
2-4	8/14

D-Jl 30-1



NEST MOVEMENT	DATE
1-2	7/31
2-3	8/3
3-1	8/7
1-3	8/11
3-4	8/15
4-1	8/16

Figure 7. Patterns of emigrations for three colonies of *Pheidole desertorum*. Dates of nest movements are shown on the right.

shading (Brian 1956, Carlson and Gentry 1973), or climatic adversity such as drought or frost (Brian 1952). A colony may also be forced to emigrate because of some biotic factor such as inter- and intra-specific competition (Hölldobler 1976, Waloff and Blackith 1962, Brian 1952, Brian et. al. 1965) and predation (Gentry 1974).

The view that emigrations occur infrequently among most ants

was recently challenged by Smallwood and Culver (1979). These investigators conducted a study in which they found that *Tapinoma sessile* and *Aphaenogaster rudis* emigrated frequently. Their study differs from ours in that colonies were marked and rechecked only after intervals of 11–21 days and no attempt was made to follow the behavior of individual colonies. Because *T. sessile* and *A. rudis* choose different nesting sites and have different life styles these investigators deduced that emigrations occur more frequently among ants than had been previously thought. However, the fact that *T. sessile*, as mentioned above, is an opportunistic nester which is expected to emigrate frequently weakens their argument.

It is difficult to apply any of the known or previously hypothesized causes of colony emigrations to explain the frequent emigrations of *P. desertorum* and *P. hyatti*. The nests of both species are excavated in the soil to a depth of 30 to 40 cm (based on excavations in oak-juniper woodland), and hence are not easily disturbed. Shading is obviously not a factor in the desert-grassland, and is negligible in the oak-juniper woodland where the canopy is not extensive. Permanent deterioration of the nest as a cause is eliminated by the fact that colonies return to former nests. Indeed almost half of all emigrations for both species resulted in a return to a former nest. This fact, and the patterns of emigrations which tended to keep a colony in the same area, argue against any hypothesis which involves a deterioration of some local condition such as might be due to interference competition or to a decrease in the local food supply.

However, in one instance the possibility that an emigration may have been the result of intraspecific competition should be mentioned. This involved colony H-Jn14-1 which was observed emigrating a distance of 4.9 m the day after it was found. This distance is considerably larger than the mean emigration distance of 1.8 m found for *P. hyatti*. Four days later, colony H-Jn19-1 was discovered emigrating 2.3 m into the nest vacated by colony H-Jn14-1. Although large-scale conflicts between these species were never observed, workers will attack any alien workers of either species discovered near their nest. Frequent encounters of this sort may have caused colony H-Jn14-1 to make its unusually long emigration.

In discussing the causation of any behavior a distinction should be made between those hypotheses that invoke a proximate cause

and those that invoke an ultimate cause (Wilson 1971). For example, it has been hypothesized that the ultimate cause of army ant emigrations is to prevent a local depletion of food resources (Wilson 1971). The proximate cause of these emigrations, at least among the Ecitoninae, was discovered to be recruitment to a new nest under periods of high colony arousal due to brood stimulation (Schneirla 1938). However, it has been recently shown that food supply may also be a proximate factor (Topoff and Mirenda 1980, Mirenda and Topoff 1980). The hypothesis we are advancing to explain the frequent emigrations of *P. hyatti* and *P. desertorum* concerns the ultimate cause of these emigrations although both the ultimate and proximate causes are the subject of further investigation by us.

Both *P. desertorum* and *P. hyatti*, which are small and lack potent stings, are easy prey for army ants of the genus *Neivamyrmex*. Mirenda et. al. (1980) found, in the same desert-grassland site employed in this study, that *P. desertorum* was the species most frequently raided by *N. nigrescens*. Our own observations also show that both *P. desertorum* and *P. hyatti* are heavily preyed upon by members of the genus *Neivamyrmex* (Tables 3 & 4). Some *P. desertorum* colonies were raided repeatedly by the same army ant colony which entered the statary phase in a nearby bivouac. On two occasions an army ant colony actually bivouacked in the evacuated nest of a *P. desertorum* colony. One *P. hyatti* colony was raided by two species of *Neivamyrmex*. Of these colonies only five appeared to be completely eliminated by the army ants. Part of the reason for

Table 3. Observed army ant raids on colonies of *P. hyatti*.

Colony	Dates of Raids	Species Raiding
H-Jn15-1	7/7, 7/8*	<i>Neivamyrmex nigrescens</i>
H-Jn15-2	7/8	<i>N. nigrescens</i>
H-Jn19-4	7/28	<i>N. texanus</i>
H-Jn21-3	8/15	<i>N. opacithorax</i>
H-Jn21-4	8/17	<i>N. nigrescens</i>
H-Jn21-5	8/15	<i>N. opacithorax</i>
	8/18	<i>N. nigrescens</i>
H-Jn23-1	8/15*	<i>N. opacithorax</i>
H-Jn26-1	8/12	<i>N. nigrescens</i>
H-Jn27-1	8/12*	<i>N. nigrescens</i>

*Colony was not seen afterwards.

this is the panic-alarm defense employed by these species against the army ants.

That defense behavior in ants can be both enemy specific and complex was established with the discovery of the alarm-recruitment defense of *Pheidole dentata* against the fire ant *Solenopsis geminata* (Wilson 1975 and 1976). Although more evidence is necessary, the defense behavior of *P. hyatti* and *P. desertorum* appears to be both enemy specific and complex. The defense, which begins when a *Pheidole* forager contacts an army ant and runs back into the nest raising an alarm, occurs in two phases. In the first, or "milling", phase, workers carrying brood well out of the nest but remain in close contact near the nest's entrance. In the second, or absconding, phase, the workers flee from the nest. *P. desertorum*'s flight is protean in nature (Humphries and Driver 1970) with workers scattering in all directions. In *P. hyatti* the exodus is more organized with the workers fleeing in columns which appear to follow recently-laid chemical trails.

After evacuating from their nest the fleeing workers tend to concentrate at temporary shelters such as that provided by leaf litter, fallen branches, rotting logs and tufts of grass. Some workers eventually find some or all of the former nests and begin to recruit other workers to them. After the raid is over workers will also start to return to the evacuated nest. In this manner the colony becomes fragmented with various proportions of the colony in some or all of the available nests. The colony then begins the process of reorganizing with segments in one nest emigrating to join segments in another nest until the colony becomes reunited in one nest. Hence it appears that the surplus nests resulting from the frequent emigrations of these species serve a dual purpose after an evacuation: they provide shelter and centers for reorganization.

After a nest evacuation, finding a place of suitable moisture before the lethal surface temperatures and low surface humidity of the approaching day is undoubtedly of vital importance for these nocturnal species. This problem becomes particularly severe in the desert-grassland where the lack of ground cover makes nests excavated in the ground the only suitable shelters. Having alternate nests becomes a necessity when an army ant colony bivouacs in the evacuated nest. The hypothesis we are proposing then is that the surplus nests which result from the emigrations of these species increases the effectiveness of the panic-alarm defense by reducing

Table 4. Observed army ant raids on colonies of *P. desertorum*.

Colony	Dates of Raids	Species Raiding
H-Jn11-1	8/1-8/5	<i>Neivamyrmex nigrescens</i>
H-Jn11-2	7/9	<i>N. nigrescens</i>
H-Jn12-1	8/4, 8/6, 8/8	<i>N. nigrescens</i>
H-Jn12-4	7/4	<i>N. nigrescens</i>
H-Jn12-5	7/2*	<i>N. nigrescens</i>
H-Jn13-1	7/12, 8/10*	<i>N. nigrescens</i>
H-Jn14-1	8/5, 8/6, 8/12-8/15	<i>N. nigrescens</i>
H-Jn18-1	7/11, 7/12, 7/16, 7/25, 7/26, 7/28, 8/1	<i>N. nigrescens</i>
H-Jn17-1	8/18	<i>N. nigrescens</i>
H-Jn25-1	8/28	<i>N. nigrescens</i>
H-Jl 4-1	8/3, 8/5-8/7, 8/9	<i>N. nigrescens</i>
H-Jl 30-2	8/13	<i>N. nigrescens</i>
H-Jl 15-1	7/28	<i>N. texanus</i>

*Colony not seen afterwards.

the secondary losses which result from the disorganization which follows the defense. If this hypothesis proves to be correct, the possibility that the frequent emigrations of these species have evolved to serve as part of a defense system against the army ants has to be entertained.

ACKNOWLEDGEMENTS

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STATARY BEHAVIOR IN NOMADIC COLONIES OF ARMY ANTS: THE EFFECT OF OVERFEEDING

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INTRODUCTION

Nearctic colonies of the army ant *Neivamyrmex nigrescens* Cresson (subfamily Ecitoninae) exhibit behavioral cycles consisting of alternating nomadic and statary phases. During the statary phase, a colony remains at the same nesting site and forages irregularly for food. The nomadic phase, by contrast, is characterized by night-long raids and frequent emigrations to new bivouacs. According to Schneirla (1957, 1958), the nomadic phase is triggered by stimulation arising from newly-eclosed callows, and is subsequently maintained by comparable excitation from the developing larvae. Experimental support for brood-stimulation theory stems from studies showing: (1) an abrupt reduction in nomadism after removing a portion of a larval brood (Schneirla and Brown, 1950); and (2) the eclosion of a pupal brood (in the absence of newly-hatched larvae) is indeed sufficient to initiate a nomadic phase (Topoff et al., 1980a). Recent studies have suggested, however, that brood stimulation may in turn depend on the degree of brood satiation. Thus, in a preliminary field study involving food augmentation, Mirenda et al. (in press) was able to halt the occurrence of emigrations during a portion of the nomadic phase in colonies of *N. nigrescens*. This was followed by more prolonged laboratory studies (Topoff and Mirenda, 1980 a,b) showing that the frequency and direction of nomadic emigrations are indeed influenced by the amount and location of food.

This paper reports findings from our continued studies of food augmentation for colonies of *N. nigrescens*. In previous studies, larval stimulation was reduced by artificially feeding colonies early in the nomadic phase, after callos eclosion. Because an additional

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goal of the present study was to reduce callow stimulation and thereby delay the onset of the nomadic phase, overfeeding commenced late in the statary period. For the first colony, emigrations were delayed approximately 6 days. In the second overfed colony, we were able to virtually eliminate the nomadic phase, together with all associated patterns of raiding and emigration behavior.

METHODS AND PROCEDURES

This study was conducted during July and August, 1980, in a desert-grassland habitat, 8 km east of Portal, Arizona. The site was chosen because the pavement-like substrate and patchy vegetation provided us with an excellent view of the ants' raiding and emigration activities. Surface soil temperatures averaged 50°C at 1500 hr (MST) and 17°C at 0200 hr throughout the summer (Mirenda et al. 1980). As a result of the severe daytime temperatures and aridity, colonies of *N. nigrescens* were usually active on the surface only between 1900–0500 hr.

Colonies were located by walking through the study area with gasoline lanterns or miner's cap lamps. Colony no. 1 was found on July 11, at the end of a nomadic phase, and observed nightly throughout its next statary period. During the subsequent nomadic phase, the colony was estimated to contain approximately 80,000 adults and 50,000 larvae. Colony no. 2 was collected on July 14, during its last nomadic emigration, and maintained in the laboratory (see Topoff et al. 1980b for details of the rearing procedure) until the pupal brood was fully pigmented. Prior to release in the field, the colony was culled to contain 4,000 adults and 4,000 pupae. By the next nomadic phase, approximately 4,500 larvae were also present in the colony. This small colony size was chosen for two reasons: (1) to increase our ability to appreciably overfeed the colony; and (2) a laboratory colony of comparable size had previously been released without food supplementation, as part of a study designed to show that laboratory rearing and population reduction do not alter qualitative aspects of nomadic behavior. This colony could therefore serve as a convenient control for our artificially-fed colony.

Food for both experimental colonies consisted of adult and brood individuals of the myrmicine ant *Novomessor cockerelli*, and workers of the termite genus *Gnathamitermes*. To collect *Novo-*

messor brood we made use of the panic-alarm behavior that this prey species exhibits when raided by army ants. Accordingly, we released several hundred adult *N. nigrescens* into the nest entrance of *Novomessor*, and aspirated the larvae and pupae that were removed from the nest by their own adult workers. Whenever colonies were artificially fed, food was given at the start of raiding in the evening, while the column was within 2 m from their bivouac. If columns emerged from more than one exit hole, booty was placed at the front of each ant column.

RESULTS

The raiding and emigration activities of colony no. 1 are summarized in Table 1. This colony was found on July 11, late in its nomadic phase. It became statary on July 13, after settling into a kangaroo rat mound (*Dipodomys spectabilis*). On the third statary night, the colony conducted a 3-m long shift to the other side of the mound. A statary shift differs from a nomadic emigration in that it is neither preceded nor followed by raiding. It consists instead of a single, unbranched column, and is presumably caused by a disturbance at the old site. For the next 13 statary days, the colony remained at the same bivouac, and staged either brief (1–3 hr) or no predatory raids. On statary day 17, however, the colony conducted a longer shift to an adjacent mound. During the move, we observed that all of the pupae were deeply pigmented, and that a few callows were being transported by mature adults to the new site. As a result of detecting the onset of eclosion, we started artificial feeding of the colony on the next night (July 30), and continued to supply food for a total of six consecutive nights (Table 1).

Each evening, a basal column appeared on the surface shortly after sunset (1800–1900 hr). As soon as the ants contacted the food, the process of mass recruitment resulted in a sharp increase in ant traffic out of the nest. On the days of heaviest feeding, when more than 30 g of booty were provided, the army ants required several hours to transport it back to the bivouac. The colony occasionally put out additional raiding columns later each night, but all captured booty was promptly brought back to the original bivouac, and no emigrations occurred. On the afternoon of August 5, the study area received 14 mm of rainfall between 1400–1550 hr. The overcast sky, coupled with cool temperatures late in the afternoon, enabled the

Table 1. Activity schedule for *Neivamyrmex nigrescens* colony no. 1

Date	Activity		Food Provided (g)	Proposed Phase-Day
	Raid	Emigrate		
7/11	+	+	—	N-?
7/12	+	+	—	N-?
7/13	+	—	—	S-1
7/14	+	—	—	S-2
7/15	—	ss*	—	S-3
7/16	+	—	—	S-4
7/17	+	—	—	S-5
7/18	+	—	—	S-6
7/19	+	—	—	S-7
7/20	—	—	—	S-8
7/21	—	—	—	S-9
7/22	—	—	—	S-10
7/23	+	—	—	S-11
7/24	—	—	—	S-12
7/25	—	—	—	S-13
7/26	—	—	—	S-14
7/27	—	—	—	S-15
7/28	—	—	—	S-16
7/29	—	ss*	—	S-17
7/30	+	—	9.1	S-18
7/31	+	—	34.7	N-1
8/1	+	—	18.5	N-2
8/2	+	—	32.6	N-3
8/3	+	—	17.6	N-4
8/4	+	—	31.6	N-5
8/5	+	+	—	N-6
8/6	+	+	—	N-7
8/7	+	+	—	N-8
8/8	+	+	—	N-9
8/9	+	—	—	N-10
8/10	+	+	—	N-11
8/11	+	—	—	N-12
8/12	+	+	—	N-13
8/13	+	+	—	N-14
8/14	+	—	—	S-1
8/15	+	—	—	S-2
8/16	+	—	—	S-3
8/17	+	—	—	S-4
8/18	+	—	—	S-5
8/19	—	—	—	S-6
8/20	+	—	—	S-7
8/21	—	—	—	S-8
8/22	+	—	—	S-9

*statary shift

colony to begin raiding earlier than usual. Thus, although we arrived at the site by 1800 hr, a long (60 m) emigration was already in progress. Given the large size of the colony, we decided to terminate food-augmentation. The colony remained nomadic for the next nine days, during which time it emigrated on six nights.

In order to determine whether we had been successful in delaying the onset of the nomadic phase, three independent types of evidence were analyzed: (1) phase length; (2) callow pigmentation; and (3) larval size. Collectively, our data indicate that the nomadic phase was indeed delayed for 4–8 days.

Phase Length: Because the colony was temporally anchored, July 13 can be considered the first statary day, August 5 the first nomadic day. Thus, the statary interval becomes 23 days (Table 1). According to Mirenda and Topoff (1980), the range of statary-phase duration for *N. nigrescens* in the same study area is 15–19 days, with a modal length of 16 days. This suggests that the minimum delay in nomadic onset for our colony was 4 days. If we use instead Mirenda and Topoff's modal duration, the delay is calculated as 7 days.

Callow pigmentation: Newly eclosed callows of *N. nigrescens* are yellow and acquire adult-like pigmentation between 7–12 days. Several hundred callows were collected from the colony during its first emigration on August 5, and compared with preserved samples collected daily from nomadic colonies in previous years. Although this form of visual comparison can not always pinpoint the exact post-eclosion day, callows from the artificially-fed colony were substantially more pigmented than those typically collected from other colonies on the first nomadic night. Our comparison between these callows and previously preserved specimens indicated a post-eclosion age of between 5–8 days.

Larval size: Several hundred larvae were collected by aspiration from the first emigration. By visual inspection, we separated the 10 largest and 10 smallest larvae and measured them with the aid of a dissecting microscope fitted with an ocular micrometer. The mean length of the large group was 4.0 mm (range = 3.8–4.2 mm), as compared with a mean of 1.5 mm (range = 1.3–1.7 mm) for the small group. When these data are compared with Mirenda and Topoff's (1980) graph of larval growth versus nomadic day, they correspond to a range of nomadic days between 4–6.

The nightly patterns of activity for colony no. 2 and for the control colony are summarized in Table 2. For this small colony, we

Table 2. Activity schedule for *Neivamyrmex nigrescens* colony no. 2 and control colony

Colony no. 2				Control colony				
Date	Activity			Proposed phase day	Date	Activity		Phase day
	Duration of raid	Occurrence of emigration	Food Provided (g)			Duration of raid	Occurrence of emigration	
8/7	2215-2300	—	9.0	S-15	7/15	—	—	S-16
8/8	—	—	—	S-16	7/16	1915-0515	—	S-17
8/9	—	—	—	N-1	7/17	1810-0340	+	N-1
8/10	2130-0120	—	7.5	N-2	7/18	2010-0640	+	N-2
8/11	—	—	—	N-3	7/19	1845-0500	—	N-3
8/12	—	—	—	N-4	7/20	1900-0400	+	N-4
8/13	1920-2210	—	6.9	N-5	7/21	2030-0515	+	N-5
8/14	0100-0235	—	—	N-6	7/22	1940-0455	—	N-6
8/15	2240-0145	—*	10.2	N-7	7/23	1850-0430	+	N-7
8/16	2140-2210	—	9.3	N-8	7/24	1800-0420	+	N-8
8/17	2315-2350	—	8.5	N-9	7/25	1820-0305	—	N-9
8/18	0210-0305	—	—	N-10	7/26	1745-0430	+	N-10
8/19	2040-0330	+	—	N-11	7/27	1830-0300	+	N-11
8/20	2215-2305	—	8.0	N-12	7/28	1840-0410	—	N-12
8/21	2300-2350	—	10.0	N-13	7/29	1920-0400	+	N-13
8/22	2030-2110	—	9.5	N-14	7/30	2010-0625	+	N-14
8/23	—	—	—	S-1	7/31	2015-0615	+	N-15
8/24	—	—	—	S-2				
8/25	—	ss*	—	S-3				

* Emigration started but reversed by feeding. See text for details.

** Statory shift forced by excavation of bivouac

were able to monitor the time of onset and the duration of each night's raid, in addition to the emigration frequency. This colony was released from a laboratory nest at 1900 hr on August 7. Because this was statary day 15, most of the pupae were fully pigmented. The colony promptly moved into a subterranean nest beneath a small hole in the desert floor. The first raiding column appeared shortly after 2200 hr, at which time 9.0 g of *Novomessor* brood and termites were placed near the raiding front. The army ants removed the booty in less than 1 hr, after which all surface activity ceased. For the next seven nights, the colony was either not active on the surface or, at best, conducted brief raids (each of which was immediately followed by artificial feeding) but no emigrations. On August 15 we arrived at the study site after 2200 hr, and found the colony emigrating 25 m to the NW. Because previously-collected food was being transported to the new nest, but no larvae had yet appeared, we considered the emigration to be in an early stage. Accordingly, 10.2 grams of booty were placed near the emigration column, 1 m from the old bivouac. This resulted in recruitment of ants both from the short column leading to the old nest, and from the longer emigration column. All of the artificially-placed food was taken back to the old nest, and the emigration was aborted.

On August 19 (nomadic day 11), after 2 days of not having been fed, the colony conducted its only successful emigration. The move took the colony 19 m to the N, beneath an *Ephedra* bush. On August 25, we excavated the colony and forced it to shift its statary bivouac. This procedure verified that the colony's larvae had pupated. Thus, throughout a nomadic phase lasting 14 days, the colony conducted only one completed emigration. On 4 nomadic nights no raiding occurred. During the 10 nights in which raiding took place, the median time for raid onset was 2200 hr, and the median duration of each raid was 1.5 hr.

The control colony, which was also released from the laboratory at the end of a statary phase, exhibited more typical patterns of nomadic behavior (Table 2). During a 15-day nomadic phase, the colony emigrated on 11 nights. Some degree of raiding took place on every nomadic night. The median time of raid onset for the control colony was 1850 hr, and the median duration of raiding was 9.7 hr.

DISCUSSION

Much of the discussion generated by Schneirla's brood-stimulation theory concerns the relative degree to which raiding and emigrations are influenced by interactions between brood and adults (internal processes), and by external environmental factors. Theoretical support for emphasizing brood-related processes stems not only from Schneirla's own research with army ants (Schneirla, 1957, 1958, 1971), but from studies of other social insects as well. For example, honeybee workers can collect protein-rich pollen or carbohydrate-rich nectar. Louveaux (1950) found that the amount of pollen collected by an incipient colony is small, but increases as the brood population increases. In another experiment (Louveaux, 1958), he removed the colony queen from a mature colony and found that pollen collection was unaffected until many of the larvae had pupated. Further evidence of larval stimulation of adult foraging came from Fukuda, 1960 (in Free, 1967), who showed that foraging workers from a recently-divided colony collected very little pollen until the eggs laid by the new queen hatched into larvae. Finally, Free (1967) demonstrated that adult worker foraging was influenced more by direct access to the brood than by brood odor alone. Perhaps most significant was the additional finding that artificially feeding a colony with pollen resulted in a decrease in pollen collection and a corresponding increase in nectar collection.

Although Schneirla was primarily concerned with the role of callow and larval excitation, he did recognize the role of food as an ecological parameter. Thus, at an early stage of his field research with the neotropical genus *Eciton*, he reported (Schneirla, 1938) that colonies frequently emigrate along the heaviest raiding route of that day. Nevertheless, it was Rettenmeyer (1963) who first suggested that the location and amount of captured food might influence not only the path of colony movements, but the very tendency to emigrate in the first place. The idea that colony excitation could be related to brood satiation has received empirical support from Free's (1967) study of honeybees and from related research with the myrmicine ant genus *Myrmica* (Brian, 1957, 1962; Brian and Abbott, 1977; Brian and Hibble, 1963). It was therefore significant that by the time of Schneirla's last field study, concerning emigration behavior in the paleotropical army ant genus *Aenictus*, he conceded that short-term variations in colony excitation may

depend upon the "alimentary condition prevalent in the brood" (Schneirla and Reyes, 1969), and that emigrations are likely to begin soon after food has run low.

In a recent series of field and laboratory studies of nomadic behavior in nearctic colonies of *N. nigrescens* (Topoff and Mirenda, 1980 a,b; Mirenda et al., in press), we demonstrated: (1) that the location of booty clearly influences the direction of raiding and therefore of emigrations; and (2) that artificially-fed colonies exhibit a lower frequency of emigrations. The present study differs from these in that food augmentation began late in the statary phase, before most of the callow population had eclosed. In addition to delaying the onset of the nomadic phase by reducing excitation from newly-eclosed callows (Topoff et al., 1980a), this was our first attempt to eliminate emigrations through a complete nomadic phase in the field.

During the six days of food augmentation for colony no. 1, we provided a total of 144 g of booty. Since the colony generated few additional raiding columns, the artificially-administered booty represents over 90% of the colony's total food intake for that period. According to Mirenda et al. (1980), colonies of *N. nigrescens* gather approximately 0.4 mg of booty/larva/nomadic night. Thus, on the average, we provided colony no. 1 each night with an amount of food that would be collected by a colony containing about 60,000 larvae. Although our estimate of colony size contains an error of $\pm 20\%$, we can be reasonably certain of having provided this colony with about 1.2 times the amount of food it would normally gather. Although the large size of this colony dictated that we could no longer supplement its food to the same degree throughout the remainder of the nomadic phase, the evidence from phase length, callow pigmentation, and larval size supports the conclusion that the onset of the nomadic phase was delayed for 4–8 days.

For colony no. 2, which was considerably smaller and more precisely counted, intensive overfeeding was more feasible. On the average, 8.8 g of booty were provided on food-supplemented nights. This is more than 5 times the amount of food that a colony of this size would collect in the field. In view of this feeding regime, it is not surprising that the colony conducted only one completed emigration throughout its 14-day nomadic phase. We must emphasize, however, that a reduction of the frequency of nomadic emigrations is by itself not sufficient to infer a relationship between food supply and

colony arousal. In all of our laboratory and field studies, we always placed food near raiding fronts, within a few meters of the bivouac. In most cases, the army ants established few or even no additional raid columns beyond the artificial feeding site. Thus, our feeding procedure reduces the ability of the ants to locate a suitable nesting site, which is a prerequisite for a successful emigration (Mirenda et al., in press). The case for a relationship between food supply and colony arousal is made considerably stronger by considering, in addition to emigration frequency, the temporal aspects of the ants' raiding behavior. Colony no. 2 conducted no raids on 4 nomadic nights. By comparison, the complete absence of raiding (on stormless nights) for a nomadic colony of *N. nigrescens* has never been reported, although it is a common occurrence for statary colonies. Finally, when we include the data on raid onset and duration for colony no. 2, we conclude that overfeeding can effectively shift the level of overall colony activity from a nomadic to a statary condition.

ACKNOWLEDGMENTS

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LIFE HISTORY OF *ANTAETRICHA* SP.
(LEPIDOPTERA: OECOPHORIDAE: STENOMATINAE)
IN PANAMA*

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The subfamily Stenomatinae (Oecophoridae) is a New World microlepidopteran group of approximately 35 genera and more than 1200 species. Its range is from the United States through Argentina; South America is especially rich in species. Little is known of the biology of these moths, but those that have been studied include leaf miners, stem borers, and seed eaters. The genus *Antaeotricha* Zeller, of similar range, comprises more than 400 species, many of which are leaf tiers.

Three individuals of *Antaeotricha* sp. near *fractilinea* (Walsingham) (Figure 1) were reared from larvae collected 29 March through 4 April 1980 on Barro Colorado Island (BCI), Panama. Two additional individuals were preserved, one in its final instar, the other as a pupa.

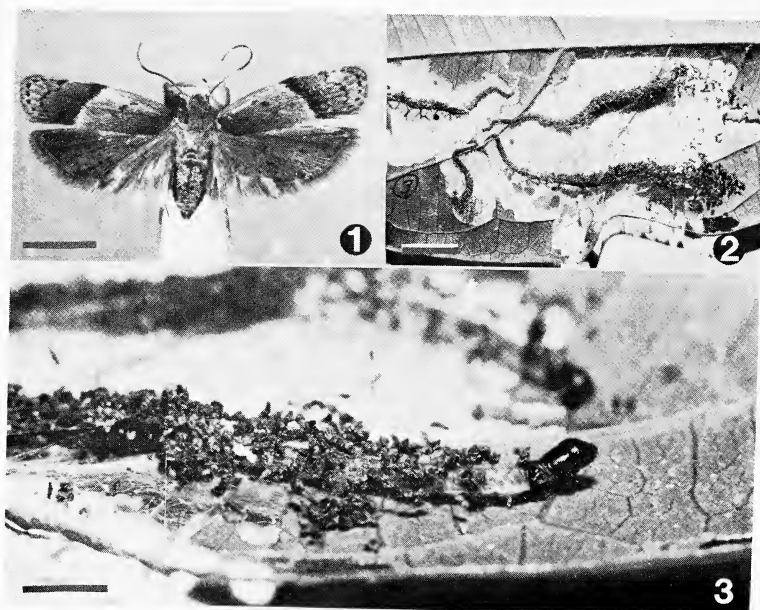
The larvae had constructed tubes (Figure 2) of silk, frass, and cast head capsules, on the undersides of the leaves of *Mascagnia nervosa* (Malpigiaceae).

At the time of collection two of the three larvae were in their final instar and these pupated five days later. The third individual, probably a first instar judging from its small size and tiny tube, molted the day after collection. Due to the uncertainty regarding instar number, letters instead of numbers are used to refer to instars.

Mascagnia nervosa is a liana which grows into the canopy of the BCI forest. Seedlings are found frequently around the edges of clearings and in tree falls. *Antaeotricha* larvae were common on the older leaves of plants 10–30 cm tall and bearing three to eight leaves each; some leaves supported as many as four larval tubes, although one or two were most common. Possibly *Antaeotricha* attacks leaves of this plant in the forest canopy as well.

Head capsule widths (Table 1) ranged from 0.18 mm (instar A) to 1.38 mm (final instar). Instar durations for the larva collected as instar A were: 5(B), 4(C), 4(D), 3(E), 5(F), and 8(G) days.

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Figures 1-3. *Antaeotricha* sp. (Rearing lot 80-30). 1. Adult (individual no. 4). Scale = 3 mm. 2. Silk and frass tubes on underside of leaf of *Mascagnia nervosa*. Scale = 7 mm. 3. Final instar larva (individual no. 1) reaching out of its tube. Scale = 2 mm.

Early instars (A, B) had pale-colored heads and green bodies. They constructed hard tubes of silk and frass, 0.5 mm in diameter, on the undersides of leaves. Most tubes were initiated along major leaf veins, a position which may offer protection to young larvae. The initial tube was dense and the larva inside could not be seen through its wall.

Subsequent instars extended the tube, each tube addition being wider and longer than previous portions.

Larvae did not leave their tubes to feed; they reached out (Figure 3) and scraped cells from the leaf surface.

Commencing with instar C, larvae had dark heads and a pink mesothorax. The remainder of the body was green as before. Intermediate instars (C, D) continued construction of the hard tube, and also fed by scraping the leaf surface immediately in front of the tube opening.

Later instars (E-G) ate whole leaf. Portions of the tube,

Table 1. Summary of variables for seven instars of individual no. 4 of Rearing lot 80-30. (P = pale, pink; D = dark; G = green; S = skeletonizer, soft; H = hard; W = eats whole leaf).

	INSTAR						
	A	B	C	D	E	F	G
Instar duration (days)	?	5	4	4	3	5	8
Head capsule width (mm)	0.18	0.25	0.35	0.48	0.63	0.83	1.38
Head capsule color	P	P	D	D	D	D	D
Mesothorax color	G	G	P	P	P	P	P
Feeding habit	S	S	S	S	W	W	W
Tube consistency	H	H	H	H	S	S	S

constructed by these instars, were soft and less dense than previous sections. The apical 2-3 cm of these tubes were extremely diffuse and the larvae inside could be seen clearly. Having consumed all nearby leaf, hungry larvae dismantled this diffuse portion and shifted it laterally until additional leaf surface was located, sometimes on other leaves of the same plant.

The final instar larva (G) (Figure 4) was about 7 mm long, lacked secondary setae; had prolegs on abdominal segments 3-6 and 10; crochets uniordinal, arranged in a circle; prespiracular wart of prothorax long, curving part way around spiracle, and bearing three setae; mesothorax with a single seta on tubercle *pi*; abdomen with setae *alpha* and *beta* widely separated, setae *eta* and *kappa* adjacent, seta *beta* on ninth segment placed higher up than *alpha*, and setae *beta* on ninth segment the same distance apart from one another across the dorsum as on previous abdominal segments; head with front extending about one-half the way to the vertex. Because the two sides of the mesothorax bore slightly different setation, on the specimen studied, both are illustrated in the setal maps (Figure 4). For ease of comparison, the map of the right mesothorax is shown in mirror image.

The day before pupation, final instar larvae abandoned their tubes and dropped to the floor of the cage. No cocoon was constructed.

The pupa (Figure 5) was ovate in outline, 5 mm long, 2 mm wide; with wings extending slightly beyond caudal margin of fourth abdominal segment; apical 1.3 mm of antennae adjacent on the meson except at their extreme tips, and bearing a distinctive raised

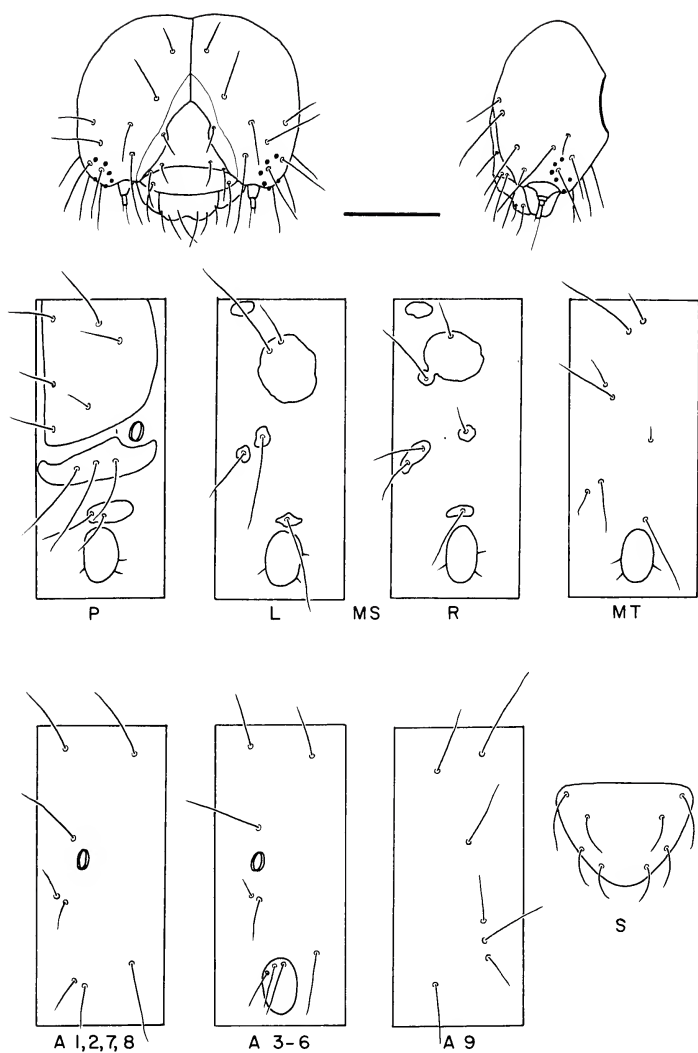


Figure 4. *Antaeotricha* sp. Final instar head capsule (front and lateral views), and setal maps. P = prothorax, MS = mesothorax, L = left, R = right, MT = metathorax, A = abdomen, S = suranal plate. Map of right mesothorax is shown in mirror image. Scale for head capsule = 0.5 mm.

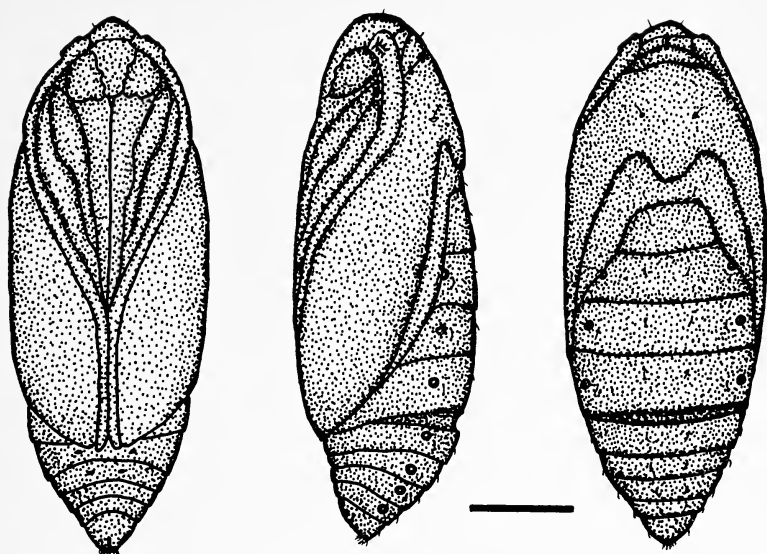


Figure 5. *Antaeotricha* sp. Pupa (ventral, lateral, and dorsal views). Scale = 1 mm.

structure on the scapes; mesothoracic legs and maxillae ending in the "V" formed by the meeting of the antennae; prothoracic legs slightly shorter than mesothoracic legs; labial palpi evident as tiny triangle between maxillae bases; fronto-clypeal and epicranial sutures distinct; abdominal segments 1-4 longer than others; spiracles evident on abdominal segments 2-8; cremaster of 8 weak setae.

Pupation lasted 10, 11, and 12 days for the three individuals reared. Total development time, for the individual collected as instar A, was 40 days. Allowing an additional three days for instar A, and four days for egg maturation, actual development time was probably close to 47 days.

Spread adults, pointed head capsules and pupal skins, and a larva and pupa in alcohol are in the collection of the author, deposited in the National Museum of Natural History, and are labelled as Rearing lot 80-30.

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POLISTES GALLICUS IN MASSACHUSETTS
(HYMENOPTERA: VESPIDAE)*

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INTRODUCTION

Polistes gallicus (Linnaeus), a common and widespread paper wasp in the palearctic region, has been introduced into the United States in the Boston, Massachusetts, area. During 1981 specimens were collected in Cambridge, Somerville, Belmont, and Newton, Massachusetts. *P. gallicus* was also collected in Cambridge in 1980, but was not seen in Belmont that year (R. J. McGinley, personal communication). Species identification was verified by Dr. Arnold S. Menke of the Systematic Entomology Laboratory of the United States Department of Agriculture. Presumably *P. gallicus* was only recently introduced; otherwise it would surely have been reported before this. It is a brightly colored and conspicuous wasp.

The purpose of this paper is to report the introduction of *Polistes gallicus*. The biology of the species in the Old World is reviewed briefly, and some observations of the wasp in Massachusetts are reported. Information on how to recognize *P. gallicus* is also included.

BIOLOGY OF *POLISTES GALLICUS* (LINNAEUS)

Polistes gallicus is ubiquitous in the palearctic region, especially in the south. It is the most common *Polistes* in Spain (Giner Mari, 1945). The species' range extends north to Paris, but *gallicus* becomes rare in far northern France. It exists in warmer parts of Belgium and Germany, but does not occur in England, Denmark, or Scandinavia (Guiglia, 1972). Spradbury (1973) states that occasionally *Polistes* are introduced into the British Isles, but for some reason the genus is not able to sustain itself there. To the south, the range of *P. gallicus* includes northern Africa, where the species is known from desert oases (Richards, 1953), and extends east through Israel and Iran. In Asia *P. gallicus* has been collected in southern

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U.S.S.R. and throughout China, east to the Pacific coast (Guiglia, 1972; Yoshikawa, 1962). Generally, the species is found in warmer and dryer localities within its range. It is not common above 1000 m elevation, although in southern Spain specimens have been collected above 2000 m (Guiglia, 1972).

The biology of *P. gallicus* varies considerably between the climatic extremes of the area it inhabits. North of the Alps, nests are built in enclosed places, such as metal containers and gutter pipes. This type of nest has also been reported by Pardi from the coast of Tuscany in Italy (Guiglia, 1972, and references therein). Throughout most of Italy, however, the nests of *P. gallicus* are built in the open, and typically hang from eaves, branches, or other protective horizontal structures. The nest hangs from a slender peduncle with its disc oriented horizontally, and the cells opening downward. Often there are several accessory peduncles. Infrequently, nests are found whose discs are oriented vertically.

In Italy, where the species has been studied extensively, nests of close to 500 cells have been reported on several occasions (Guiglia, 1972). It is apparently common for colonies of this species to become quite large in the south.

Polistes gallicus colonies are haplometrotic (with a single foundress) in northern Germany and presumably throughout the northern extent of the species' range. Further south, for instance in southern Germany, pleiometrotic colonies (with several foundresses) are occasionally reported (Richards, 1953). In Italy the species is typically pleiometrotic, although as with the pleiometrotic colonies reported from Germany, one queen is clearly dominant and lays most of the eggs. The subordinate, or accessory females function as workers in the nest. According to Pardi (1948), after the first workers emerge the accessory females are chased off the nest or killed by the queen. This situation resembles nest founding in *P. fuscatus* (Fabricius), the common paper wasp in northeastern United States, except that in *P. fuscatus* subordinate females are usually allowed to remain on the nest after workers have emerged (West, 1967). In Africa *P. gallicus* colonies reproduce by swarming, with a reproductive female leaving her nest in the company of several workers (Richards, 1953).

LOCAL OBSERVATIONS

I report here on 2 nests of *P. gallicus* in Cambridge, Massachu-

setts. Both were in enclosed situations, similar to those described as typical in the northern parts of the species' range in Europe. The first nest was located inside a metal pole supporting a stop sign. The pole was $7\frac{1}{2}$ cm in diameter, and open at the top. The single peduncle of this nest was located 28 cm from the top of the pole. The nest was suspended from the pole's side and faced north. This nest contained 134 cells, and measured 8 cm high and 5 cm across.

A second nest was located inside an open vertical pipe, 35 cm tall and 8 cm in diameter. The nest was suspended from the side of the pipe and faced west-north-west. Its peduncle was located 6 cm from the top of the pipe. This nest contained 153 cells and also measured 8 cm \times 5 cm.

P. gallicus does not seem to be an aggressive species. I have been able to observe a nest from as close as 15 cm, apparently without disturbing the wasps.

The prognosis for permanent establishment of *P. gallicus* in the western hemisphere appears good. The species seems quite able to withstand the climate in the northeast. 1980–1981 was an unusually cold year in Boston, with 5,819 degree days accumulated between June 1 and May 30, as opposed to the 30-year normal of 5,597 (United States National Weather Service statistics, telephone information).

RECOGNITION OF *POLISTES GALLICUS*

In northeastern United States *P. gallicus* would more likely be confused with a yellow jacket (*Vespula* spp.) than with another paper wasp. Although its shape and flight are similar to the native *Polistes*, it is relatively small and its markings and coloring are strikingly different. *P. gallicus* is black with bright yellow maculations (see figure 1).

Specimens collected in Massachusetts have varied considerably in their markings, with some showing more yellow than others, especially on the clypeus. This has also been true of specimens collected from the same nest. *P. gallicus* is known to be quite variable in Europe (Guiglia, 1972).

Males have completely yellow faces and their antennae are curled at the tips, a characteristic common in the genus. Their antennae are quite short, however, compared to males of other species. In other superficial respects, males of *P. gallicus* resemble the females.



Figure 1. *Polistes gallicus* worker (left) and male (right) collected in Cambridge, Massachusetts. Length of worker, 1.4 cm.

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NOTES ON THE POPULATION ECOLOGY OF CICADAS
(HOMOPTERA: CICADIDAE) IN THE CUESTA ANGEL
FOREST RAVINE OF NORTHEASTERN COSTA RICA*

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INTRODUCTION

Several previous field studies of cicadas (Homoptera: Cicadidae) in Costa Rica have revealed that different sympatric genera and species often exhibit allochronic (seasonal) annual adult emergence patterns and habitat associations (Young 1972; 1974; 1975a; 1976; 1980a,b,c; 1981a,b,c). Most of these studies concerned cicadas associated with lowland tropical forest and the Central Valley regions of Costa Rica, although one study in particular (Young 1975) examined some aspects of the population ecology of cicadas in a mountain forest. Because different species, and sometimes genera, of cicadas are found in different climatic and geographical regions of Costa Rica (Young 1976), it is necessary to examine the population ecology of these insects in as many of these ecological zones as possible. This paper summarizes an ecological survey of the cicadas thriving in the steep and very rugged forest ravine known as "Cuesta Angel" in the Central Cordillera of northeastern Costa Rica. The information reported here complements the studies of cicadas in other ecological zones of Costa Rica, although by no means does as extensively owing to the difficulties working on the very steep slopes of the ravine. It is shown tentatively that (a) the cicada fauna of this region includes at least two species not discussed or found in the other regions studied, (b) the resident species exhibit different annual emergence patterns, and (c) nymphal skins of several species are distributed at very low densities and in association with various genera and species of leguminous canopy-size trees in the ravine habitat.

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Fig. 1. The ravine forest at Cuesta Angel, near Cariblanco, Heredia Province, Costa Rica.

METHODS

The Cuesta Angel ravine is an extensive strip of very steep primary and river-bottom forest (Fig. 1) filtering down from the highest mountains of Costa Rica's Cordillera Central and tapering into the northeastern lowlands known as Sarapiquí. Because of its rugged profile much of the ravine remains blanketed in forest even though surrounding level areas have been largely converted to pastures. This ravine is within the recently extended Carillo National Park. There have been relatively few field studies of plants and animals in the ravine, even though both its invertebrate and vertebrate faunas contain many forms not found in other parts of Costa Rica. "Cuesta Angel" is located about 10 km south of the village of Cariblanco ($10^{\circ} 16'N$, $84^{\circ} 10'W$), Heredia Province, and is classified as montane tropical wet forest (elev. about 1200 m) (Holdridge 1967). The vertical drop in the ravine is about 300 m.

As shown by 1972 and 1973 rainfall data, the region is very wet and with a short and erratic dry season during January and February (Fig. 2). For either collections of nymphal skins or determination of species active by calling songs or collection of specimens, the locality was visited the following dates: 27–30 June 1972, 14 August 1972, 15–17 February 1973, 20–24 March 1973, 18–20 April 1973 (beginning of nymphal skin regular censuses), 22–25 May 1973, 6–10 June 1973, 4–7 July 1973, 7–9 May 1975, 3 April 1976, 1 and 5 November 1980. Dates of visit included both wet and dry periods for this region. During the April 1976 visit, Dr. Thomas E. Moore recorded calling songs of the species active at that time.

The 1973 visits were concerned primarily with attempting to census the nymphal skins of various species active at different times of the year while other dates were devoted to listening and collecting adult specimens. The nymphal skins of recently emerged cicadas are relatively easy to distinguish from those of a previous years' emergence owing to discoloration and disintegration of some parts (Young 1980a) and therefore provide an accurate record of a recent or current emergence within the year. The locations of nymphal skins in the habitat also provide information on the possible feeding associations of the nymphs in the ground and other aspects of microhabitat. I censused nymphal skins, with the assistance of at least one, and usually two, trained student assistants by marking off rectangular or square plots (usually 5×5 meters) immediately beneath a tree or other spot where at least one nymphal skin was found. Initially we crawled through the forest along transects to determine where nymphal skins were found and then marked off the trees and places having them. The transect approach was used in the survey of the very rocky terrain comprising the river-edge forest on relatively flat ground, but working on the steep slopes entailed spot-checking various places owing to the difficulty of the terrain and often very misty conditions. Thus the nymphal skin census program involved repeated censuses at twelve marked canopy-size trees on the slopes, and four large river-edge plots of forest, each plot containing many trees. The four river-edge plots, each one widely separated from the other by at least 100 meters of forest, ranged in size from 462m² to 300m², the differences being due to rivulet channels and other interruptions in the forest. With the exceptions of marked trees 2, 6, and 7 (each of which was a plot of about 90m²),

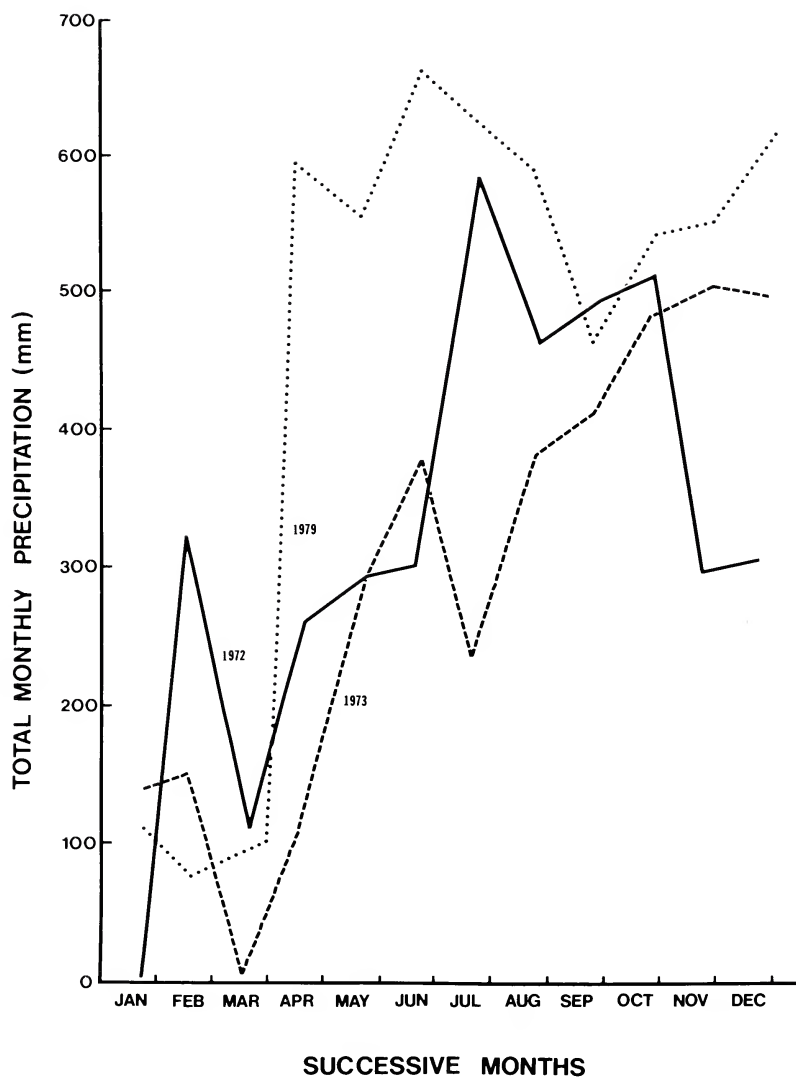


Fig. 2. A sample of three separate years of monthly rainfall patterns at Cariblanco. In all three years portrayed, a short dry spell occurs between January and March, although conditions are not completely dry as in other regions of Costa Rica with distinct dry seasons.



Fig. 3. The forest habitat at the top of the ravine, and above the Sarapiqui roadcut. The cicada *Fidicina* n.sp. is abundant here.

most tree plots on the slopes were 25m^2 . The twelve tree plots gave a total habitat area of about 484m^2 sampled for nymphal skins several times and a total of $6,957\text{m}^2$ of river-edge forest sampled as well (total sample area of $7,441\text{m}^2$). The tree plots were widely scattered with the closest being no less than 30 meters apart. The sample included the hill-top forest above the Sarapiqui roadcut (Fig. 3) as well as the forest habitat to either side of the secondary road down into the ravine (Fig. 4). A census consisted of making an exhaustive collection of all cicada nymphal skins found within each plot, including those attached to plants and tree trunks and those lying in the ground litter. The contents were placed into a plastic bag and labeled appropriately. Later the skins were determined to species and sex. The nymphal skins of the cicadas studied were readily separated to species in my field samples on the basis of marked differences in size, color, and body profile. Skins were matched with

others obtained from collecting skins when adults were emerging. In previous studies (Young 1972; 1975a; 1980a,b; 1981a,c) I have illustrated and discussed distinguishing features of cicada nymphal skins. Based upon these materials, a key to the Costa Rican cicada fauna, using both adults and nymphal skins, is being formulated (T.E. Moore and A.M. Young, in preparation). In the present study, it was very easy to distinguish nymphal skins of *Fidicina* species (three species) on clear-cut differences in color pattern and size; the *Zammara* species studied has nymphal skins very different in color and body profile from the others (see also Young 1972), while the two species of *Carineta* species had nymphal skins differing in color, even though of very similar size. One species has a very dark brown nymphal skin, and the other, light brown. Based upon matching of skins with adults done by myself and T.E. Moore, I am reasonably certain that matches of field collections of skins with adults is very reliable. Voucher specimens of fruits and leaves of the trees having nymphal skins beneath them were collected and sent to specialists for determination.

Other observations included determining the places on the ravine where adult cicadas were heard chorusing as a means of estimating preferences among species for the river-edge area and top of the ravine. In some instances, diurnal patterns of calling were also noted and the trees used for calling. Once the species were determined, records of captures of cicadas in other regions of Costa Rica were checked by examining the University of Michigan collections and data bank on Neotropical species in other museums, as a means of determining if the Cuesta Angel species were found elsewhere in Costa Rica. Because virtually nothing is known about the geographical distributions and habits of Neotropical cicadas in general, vouchers of both adults and nymphal skins were saved and placed in collections at the University of Michigan and the Milwaukee Public Museum.

Owing to the steep terrain and heavy rains of the region, a small experiment was conducted on estimating the rate of disintegration of cicada nymphal skins on both forested slope and river-edge forest. Such a test would tell me how many skins were being missed between census intervals because they were possibly disintegrated, particularly on the slopes, before the next census was taken. Thus in the May 1973 census, two groups of fresh skins of one of the larger species, each group containing ten skins, were established, one



Fig. 4. The forest habitat along the secondary road going to the bottom of the ravine. Cicadas such as *Fidicina sericans*, *F. mannifera*, and two species of *Carineta* are heard in the trees along this road.

group of a patch of forest slope where this species emerges, the other on a level area adjacent to the Sarapiquí River. The skins in each group were randomly distributed (by throwing) within a one-meter square area of ground. The numbers of skins remaining in each plot were then checked in June and July 1973.

RESULTS

The six species of cicadas found and studied at Cuesta Angel are shown in Fig. 5, and they are: *Zammara tympanum* Distant, *Fidicina sericans* Stal, *Fidicina* "new species" (n.sp.), a new species, *Fidicina mannifera* Fabricius, *Carineta postica* Walker, and *Carineta* sp. Three of these, *Z. tympanum*, *F. sericans*, and *F. mannifera*, are large-bodied cicadas with very loud calls, while *F. n.sp.* is medium-sized, and the two species of *Carineta* are considered small-sized (or at the low end of the medium-size range), the latter two

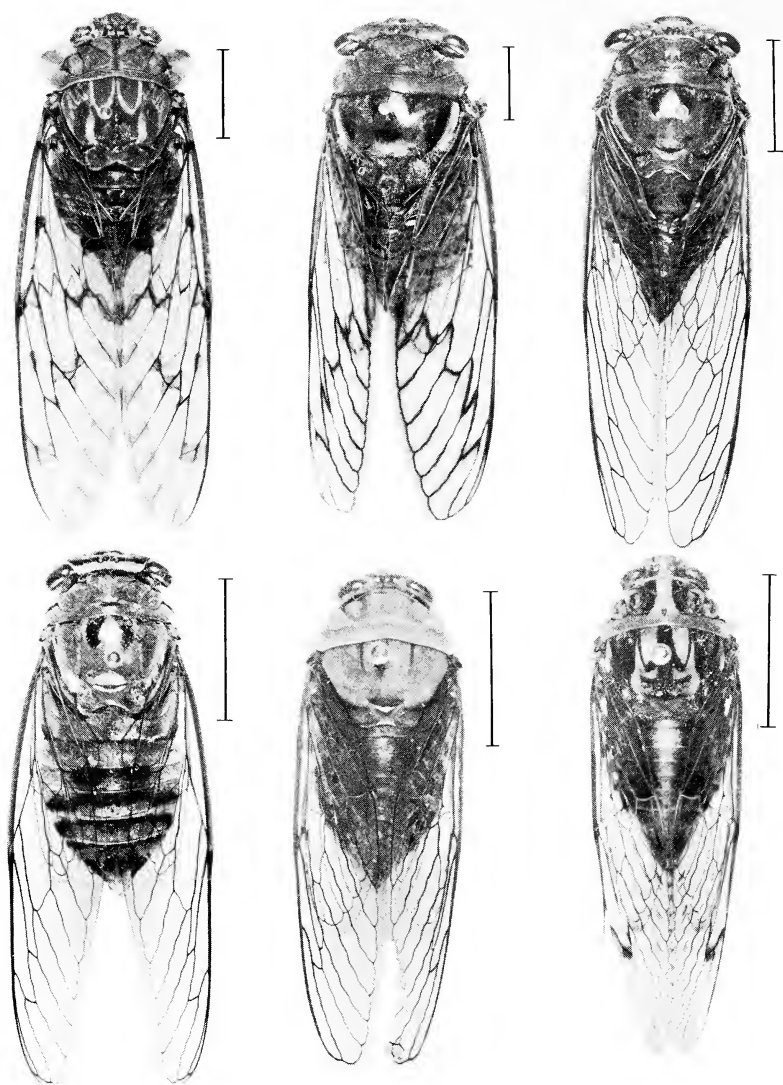


Fig. 5. Cicadas found in the Cuesta Angel ravine forest, top, from left to right: *Zammaria typanum*, *Fidicina mannifera*, *F. sericans*; bottom, left to right: *F. n.sp.*, *Carineta sp.*, and *C. postica*. The vertical black line to the left of each cicada gives the scale of one cm. relative to the body shown in each photograph.

cicadas having very soft calls. *Zammara tympanum* adults are heard throughout most of the year and sometimes during the dry season and they call from the moss and other epiphyte-covered trunks of forest trees primarily along the river-edge. This cicada is mottled green and brown and has brown spots on the wings, immediately distinguishing it from the others. The call is a "winding up-like pulsating buzz. Adults when calling occur at one per tree, and there are usually no more than two or three calling males present within approximately 800m² parcels of river-edge forest during an optimal calling period. Males call throughout the day, including overcast and light drizzle conditions. Males are bright green with brown markings while females are drab olive green and brown.

Fidicina sericans, both sexes, are black with green markings on the thorax and smoky wings. The call is a steady rather high-pitched buzz most frequently heard during sunny weather and during the dry season. Sometimes several males congregate in the same tree, particularly if it is along an edge of forest, and sometimes, under these conditions, several adjacent exposed trees may have males calling at the same time. The calling males are seen perched on the upper portions of the trunk and on branches, and they are easily spotted on light-colored bark species such as *Pourouma* and *Cecropia*. Adult densities, as indicated by calling males, probably are about 1–20 cicadas per 800m² of forest during a period of peak calling, although this may be an underestimate since only a fraction of males may chorus at any one time. Calling males are heard primarily on the forest slope and less so at the bottom of the ravine and at the very top.

Fidicina n.sp., both sexes, possesses a green head and thorax and black and orange-banded abdomen, sometimes with patches of silvery hairs laterally. Of all of the cicadas in Costa Rica, this species is the most difficult one to catch because of their habit to perch very high in trees and to change trees after one call. Based on comparisons with type materials and other specimens, this is most likely a new species. It has a very distinctive two-part call: the first part is a series of pulsating chirps followed by a longer period of siren-like and pulsating calls. Unlike this species, both *Z. tympanum* and *F. sericans*, as well as the other species to be discussed, often make repeated complete calls from the same perch, even if interspersed with periods of silence lasting several minutes or an hour or two. *F.* n.sp. is heard during the dry season and it occurs in the ravine and

above the Sarapiquí roadcut. Adult densities appear to be very low, similar to that of *Z. tympanum*, but difficult to determine due to the highly mobile habits of males.

Fidicina mannifera, both sexes, is dark brown with some dark green markings on the head and thorax and with tinges of brown along the veins of the wings. The body is very pubescent. Males generally call at dusk and dawn and usually for about 15–20 minutes during each period. The call is a very intense pulsating shrill buzz. Based upon observing a total of close to 20 individuals at this locality, there is about a 50:50 chance that a male just completing a call will stay in the same tree. Males are heard primarily inside the forest and on the lower slope and along the river. Densities are very low with probably only one or two males per 1000m² of forest habitat.

Carineta postica, also illustrated in Young (1975), is black with green markings on the head and thorax and with the entire body blanketed in setae. The wings are smoky and calling males have the habit of perching head-downward on the trunks of forest trees, a behavioral trait separating the larger-sized members of the genus from all other Neotropical cicadas. Males sing from moss-covered tree trunks and branches inside the river-edge forest and along the river itself. Densities are low, with 1–5 calling males per 500m² of forest and with calling limited to the late afternoon or overcast conditions during the dry season. The call consists of repeated coarse “zip-zip” sounds, and is reminiscent of a muted version of the call of the familiar cone-headed grasshopper of North America. This species may also be *C. trivitatta* Walker as specimens of both species are very similar in size and coloration. Clarification awaits further study.

Carineta sp. is pea-green with clear wings and calls from forest edge trees such as *Cecropia* during the wet season. It is of same size and profile as *C. postica* but is most abundant near the top of the ravine. The call is also similar to that of *C. postica* but somewhat louder and calling is generally a dusk phenomenon. Sometimes as many as eight males have been seen perched at different heights on the trunk of the same *Cecropia* tree.

The data on temporal emergence patterns annually from the censuses of nymphal skins present a more diffuse picture of seasonality in the cicadas at Cuesta Angel (Fig. 6). Caution is given here in that these data are very fragmentary and discontinuous,

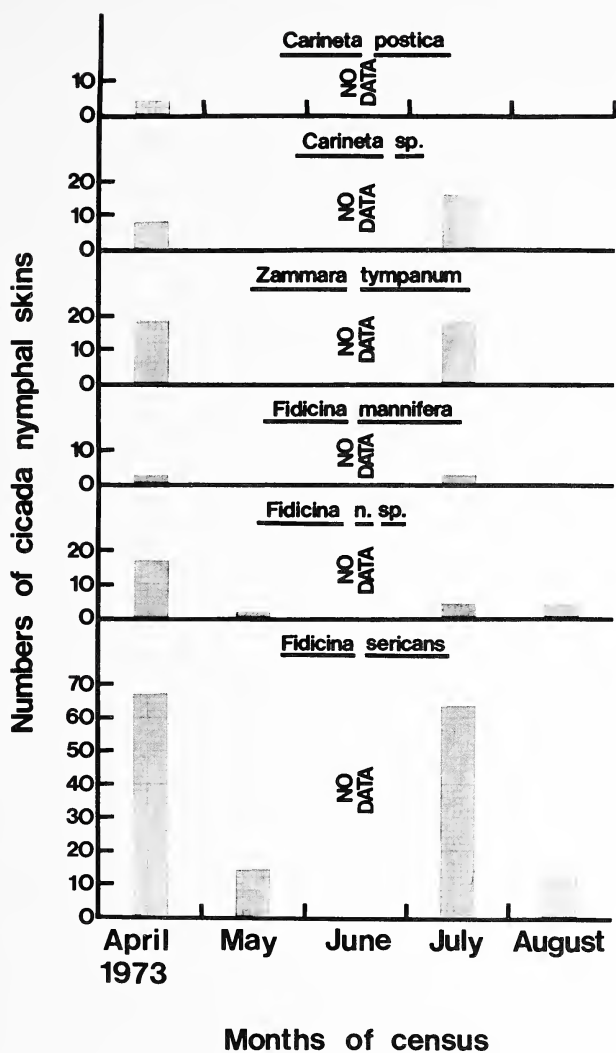


Fig. 6. Monthly collections of cicada nymphal skins from tree plots and river-edge plots at Cuesta Angel.

although the best there are at this time. With the exception of *C. postica*, there appears to be a trend for most species to emerge during both wet and dry seasons, when considering both the nymphal skin and call records together. Thus although *F. sericans* is heard in abundance during the short dry season, there is some evidence of emergence well into the wet season (Fig. 6). But examining the 1973 rainfall data shows a marked dip in rainfall during July (Fig. 2), giving a brief dry spell that month. If it is assumed that the data are actually representative of emergence patterns of cicadas at Cuesta Angel, it then appears that another dry season species, *C. postica*, did not respond to the July 1973 dry spell as there was no emergence (Fig. 6). At the same time, the dry spell was apparently insufficient in intensity to block the emergence of wet season species such as *Z. tympanum*. Perhaps even more interesting is the wet season emergence of another supposedly dry season species, *F. n.sp.* (Fig. 6). Adults of such species were not heard at these times although my sample sizes are very small. Different patterns of emergence may be associated with different years in which monthly rainfall regimes are very different. For example, during 7–9 May 1975, there was an abundance of *F. n.sp.* calling in the ravine as was the case for 4–7 July 1973. Both of these months, in different years, were drier than in other years, and the rainfall data for 1972 and 1973 clearly show the year-to-year variation in monthly rainfall patterns at this locality (Fig. 2). Furthermore, when *F. n.sp.* emerged during the wet season, calling was restricted to the dry periods of the day. All of the cicadas studied exhibit bursts of calling near dusk (see also Young 1981b).

The distribution of nymphal skins for each species studied by marked trees is given in Table 1. Even though approximately 70 species of canopy-size trees were included along the initial transects to determine the locations of cicada emergence patches in the ravine, patches were found to be confined to the species of Leguminosae listed in Table 1. Note that the estimation of relative abundance of adults among the species discussed above is confirmed here in terms of nymphal skins: by far the most abundant species is *F. sericans*, whose nymphal skins comprised almost 64% of the total 241 skins collected in the 1973 survey of tree plots alone (Table 1). *F.n.sp.*, *Z. tympanum*, and *Carineta sp.* are about evenly distributed in terms of abundance of nymphal skins in the tree plots. As in previous studies of cicadas in Costa Rica, sex ratios are close to

Table 1. Census history of cicada nymphal skins in legume tree plots* in the forest ravine, "Cuesta Angel", near Cariblanco, Heredia Province, Costa Rica.

Tree No. and Species**	Distributions and Abundances of Nymphal Skins per tree over all census dates					
	<i>Fidicina sericans</i>	<i>Fidicina n.sp.</i>	<i>Fidicina mamifera</i>	<i>Zammara tympanum</i>	<i>Carineta sp.</i>	<i>Carineta postica</i>
(1) <i>Pitnecollobium latifolium</i>	0	0	0	0	4	0
(2) <i>P. latifolium</i>	72	7	1	13	1	0
(3) <i>Inga</i> sp.	13	1	0	3	0	0
(4) <i>Pithecollobium</i> sp.	1	0	0	0	0	0
(5) <i>Inga</i> sp.	1	3	1	0	1	1
(6) <i>Inga</i> sp.	34	2	0	0	0	0
(7) <i>Pentaclethra</i>	6	4	0	1	4	0
(8) <i>Inga</i> sp.	7	0	0	7	0	2
(9) <i>Planifolium</i>	0	0	0	1	2	0
(10) <i>Inga</i> sp.	4	5	2	4	10	0
(11) <i>Inga edulis</i>	15	0	0	1	0	0
(12) <i>Inga enfusa</i>	0	1	0	5	1	0
(12) <i>Inga edulis</i>						
Total skins	153	23	4	35	24	3
Range per tree	0-72	0-7	0-2	0-13	0-10	0-2
Mean ($\bar{X} \pm S.D.$)	12.75 ± 21.07	1.91 ± 2.35	0.33 ± 0.65	2.91 ± 3.91	1.91 ± 2.93	0.25 ± 0.62

* Each plot ranged in size from 5×5 meters to 10×9 meters around the base of individual legume trees.

** All trees and cicadas were censused 18-20 April, 22-25 May, 4-7 July, 15 August 1973 (total of 14 days), except for trees 9, 10, 11, and 12, which were added to the census program on 4 July 1973.

unity. Taking the most abundant species, *F. sericans*, there is considerable range in numbers of skins found in the different tree plots, although close to 40% of all skins of this species were found beneath one individual of *Pithecollobium latifolium* (Table 1). Yet a second individual of this tree species yielded only four skins of cicadas overall and none of *F. sericans*. Such data, although limited, indicate the considerable variation encountered over different patches of the same resource for a cicada species in tropical forests. Two different individuals of *Inga* and one *P. latifolium* together account for almost 65% of all skins found. That such data may be underestimates of true values, even for an abundant species such as *F. sericans*, is suggested by the results of the estimate of rate of disintegration of nymphal skins: at the end of a five-week period, between 50% (level ground) and 80% (slope) of the *F. sericans* nymphal skins studied had disappeared. These samples are pitifully small, but it is the best we have at this time. The intervals between censuses in my study are of this magnitude and greater, thereby indicating the likelihood that some skins were missed owing to their rapid disintegration under very wet conditions. The examination of nymphal skin distributions by tree plots and river-edge plots separately provides further confirmation of the data shown in Table 1 (Table 2). Although high percentages, if not all, of plots are occupied by skins of *Z. tympanum*, the emergence is one of very low density since only a small number of skins occur in the plots studied (Table 2). The tree plots, although only representing an area of about 6.5% of the combined area of tree plots and river-edge plots, account for almost 80% of all skins recovered (Table 2). The larger river-edge plots include a wide variety of tree species whereas the tree plots each include one individual of a leguminous tree species and understory plants. Most striking is the relatively high density of the nymphal skins of *F. sericans* in the tree plots, almost 0.4 skins/m² (Table 2). Yet the same cicada, in a much larger and representative tract of forest, representing an area about five times that of the tree plots, has the very low density of about 0.010 skins/m² (Table 2). Other patterns of nymphal skin density between tree plots and river-edge plots are self-evident and support the pattern discussed for *F. sericans* (Table 2). From such results, one can readily appreciate the distortion of density estimates when different size patches of the environment, with different biological attributes, are combined to give a summary figure (Table 2). And

Table 2. Some population parameters of cicada species in the ravine forest, "Cuesta Angel", Costa Rica

Cicada Species	Body Size (mm)	Distribution and Abundance of Nymphal Skins						
		River-Edge Plots (4)*			Tree Plots (12)***			
		Total Skins	# Plots with Skins	Density**	Total Skins	Ratio Occupied Plots	Density	
<i>Zammaria tympanum</i>	28 mm	10	4	0.001 m ²	35	8	0.106 m ²	0.006 m ²
<i>Fidicina sericans</i>	31 mm	21	1	0.010 m ²	154	9	0.377 m ²	0.069 m ²
<i>Fidicina</i> n.sp.	25 mm	7	2	0.002 m ²	23	7	0.064 m ²	0.006 m ²
<i>Fidicina mannifera</i>	39 mm	1	1	0.004 m ²	4	3	0.024 m ²	0.002 m ²
<i>Carineta postica</i>	10 mm	3	3	0.001 m ²	3	2	0.060 m ²	0.001 m ²
<i>Carineta</i> sp.	18 mm	9	3	0.002 m ²	23	8	0.060 m ²	0.005 m ²

*There are four river-edge plots of these sizes: 2,145m², 1,350m², 462m², and 3,000m² for total area of 6,957m².

**All estimates of density based on occupied plots only; no empty plots included.

***Most of these plots are 25m² for a total area of 484m².

the data also show, that for larger areas of environment as typified here by the river-edge plots, there are not necessarily going to be increases in densities of insects recovered.

DISCUSSION

Of the six species studied at Cuesta Angel, none are exclusive to the locality, but other locality records from Costa Rica indicate similar elevations and habitat. *Fidicina* n.sp., *Zammara tympanum*, and both species of *Carineta* have been collected at Turrialba, Cartago Province as shown by specimens in the collections at The University of Michigan Museum of Zoology. The species I term *C. postica* may also be *C. trivitatta* Walker, which has also been collected from the San Jose area, Guapiles (Limon Province) and Bajo La Hondura (San Jose Province). Two other cicadas, *F. sericans* and *F. mannifera*, have much more extensive ranges in Costa Rica as both have been collected and studied in premontane and lowland tropical wet forest regions of the Atlantic coastal watershed (Young 1972; 1980b), and *mannifera* also occurs in the semi-dry to dry forest region of the western provinces of Puntarenas and Guanacaste (Young 1981a,c). Given the topography of the Cuesta Angel region relative to the adjacent lowlands, it is not surprising to find species such as *sericans* and *mannifera* along a more or less continuous elevational gradient within the wet forest region and over a range of about 90–1100 meters. Yet this is not true for the genus *Zammara* or *Carineta* since entirely different species occur in the adjacent premontane and lowland wet forest regions of northeastern Costa Rica (Young 1972; 1976; 1980b). From both records of adults calling and nymphal skins, both *sericans* and *mannifera* occur at much lower densities in the Cuesta Angel montane wet forest than they do in adjacent premontane and lowland wet forests. Given these records, it is concluded tentatively that cicadas such as *F. n.sp.*, *Z. tympanum*, and the two species of *Carineta* studied are montane species associated with wet forests while *F. sericans* and *F. mannifera* are lower elevation forms also associated with generally wet forests and semi-dry forests. Thus the Cuesta Angel cicada fauna is a mixture of montane and lower elevation tropical wet forest cicadas.

Both generic and specific richness of cicadas at Cuesta Angel are not as high as they are in the adjacent lower elevations. There are six

genera and about ten species of cicadas found in the adjacent premontane tropical wet forest (Young 1980b) as studied about 25 km from the Cuesta Angel locality. Young (1975) found only two genera, each monospecific, at another montane wet forest locality, Bajo La Hondura. There are also greater numbers of genera and species found in mid-elevation moist forest (Young 1980a) and lowland tropical dry forest (Young 1981a) in Costa Rica. Cicadas such as *F. sericans* and *F. mannifera* are tentatively interpreted as being ecological "leaks" into the forested ravine at Cuesta Angel. Given the continuous accessibility to lower elevation wet forest habitats moving along the ravine into the lowlands, it is unreasonable to expect some highly mobile insects to colonize at either end (Young 1975b).

Elsewhere in Costa Rica, cicadas have been found to have distinct seasonal patterns of adult emergences each year (Young 1972; 1975a; 1980a,b; 1981a,c) with the recognition of usually three kinds of cicadas: dry season, wet season, and transitional forms between dry and wet seasons. From the studies of cicadas in premontane tropical wet forest in particular (Young 1980b), however, it became apparent that brief spells of wetness in a dry period and of dryness in the wet season may trigger emergence of wet season and dry season species respectively. In the premontane tropical wet forest zone of northeastern Costa Rica, typically wet season cicadas such as *Z. smaragdina* Walker will emerge in low numbers during a rainy spell of about five days or longer within the dry season (Young 1980b: pers. obs.). During a dry spell within the long rainy season at the same locality, *F. sericans*, a typical dry season cicada, can also be heard and fresh nymphal skins found (Young 1980b: pers. obs.). Such observations indicate that "seasonality" in tropical cicadas is a very flexible sort of emergence strategy, perhaps determined by critical periods of wetness or dryness, depending upon the species and locality. Such an effect may explain the anolamous emergence of *F. sericans* in the wet season at Cuesta Angel. The data from Cuesta Angel very tentatively provide additional support for this phenomenon, as shown for species such as *F. n.sp.* The proximal cues triggering emergence in tropical cicadas have not been studied to my knowledge, although some ideas have been suggested for study (Young 1975; 1980a,b; 1981a). What are also needed are detailed studies of the effects of small changes in air temperature and humidity, and light intensity on the behavior of adult cicadas in

the tropics over a typical diurnal cycle. Different species may possess different levels of physiological capacity to cope with stressful environmental conditions imposed by either too much wetness or too little wetness. From my work on cicadas in Costa Rica over the past eleven years, and particularly from data on densities of nymphal skins of co-occurring species in the same patches of habitat, it seems doubtful that seasonal emergence patterns in cicadas is related to interspecific competition in developing cicadas. From what little information I have, there is little reason to suspect competition for oviposition sites. But the great diversity in the properties of the calling songs among co-occurring species in tropical forests, and the tendency for several species to form single species aggregates of chorusing males (Young 1980c) suggest that there might be competition for optimal calling conditions. In cicadas, the calling song is a major component of fitness since it presumably functions in mating, and there might be strong selection to evolve allochronic emergence patterns when the calling songs of species conflict and reduce mating success. Certain types of seasonal changes in the environment, yet to be determined, may provide the most ready cues for these insects to exploit in evolving allochronic emergence patterns to reduce losses in mating success. The whole system warrants considerable detailed study as it involves different stages in the life cycle. Seasonal emergence may or may not have anything to do with conditions being intrinsically optimal for a certain species in a certain region at a certain time of the year. If the latter, the cicada is merely locking in to a convenient cue since, under this hypothesis, both wet and dry periods provide suitable resources for adults, including those associated with mating needs.

Under the mating conflict hypothesis, it is implied that cicadas with very low densities and with unusual calling habits may forego entering into such a selection arena, thereby circumventing this adaptive pathway and emerging throughout most of the year, other things being equal. A typical case in point is the almost catholic habit of *F. mannifera* to sing for a brief period at dusk and under conditions of low population densities in Costa Rica (Young 1972; 1980b; 1981b; this paper). The intensity of the presumed mating conflict is considered to increase as population densities of co-occurring species increase individually.

In virtually all other regions studied, the greatest numbers of cicada nymphal skins occur beneath adult legume trees (Young

1972; 1980a,b; 1981a,c) although precise data on the abundances of skins in legume plots versus non-legume plots is still lacking. At Cuesta Angel cicada nymphal skin patches too were found beneath legume trees. If legume trees provide some form of highly suitable environment for developing cicadas in tropical forests, emerging populations each year will be spatially disjunct according to the spatial distribution of the legume trees whose root crowns provide a primary resource for developing nymphs. The suitability of Leguminosae for developing cicadas may involve both physical and chemical properties of the classes of root sizes exploited by various age-classes of nymphs. The observed low densities of nymphal skins in all of the plots at Cuesta Angel, relative to previously obtained densities of the same or similar species in other regions (e.g., Young 1980a,b; 1981a), may therefore be a function of the very dispersed condition of the legume trees at this locality. A striking contrast is made with the association of nymphal skins of species such as *Z. smaragdina* and *F. sericans* in relatively large patches of adult *Pentaclethra macroloba* in nearby premontane tropical wet forest (Young 1980b). Densities of these cicadas range from 5.4 to 9.3/m² in patches of two or more *P. macroloba*, estimates considerably greater than for the same species at Cuesta Angel. I interpret such observations to be the result of *P. macroloba* occurring as clumps of several trees thereby increasing the size of a single resource patch for cicadas, which results in either greater oviposition in the patch or greater survival of nymphs, or both. The river-edge plots in the Cuesta Angel study illustrate quite well such an effect. Such plots, although quite large, only contained one or two widely scattered legume trees and not clumps of such trees, and some did not contain legumes at all but were situated near such trees. The observed very low densities of cicada nymphal skins in these large segments of forest is due to an absence or scarcity of suitable root crowns for cicadas. The tree plots, on the other hand, although very small, are highly suitable for cicadas and therefore densities are high.

The pattern of cicada nymphal skins being associated with legume trees in tropical forests can have other explanations as well, ones not involving a presumed coevolved interaction of the sort suggested above. For example, selective logging of tropical forests may leave behind the relatively soft-wood legumes thereby increasing their relative abundance as a resource for insects such as cicadas. Thus the likelihood for an ovipositing cicada to discover a legume tree

increases greatly over a period of years, even though the root crowns and other cicada-related characteristics of other trees are equally suitable for cicada development.

Since all plots were located at or within the lower one-fourth of the ravine, the instances in which some species, such as *F. n.sp.* and *Carineta* sp. call primarily from the top of the ravine and not at the bottom suggests a behavioral response associated with mating requirements. Such species presumably emerge near the bottom of the ravine and fly up to the top for courtship. Such species may also emerge near the top as well although this was not determined in this study. The observed patterns of adult calling sites within the ravine are presumably related to the acoustical and thermoregulatory needs of each species.

SUMMARY

The genera and species of cicadas, their seasonal distributions, habits, and emergence sites were studied discontinuously over several years at the Cuesta Angel ravine, a rugged mountain tropical wet forest locality in the northern portion of the Central Cordillera of Costa Rica. Emphasis was placed on determining the distribution of cicadas down one steep forested side of this approximately 300-meter deep ravine and along a representative portion of its bottom (Rio Sarapiquí). Some evidence of seasonal fluctuations in abundance was obtained for the six species found here, and the greatest densities of nymphal skins of all species were found in small plots around individual legume trees. Densities in the large river-edge plots, containing many different kinds of trees, were relatively very low. The data are compared to similar data on cicadas from other regions of Costa Rica. Tropical cicada seasonality, interactions with Leguminosae, and possible mechanisms underlying population densities, are discussed.

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support. Dr. Dieter C. Wasshausen of the Smithsonian Institution provided identifications of the tree species discussed. Dr. Thomas E. Moore of The Museum of Zoology at The University of Michigan assisted with the identification of the cicadas, gave the author access to the UMMZ cicada collections and other information concerning cicadas, accompanied the author on one of the visits to the locality to record the calls of cicadas, and discussed cicada biology with the author. I thank Dr. Henk Wolda, who, in the capacity of a referee for this journal, made many helpful suggestions on the manuscript.

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No. 3-4

CONTENTS

Dedication: Robert E. Silberglied. <i>Frank M. Carpenter</i>	197
Sound Production by Courting Males of <i>Phidippus mystaceus</i> (Araneae: Salticidae). <i>G. B. Edwards</i>	199
Maternal Behavior and Alarm Response in the Eggplant Lace Bug, <i>Gargaphia solani</i> Heidemann (Tingidae: Heteroptera). <i>R. S. Kearns</i> and <i>R. T. Yamamoto</i>	215
Polymorphism and Division of Labor in the Dacetine Ant <i>Orectognathus versicolor</i> (Hymenoptera: Formicidae). <i>Norman F. Carlin</i>	231
Trail Communication of the Dacetine Ant <i>Orectognathus versicolor</i> (Hymenoptera: Formicidae). <i>Bert Hölldobler</i>	245
Francis Walker Types of, and New Synonymies for, North American <i>Hydropsyche</i> species (Trichoptera, Hydropsychidae). <i>Andrew P. Nimmo</i>	259
Territoriality, Nest Dispersion, and Community Structure in Ants. <i>Sally C. Levings</i> and <i>James F.A. Traniello</i>	265
The Effect of Flower Occupancy on the Foraging of Flower-Visiting Insects. <i>V. J. Tepedino</i> and <i>F. D. Parker</i>	321
Abdominal Trophallaxis in the Slave-Making Ant, <i>Harpagoxenus americanus</i> (Hymenoptera: Formicidae). <i>Robin J. Stuart</i>	331
New Name for the Extinct Genus <i>Mesagyrtes</i> Ponomarenko (Coleoptera: Silphidae S.L.). <i>Alfred F. Newton, Jr.</i>	335
Historical Development of Bee Foraging Patterns in Central New York State. <i>Howard S. Ginsberg</i>	337
Myrmecophilic Relationship of <i>Pella</i> (Coleoptera: Staphylinidae) to <i>Lasius fuliginosus</i> (Hymenoptera: Formicidae) <i>B. Hölldobler, M. Möglich, and U. Maschwitz</i>	347
Behavioral Origin of Tremulation, and Possible Stridulation, in Green Lacewings (Neuroptera: Chrysopidae). <i>Peter Duelli</i> and <i>James B. Johnson</i>	375
Arthropods Attracted to Luminous Fungi. <i>John Sivinski</i>	383
Index to Volume 88	391



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Robert Elliot Silberglied

This issue of *Psyche* is dedicated to the memory of Robert E. Silberglied, a victim of the Air Florida accident in Washington, D.C., on January 13, 1982.

Born in Brooklyn, N.Y., in 1946, Bob was already an enthusiastic naturalist and entomologist even in his school days. He graduated from Cornell University in 1967 and received his PhD from Harvard in 1973. He remained at Harvard until July of 1981, as Assistant Professor and later as Associate Professor in the Department of Biology, teaching mainly the courses in entomology that I had given for many years as his predecessor. He was also Assistant Curator and later Associate Curator in the Entomology Department of the Museum of Comparative Zoology. During the same period he was associated with the Smithsonian Tropical Research Institute, spending about half of each year in Panama or other parts of the American tropics. At the time of his death he was Staff Scientist (Research Entomologist) at the Institute.

Bob joined our society on his arrival in Cambridge in 1968 and for the next 14 years he was one of our most active and enthusiastic members. He served as vice-president and president, and was a member of the editorial board of *Psyche* for the past decade. At our fall and winter meetings, he could always be depended upon to relate some unusual collecting experience or to demonstrate with superb photographs and specimens some of the remarkable insects that he had collected in the tropics. He combined a warm and sympathetic personality with a brilliant and imaginative mind. In both respects he has left a lasting impression on our society and its members.

The Smithsonian Institution has established the *Robert E. Silberglied Memorial Fund* to support student research and training in tropical entomology. Those who wish to contribute a gift of any size may send it to: Robert E. Silberglied Memorial Fund, Accounting Office, Smithsonian Institution, L'Enfant 3500, Washington D.C. 20560.

Frank M. Carpenter, editor



ROBERT ELLIOT SILBERGLIE

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SOUND PRODUCTION BY COURTING MALES OF *PHIDIPPUS MYSTACEUS* (ARANEAE: SALTICIDAE)¹

BY G. B. EDWARDS²

The courtship rituals of male salticids generally are considered to be visually-oriented, despite the fact that a primarily tactile type of courtship has been demonstrated for 2 species of *Phidippus* (Edwards, 1975; Jackson, 1977). In addition, chemotactic cues probably assist a male in locating a female in most species of jumping spiders (Crane, 1949; Richman, 1977). I report here that males of *Phidippus mystaceus* (Hentz) produce sound by means of a palpal stridulatory mechanism as an integral part of their courtship. This is the first known case of a salticid producing sound with this type of mechanism; a similar stridulatory organ has been reported for lycosid spiders (Rovner, 1975).

Petrunkévitch (1926) reported that the salticid *Stridulattus stridulans* Petrunkévitch has a stridulatory organ (of type "d", chelicera-palpus; Legendre, 1963). However, he did not detect sound production. The only other records of a salticid producing sound were by Bristowe (1958), who reported that *Euophrys frontalis* (Walckenaer) made a "distinct sound as the tarsal claws (of the legs I of the male) hit the ground . . .," and by Bristowe and Locket (1926), who had reported earlier on the same species, but had implicated the legs II as the sound producers. In either case, it was not clear if the sound produced by *E. frontalis* was an integral part of the courtship or incidentally produced by the movement of the legs.

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²Florida State Collection of Arthropods, Division of Plant Industry, P. O. Box 1269, Gainesville, FL 32602.

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EXPERIMENTAL PROCEDURE

Four females and 2 males of *P. mystaceus* were reared to maturity from an eggsac containing 12 eggs.³ The spiders were housed separately in 9 x 1 cm plastic petri dishes; twice a week they were provided with water by moistening a wad of cotton within the dish and were fed larvae of the cabbage looper, *Trichoplusia ni* (Hübner).

Two different techniques were used for observing courtship. In one method, the male was placed directly into a female's petri dish, on the side opposite the female. In the other method, the male and female were placed 5–15 cm apart on a 30 x 10 cm section of a live-oak branch, in order to simulate natural conditions. Temperature ranged from 24–26°C for all sessions.

Six separate filming and/or recording sessions lasted 10–90 min. each. Films were made using a Beaulieu Super-8-mm movie camera and an Auricon Pro 600 16-mm movie camera. Sound recordings were made with a Sony TC-756-2 reel-to-reel tape recorder and a Turner S22D microphone. The audiospectrogram was produced on a Kay 7029A Sound Spectrograph.

RESULTS

Courtships were observed for one of the males (the second male was killed by the first female with which he was placed). Typically a male placed into the petri dish housing a female almost immediately begins palpating the female's draglines and her abandoned nests, continuing this palpal exploration until he detects the female visually.

If the female is not inside a nest when first seen by the male (usually from 3–6 cm), the male begins producing a soft, audible trill that is systematically repeated. By apparently engaging the substrate with enlarged setae (macrosetae, Fig. 1; similar to those observed on lycosids by Rovner, 1975), leverage is produced enabling a stridulatory mechanism on the palpus to be operated. This mechanism consists of a plectrum-like projection of the tibial apophysis which fits into a bowl-shaped area on the cymbium containing a complicated file system. The entire mechanism is located laterally (ectally); in lycosids it is located dorsally. Also, lycosids have the file on the

³Gravid female *P. mystaceus* collected by Robert Dye, 26 October 1975, 4 miles north of Texas state line at a rest stop on I-35 in Oklahoma, under a rock. Eggs were laid November, 1975.

tibia facing a cymbial plectrum, the reverse of the condition in *P. mystaceus*. The file system of *P. mystaceus* appears to consist of 2 types of adjacent file fields which blend into one another. Within the concavity is a fan-shaped file, while along the distal edge of the concavity is a linearly-arranged file similar to lycosid files. Neither file is as well-defined as the lycosid files. The individual ridges of *P. mystaceus*' files are rounded, whereas those of lycosids have distinct edges; however, in *P. mystaceus*, both types of file are overlaid with numerous short ridges of variable length (Fig. 2).

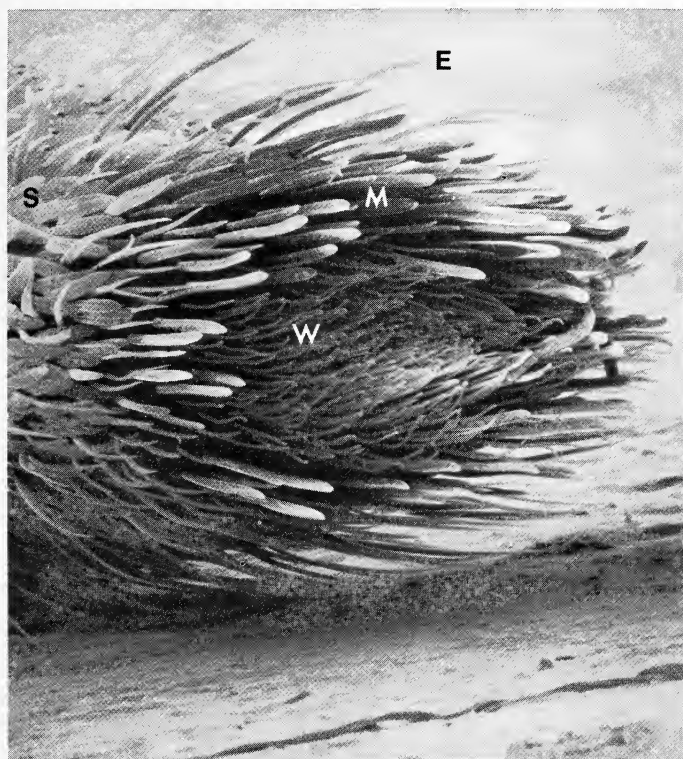


Fig. 1. Distal tip of palpus of male *P. mystaceus* showing ring of macrosetae (M) encircling whorled chemotactile setae (W). On extreme left are scale-like setae (S) which form part of a white and/or yellow spot which probably contributes to the overall visual stimulus of a courting male (100X). Note the greater number of macrosetae on the ectal edge (E); see text for explanation. The curved macrosetae (extreme right) at the tip of the cymbium first contact the substrate and may facilitate the backwards sliding motion of the palpi by reducing friction with the substrate.

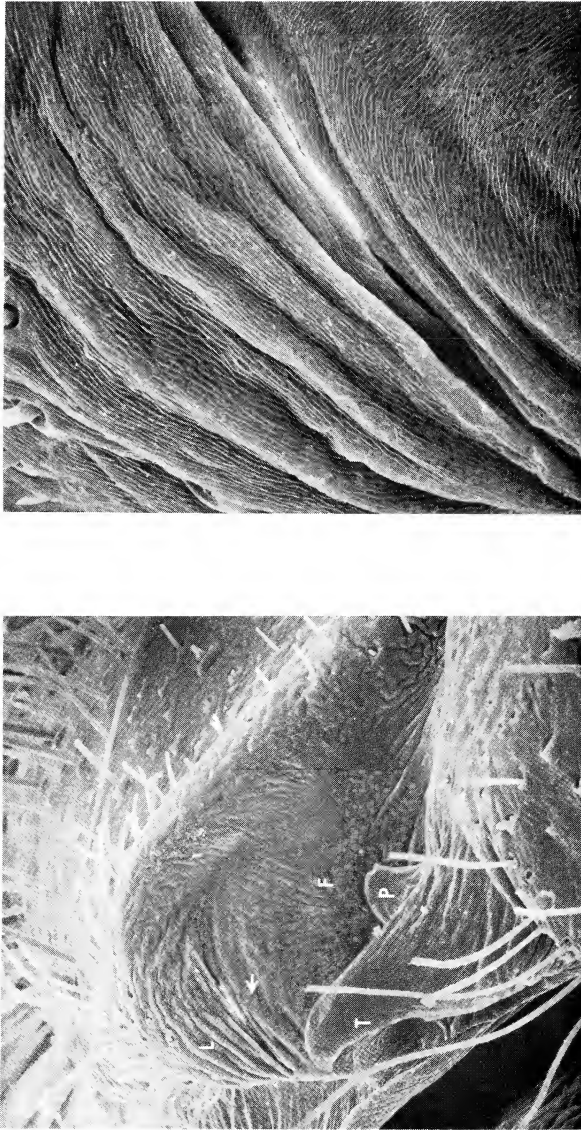


Fig. 2. Left: stridulatory area of male *P. mystaceus* on ectal edge of cymbium of left palpus, showing fan-shaped file (F), linear file (L), and pectrum (P), which is a branch of the tibial apophysis (T) (250X); Right: closeup of portion of file indicated by arrow (1300X).

For each sound sequence, both palpi become engaged nearly simultaneously by a backward movement in which the palpi appear to be dragged along the surface of the substrate for a distance of about 1 mm. Halfway through the backward movement, the cymbia are bent backward at an angle to the palpal tibiae (Fig. 3). At the end of the backward movement, the palpi remain stationary for a fraction of a second while the cymbia are rotated outward (left palpus clockwise, right palpus counter clockwise). The palpi are then returned to their most anterior position, apparently by lifting the palpi from the substrate and moving them forward. When the palpi are in their most anterior position, they are clearly off the substrate. A single cycle of palpal movement is approximately 0.8 second (5 frames at 6 frames per second).

Audiospectrograms indicate that 13–20 ($\bar{x} = 17$, $n = 8$) paired stridulations are made consecutively, separated by pauses subequal in timing to the sound sequences (Fig. 4). Alternation of stridulations and pauses occurs at the rate of 1.5 sound sequences per second (at approximately 25°C).

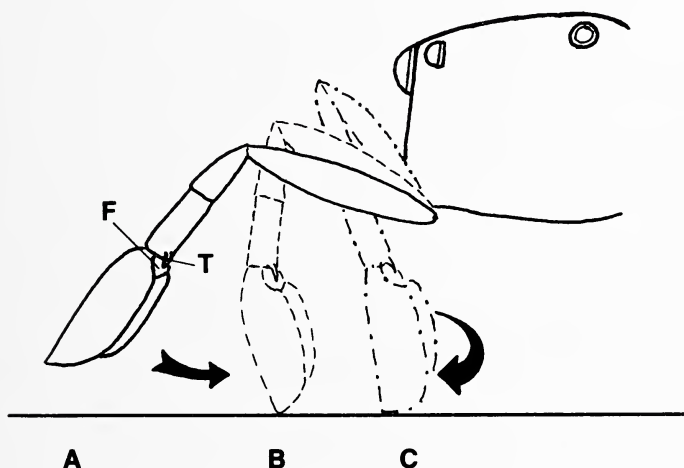


Fig. 3. Diagrammatic illustration of movement of left palpus (ectal view) by male *P. mystaceus* during stridulation. A. Anterior position. B. Backward movement, during which cymbium is bent backward, moving fan-shaped file across plectrum. C. Rotary movement, during which macrosetae are engaged in substrate and cymbium is rotated outward, moving linear file across plectrum. F = File cavity, T = Tibial apophysis.

Simultaneous with the initiation of sound production, the male extends his legs I forward, positioning them just above and parallel to the substrate, and spread approximately 40° apart. The tarsi and metatarsi are turned upward about 15° and occasionally flicked upward together. On 1 occasion, at a distance of about 1 cm from the female, the tarsi and metatarsi were flicked continuously for several seconds at approximately 2 flicks per second.

The male's approach usually is direct, without the zigzag movement (lateral stepping movement) characteristic of some other *Phidippus* species and many other salticids. Forward movement is slow and halting, the male often remaining in one spot for several minutes. Total courtship time is long compared to the rapid advance of the males of some *Phidippus* species, on 3 occasions lasting approximately 8 minutes before the female terminated the courtship by leaving the vicinity. These 3 longest courtships reached an advanced stage, wherein the male brought his legs I closer together, touched the female, and attempted to mount her; however, none of the 4 females allowed their male sibling to mate with them. Instead, each raised her legs I to repel him, and, if the male was persistent, lunged sharply forward with open fangs, struck downward with the legs I, and forced him backward; the female then left the vicinity.

On 2 occasions, the male performed a zigzag display; once prior to assuming his stridulatory stance, and once in the middle of courtship after several sequences of stridulation. In the first instance, the zigzag display was brief, lasting less than 30 seconds and consisting of 4 changes of direction, with a pause between each lateral move. In the second instance, during mid-courtship, 7 multiple zigzags occurred which included 1–3 changes of direction during each lateral stepping sequence; total elapsed time was about 3 minutes.

If the female is initially in and remains in a nest when the male is introduced into the petri dish, the male alternates palpation of the substrate with sequences of stridulation. Upon finding the nest sheltering the female, the male attempts to gain entrance by probing and pulling at the silk with his legs I, interspersing sequences of palpal vibration on the silk. (Note: other species of *Phidippus* known to use a tactile courtship vibrate their entire body). I could not determine the movement pattern of this palpal vibration (it

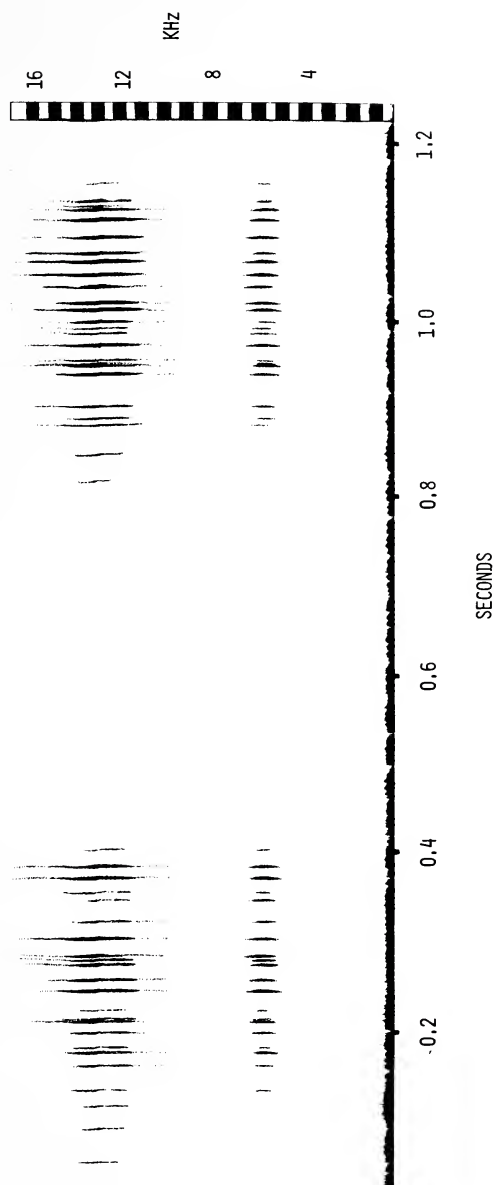


Fig. 4. Audiospectrogram of male *P. mystaceus* stridulating on live-oak bark at $25 \pm 1^\circ \text{C}$. Frequencies are much higher than previously reported for any other spider.

appeared to be similar in timing to stridulation), but the palpi were not in contact with the petri dish, and no audible sound was produced.

DISCUSSION

Known reproductive behavior of the males of species of *Phidippus* involves a male locating a female by visual or chemotactic means (Richman, in press), a visually-oriented courtship by the male consisting of a series of movements with the legs I and palpi (usually while advancing in a zigzag path), mounting of the female by the male, and mating. Typically the male is conspicuously marked with bright and/or contrasting colors both anteriorly and dorsally; the anterior patterns are displayed during courtship. Unlike most other species, both males and females of *P. mystaceus* are cryptically-colored gray spiders that live in trees (Specht and Dondale, 1960; Warren et al., 1967, as *P. incertus*; see Edwards, 1977, for nomenclatorial comments); males have mostly anteriorly-oriented modifications (Fig. 5). While anterior modifications are probably used by each sex to identify the other (especially the female recognizing the male as a conspecific and potential mate) from distances of a few centimeters, visual identification at longer distances might be severely handicapped by cryptic coloration. A mechanism which increases the chance of one sex locating the other could be selected for under these circumstances.

The role of acoustic or vibratory signals in the courtship of *P. mystaceus* may have co-evolved with cryptic coloration. As selection for cryptic coloration increased in association with exploitation of a new microhabitat (most *Phidippus* species live in the herb-shrub zone), the role of visual communication might have been in part supplanted by sound during courtship. The use of sound, whether airborne or substrate-borne, would have several advantages over conventional visual courtship, if the sound extended the male's communicatory distance from a few centimeters to over a meter (as it appears to do based on the audible component available to the human ear). Sound is transmitted well through solids, and considering that in this case sound is produced on the substrate, vibrations through this medium may be most important for female-to-male orientation (as Rovner, 1967, showed to be the case for wolf spiders). By orienting toward the male upon perception of the

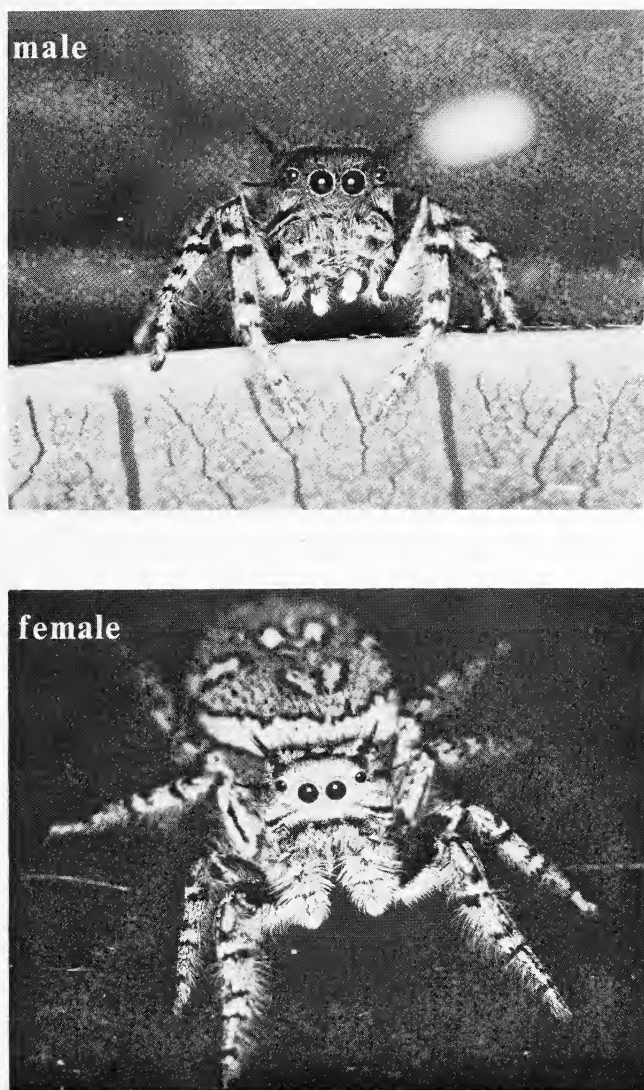


Fig. 5. Anterior views of male and female *P. mystaceus*, offspring of female collected in Oklahoma, which were used in this experiment.

sound, the female might sooner visually detect and be able to evaluate the male as a prospective mate, and thus sooner choose to wait for or flee from him. The advantages gained by the male by increasing his communicatory distance might be: 1) alerting a receptive female to his presence at a greater distance, possibly causing her to remain in the vicinity for a longer period of time (and perhaps inhibiting her predatory instincts), so that the male has a greater chance of finding and courting her; 2) based on many observations of *P. mystaceus* and of other *Phidippus* species, non-receptive females usually avoid advancing males; thus, by alerting a female to his presence at a greater distance, a male would reduce the chance of stimulating an aggressive response by a non-receptive female.

As evidence for these probable advantages, analysis of courtships showed that the male began courting a female from 2-4 times further away when unconfined (on the live-oak branch) than did other species of *Phidippus* when observed under unconfined experimental conditions (Edwards, 1975). At the greater distances, only sound was used initially by a *P. mystaceus* male upon sighting a female, indicating that this form of communication was important in alerting a female to his presence. Sound was also used alternately with palpal exploration of the silk when the male was in contact with the female's draglines in the petri dish, even though she was not visible. Under natural conditions, a male likely would often encounter a female's dragline prior to locating her; he could maximize his chances of mating by beginning to signal immediately, regardless of whether or not the female was visible to him.

COMPONENTS OF BEHAVIOR AND MORPHOLOGY

The male's initial palpal exploration of the female's silk draglines and nests has been noted for other salticids (Richman, 1977). The presence of a contact pheromone on the silk could indicate to a male that a female was, or had been, in the vicinity. Contact pheromones (Hegdekar and Dondale, 1969) and dragline following by males (Tietjen and Rovner, 1980) have been demonstrated for some lycosids, but have not yet been conclusively demonstrated for any salticid. Foelix (1970) demonstrated the presence of chemosensitive setae in certain araneid spiders and hypothesized that those setae were contact chemoreceptors. He showed that the suspected chemo-

sensitive setae in araneids were innervated and structured in essentially the same manner as pheromone receptors of insects. Hill (1977a, b) noted that the whorled setae on the tarsi and palpal cymbia of several species of *Phidippus* also resembled insect pheromone receptors; male *P. mystaceus* have the same type of setae on their palpal cymbia (Fig. 1).

The behavior in *P. mystaceus* of engaging the palpi against the substrate is probably derived from similar behavior among its relatives. Males of other species of *Phidippus* move their palpi up and down or back and forth during courtship. This behavior appears to pre-adapt them for engaging the substrate, since only a slight change in the amplitude and/or attitude of these movements would bring the palpi into contact with the substrate. The same movement occurs more intensely and rapidly when a male encounters silk made by a female, in association with presumed chemotactile exploration; it is likely that this is the evolutionary pathway of the development of the use of sound in *P. mystaceus*.

The shape and arrangement of the macrosetae at the tip of the cymbium are such that a downward, forward pressure would engage them with the substrate. By dragging the palpus backward, enough leverage apparently is produced to move the fan-shaped file across the relatively stationary plectrum; however, the backward movement and bend of the palpus also may be a prerequisite to positioning the macrosetae onto the substrate. Once the palpus is anchored onto the substrate, the cymbium is rotated laterally outward, then the palpi are returned to their starting position. The macrosetae are arranged in a circle around the tip of the cymbia in *P. mystaceus*, with more macrosetae on the ectal edge than on the ental edge, which enables the palpus to remain engaged with the substrate as it rotates outward. The structure involved in sound production by rotating is the linear file; the cymbium must be rotated sideways due to the lateral position of the file.

By simulating the direction of palpal movement with a model, it is apparent that the backward movement would cause the fan-shaped file to be drawn across the plectrum, while the rotary movement would bring the linear file into contact with the plectrum. The fan shape of the proximal file would accommodate the arc-shaped movement as the palpus is bent on the backward stroke; however, sound does not seem to be produced by the fan-shaped file. Only

one type of stridulation is produced, evidently from the linear file (see figure 4); the function of the fan-shaped file remains unclear. Although the files appear to be oriented so that they could be stroked from either direction, the timing of a complete palpal movement indicates that sound is produced only on the backstroke and not on the return stroke. The mechanics of stridulation by *P. mystaceus* are still incompletely understood, and need further study with more sophisticated filming techniques.

COMPARISONS TO OTHER STRIDULATORY MECHANISMS

The behavioral application of the palpi to the substrate by *P. mystaceus* differs from lycosids in that *P. mystaceus* moves the tips of the palpi while stridulating during each brief sound sequence, whereas the lycosids apparently remain attached in one place to the substrate for a prolonged sequence of sound production. The mechanics of sound production with the linear file are similar to those of the lycosids with respect to the palpus anchored by macrosetae and the similar file structure, but *P. mystaceus* differs from the lycosids in the location of the stridulatory organ, the type of movement needed to engage the file, and the reversed positions of the file and plectrum. Rovner (1975) proposed a new category of stridulatory organ (as an extension of the classification of Legendre, 1963), type "h" to accommodate those types of mechanisms in which the file and plectrum (scraper) were on adjacent surfaces of a joint within the same appendage. I propose a subdivision of Rovner's category, following Legendre's method of subdividing categories: type "h I" in which the file is on the more proximal segment (as in lycosids), and type "h II" in which the file is on the more distal segment (as in *P. mystaceus*).

The stridulatory mechanisms known in other spiders incorporate plectrum and file systems on opposing faces of the chelicerae and palpi, legs I and II, carapace and legs I, carapace and abdomen (Gertsch, 1979), or between palpal tibia and tarsus (Rovner, 1975). In each of these cases, either the plectrum is moved across a stationary file or both plectrum and file are moved together. The stridulatory mechanism of *P. mystaceus* differs from all of these in that the primary moving part is the file. Although the plectrum is passively moved in space during the movement of the palpus to

engage the substrate, the cymbium containing the files is actively moved against the plectrum on the tibia. When the palpus is fixed on the substrate with the macrosetae, again it is the cymbium that is moved against the stationary plectrum.

OTHER TYPES OF VIBRATORY SIGNALING

A third method of sound production in spiders, vibration (producing a "buzz" similar to that of a fly), has been demonstrated for the sparassid spider, *Heteropoda venatoria* (L.) (Rovner, 1980). In the same paper, low amplitude appendage oscillations resulting in a faint whirring sound were reported for *Lycosa rabida* Walckenaer. *Phidippus whitmani* Peckham and Peckham employs entire-body (?) vibration (lacking an audible component, but with a widely-spaced stance similar to *H. venatoria*) during its Type I visual courtship (Edwards, 1980). This is probably an adaptation to its microhabitat (mesophytic leaf litter), the same substrate used for vibratory signaling by many lycosids. I have noted another vibratory behavior that also seems similar to that of *H. venatoria* during the Type II tactile courtship of *Phidippus regius* C. L. Koch, while the male is contacting the nest of the female (Edwards, 1975). Subsequent laboratory observation showed a similar behavior for *P. whitmani*, although the timing of vibratory sequences was different from those of *P. regius*, probably a species-specific difference. Jackson (1977) reported a similar behavior for *P. johnsoni* (Peckham and Peckham) and suggested a similarity in some respects to the vibratory courtships of web-building spiders. I suspect that the vibratory courtships of *Phidippus* species, although not producing an audible component that I could detect, may be more like the courtship of *H. venatoria* than like web-builders, or perhaps all 3 groups produce vibrations in essentially the same way (i.e., "juddering" as in araneid males; Robinson and Robinson, 1980). It is curious that all known forms of non-tactile direct inter-individual communication not involving vision in salticids are acoustic or vibratory signals (despite the contention of Crane, 1949, and other authors, the use of airborne pheromones by salticids has never been proven). In the case of *P. mystaceus* and *P. whitmani*, both visual and vibratory signals are used simultaneously, although the 2 species produce vibrations in different ways.

CONCLUSION

The use of stridulation to produce sound by *P. mystaceus* appears to represent a third method of communication for salticids (a fourth method, if the tarsal percussion of *Euophrys frontalis* is a valid communicatory process). Despite the fact that females used for the present research failed to respond favorably to courtship by their sibling male, the behavioral and morphological evidence in the male of a functional role for sound production during courtship is substantial.⁴

SUMMARY

Males of *Phidippus mystaceus* have a stridulatory organ located on the tarsal and tibial segments of the palpi. This organ is employed by males in the potential or actual presence of adult females, and forms the most significant part of courtship by males. The mechanics of stridulation are somewhat similar to those of lycosids, and as with the lycosids, substrate vibrations may be the most important component of stridulation. Evolution of sound production by *P. mystaceus* is hypothesized to have occurred in conjunction with the evolution of cryptic coloration. Sound production is thought to extend the males' communicatory distance, compensating for fewer visual identification opportunities due to the spiders' cryptic coloration.

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⁴Two antepenultimate *P. mystaceus* were collected by G. B. Edwards, 28 July 1979, Ocala National Forest, Marion Co., Florida, beating young scrub live oaks, and reared to maturity (October, 1979). Although these specimens were collected and reared after the research on the Oklahoma specimens was completed, and the courtship was neither filmed nor recorded, a courtship and mating was observed for this pair. Courtship appeared in all respects to be identical to that of the Oklahoma male, including type of sound, stance, and the rapid upward flicking of the tarsi and metatarsi at less than 1 cm distance from the female. Mating occurred in the female's nest and lasted 87 minutes until the female left the nest. Upon separating, the male renewed courtship, initially showing a single lateral stepping sequence as in the Oklahoma male. The female avoided the male, and the pair was separated.

aid in filming (16-mm); Mr. Lloyd R. Davis, Jr., for obtaining the gravid *P. mystaceus* female for me; and Drs. Jerome S. Rovner, Jonathan Reiskind, Thomas J. Walker, and Robert L. Crocker for reviewing the manuscript.

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MATERNAL BEHAVIOR AND ALARM RESPONSE IN THE EGGPLANT LACE BUG, *GARGAPHIA SOLANI* HEIDEMANN (TINGIDAE: HETEROPTERA)¹

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INTRODUCTION

Maternal behavior in the eggplant lace bug, *Gargaphia solani* Heidemann (Tingidae: Heteroptera) was first reported by Fink (1915). He described the female's guarding of the eggs and shepherding of the nymphs from leaf to leaf. *G. solani* is found on the native horse nettle (*Solanum carolinense*) and on the introduced eggplant (*Solanum melongena*). Overwintering adults appear in late spring, and females lay eggs in circular masses on the underside of leaves. Fink reported that the number of eggs is greater than 100, oviposition lasts 4 to 5 days, and the incubation period is about 6 days. Maternal care persists through the development of the nymphs, and the life cycle is approximately 20 days. Females observed in this study usually laid less than 100 eggs over a period of 3 to 4 days (Kearns 1980).

Maternal behavior has been reported for a number of heteropterans (Melber and Schmidt 1977) and for two other species of the genus *Gargaphia*: *Gargaphia tiliae* (Weiss 1919, Torre-Bueno 1935, Sheeley and Yonke 1977) and *Gargaphia irridescentis* (Torre-Bueno 1942). These accounts give few details. The maternal behavior of *G. solani* has much in common with that exhibited by treehoppers (Membracidae: Homoptera) (Wood 1974, 1976a, 1976b, 1977 and Hinton 1977). The complex behavior patterns of membracids and of *G. solani* suggest that aggregations of these insects depend upon a

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pheromonal communication system which facilitates group movements. In the membracids, there is indirect evidence for aggregation pheromones (Hinton 1976, 1977). Alarm pheromones of membracids are released only when the body wall is ruptured, and this type of release has not been reported for any other insects. Pheromones causing alarm responses are known to be present in at least 3 membracid species. They are interspecific in action but have not been identified (Nault et al. 1974).

This study reports an examination of the movements of *G. solani* aggregations on host plants with particular emphasis on the female's behavior.

MATERIALS AND METHODS

MAINTENANCE OF INSECTS

G. solani was collected from horse nettle growing in or near Raleigh, N.C., and aggregations were maintained for more than a year on horse nettle or eggplant either in the laboratory on a 16:8 light:dark cycle or in a greenhouse. The movements of nymphs were studied after an aggregation consisting of nymphs and a female had been transferred to a small sprig of horse nettle having an unbranched stem with 5 or more leaves. A piece of leaf containing a group was pinned to the upper surface of the second or third leaf from the bottom of a horse nettle stem. In time, the aggregation moved off the leaf fragment and onto the fresh leaf.

FEEDING MOVEMENTS

Feeding movements were measured in light, darkness, and with a light placed below the aggregation. Groups chosen for these studies were nymphs in the third or fourth instars, with smaller numbers of the other instars present. For dark conditions, an aggregation on a horse nettle sprig was placed in a tightly covered metal can which had been sprayed inside with a dull-finish black paint. Directional lighting was provided by placing the sprig or plant within a darkened enclosure and positioning a light about 0.6 m from the bottom of the plant.

ALARM RESPONSE AND ALARM PHEROMONE

G. solani nymphs exhibited an alarm response after they were presented with a nymph, freshly squeezed and held by fine forceps,

Table 1. Elements of behavior of *G. solani* females when their broods were responding to alarm pheromone

Behavior	% of responses observed (1)
1. Female positioned slightly below exit axil	17
2. Female positioned at exit axil	50
3. Female positioned between axils	39
4. Female positioned at entrance axil	61
5. Female moved off leaf shortly after nymphs left	78*
6. Female followed nymphs onto new leaf	78*
7. Female returned to old leaf after group had moved	33
8. Female used at least one of the first four elements listed	89*

(1) 18 different trials

* Significant at the 95% confidence level (Binomial distribution. Table 2, partial sums, Eisenhart 1952. Confidence intervals, Table A-22, Natrella 1963.)

or a nymph pierced with a pin against a small disk of filter paper (after Nault et al. 1974). Blank disks of filter paper placed near an aggregation did not elicit an alarm response. Nymphs of *G. solani* were also collected and stored in a small container of chloroform. Several hundred were sufficient to provide a crude extract. Before the extract was tested for activity, the chloroform was allowed to evaporate from a small sample contained in a Pasteur pipette. The tip was then brought close to an aggregation, and the bulb was pressed gently to force the remaining volatile pheromone from the tip. As a control, a pipette with evaporating chloroform was also used. Chloroform vapors disturbed resting aggregations, causing individuals to move away from the pipette; but chloroform alone did not elicit a full alarm response with characteristic group movement to a new leaf. Alarm responses were studied under well-lighted conditions with and without the female present.

RECORDING OF DATA

Observations were written, tape recorded, or photographed. Direction of movement of aggregations on the host plant was recorded as up, down, or "up and down" (part of the group moved up, part moved down). Movement up *or* down was considered "directed"; movement both up and down, "undirected". The new

position of the group was recorded as 1, 2, 3, or 4 or more leaves above starting position. The designation "4 or more" included leaf no. 4 and several small leaves at the growing tip of the plant.

RESULTS

Egg masses of *G. solani* are deposited on the underside of leaves, and first instar larvae feed from the leaf surface between the eggs and then from the areas adjacent to the eggs. The larvae are usually in a compact circular formation while feeding, and the aggregation moves away from the oviposition site as leaf tissue is destroyed. Feeding sites become yellow or brown in color and also brittle. On a large eggplant leaf, nymphs may pass through several instars before consuming most of the leaf's soft tissue. On the relatively smaller horse nettle leaf, an aggregation consumes the edible portion of a leaf more quickly and then moves to another leaf.

MOVEMENTS TO NEW FEEDING SITES

Movements to new sites on the same leaf seemed to proceed gradually and with little intervention from the female. As individuals in the aggregation withdrew their stylets, they moved away from where they were feeding, bumping into adjacent nymphs. These bumped nymphs in turn withdrew their stylets and moved or milled about, bumping into other nymphs until the entire aggregation was activated. Movement from the feeding site to another feeding site on the same leaf then ensued. Movement to a new leaf usually occurred after 75% or more of the leaf was damaged and often lasted for about an hour. The parent female, also activated by the milling nymphs, usually moved slowly down the petiole while keeping close physical contact with the nymphs immediately behind her. If there was any break in contact, the nearest nymphs moved forward and touched the tips of the female's wings with their antennae, or the female turned around and touched her antennae to those of the nearest advancing nymphs. During one group movement, the female waited first at the axil of the new leaf and then on the underside of the petiole, as nymphs filed by her. This behavior was identical to that observed during alarm responses. On two occasions, the female seemed to initiate movement of the nymphs by forcing her way into the cluster of feeding nymphs; but this occurred only when the nymphs were in the earlier instars and were moving

Table 2. Direction of movement of *G. solani* aggregations on a host plant

Feeding Movements	<i>Female Present</i>		<i>Female Absent</i>	
	% of groups observed		% of groups observed	
	Upward movement	Directed movement	Upward movement	Directed movement
In light	82*	96* (1)	78	100* (2)
In darkness	89*	100* (2)	100*	100* (3)
Light source below aggregation	71	78 (2)	75	67 (3)
<i>Alarm Response</i>				
In light	90*	100* (4)	62	67 (5)

(1) 23 observations

(2) 9 observations

(3) 6 observations

(4) 19 observations

(5) 12 observations

* Significant at the 95% confidence level

from one surface of the leaf to the opposite surface. At no time was "herding" by the female observed as described by Fink (1915).

Movements to a new leaf were difficult to predict and lengthy to monitor. Because of time considerations, it was not feasible to make a statistical study of the female's total behavior pattern during these group movements. When a female was present, she led the group to a new leaf. In the absence of a female, the nymphs moved on their own. Females sometimes wandered about on adjacent leaves but usually returned to their aggregations.

ALARM RESPONSES

When an aggregation of the third through fifth instar nymphs of *G. solani* was alarmed with a squashed fifth instar nymph, the group responded quickly, usually within 10 seconds. The duration of the response was from 4 to 20 minutes. If the nymphs were on the top surface of the leaf they moved to the underside, and conversely. In either case, at least some of the nymphs moved quickly to the midrib and from there to the petiole of the leaf. At the exit axil, the nymphs moved up or down the stem; but they were more likely to move up the stem (Table 2, Female Present). During this activity, the female



Figure 1. Adult female of *G. solani* positioned at the exit axil during an alarm response.

moved quickly to the axil of the leaf and oriented herself a little to one side of the nymphs' path (Fig. 1). When she was in this position, the nymphs moved up the stem rather than down.

As more of the nymphs left the leaf, the female sometimes moved about the axil and positioned herself along the side of the stem as the nymphs moved past her. When she was in these positions, she seemed to have little physical contact with the nymphs which filed past her unless they happened to bump into her in passing. Part way through an alarm response, the female moved quickly up the stem, usually to the axil of the first leaf above the previously occupied leaf. Many of the nymphs had already reached this axil and had moved down the petiole onto the new leaf. A few nymphs often proceeded above this axil and continued up the plant before returning to the group. The female oriented herself at the axil of the new leaf (Fig. 2) and waited there as more nymphs arrived. After most of the nymphs had passed along the petiole, the female joined the aggregation on the new leaf.

There were always a few nymphs that remained behind or that failed to keep up with the bulk of the aggregation. These slower individuals wandered out onto other leaves but did not settle down until they found the group. Apparently the nymphs maintain locomotor activity unless they have sufficient physical or chemical contact with other nymphs. There were variations in the female's behavior (Table 1), but it was not obvious what environmental conditions might cause the female to include or change a particular element of her behavior. When an aggregation of first and/or second instars was alarmed, the group was likely to relocate on the same surface of the leaf rather than to move to the opposite surface or off the leaf.

Certain elements of the female's behavior were clearly recognizable and repeated more than once. These elements are recorded in Table 1 with the frequency of their occurrence in 18 different experimental responses to alarm pheromone. In 89% of the alarm responses, the female exhibited at least one of the first 4 elements



Figure 2. Adult female of *G. solani* positioned at the extrace axil during an alarm response.

listed. The fourth element, female positioned at the entrance axil (Figure 2), was repeated most frequently, although the element was not itself significant. There was more variation in the female's position on the stem at the beginning of the alarm response than at the end.

DIRECTION OF MOVEMENT

Aggregations with and without the female present were studied in order to determine the significance of the female's role in feeding movements or alarm responses. It was hypothesized that the female's presence would keep the aggregation together and inhibit random movements on the plant. The relocation of the group was studied in terms of the direction of movement on the plant (up, down, or in both directions) and the choice of a new leaf on which to feed. Movement was considered directed if a group moved in one direction or the other, but not in both. A table for a binomial distribution was used to evaluate significance at the 95% confidence level (Table 2, partial sums, Eisenhart 1952; Table A-22, confidence intervals, Natrella 1963). The results for upward and directed movements of aggregations, with and without the female present, are recorded in Table 2 as percentages of groups observed. Those results significant at the 95% confidence level are marked with an asterisk.

Feeding Movements

In light or in darkness, feeding movements with or without the female present were directed rather than random, and the group usually moved upward. When the source of light was 180° away from the usual direction, neither moving upward nor directed movement was significant; but the aggregations did not reverse their direction of movement and move toward the light. It is possible that the abnormal position of the light source acted as a conflicting stimulus which confused some of the aggregations.

A small field sample of horse nettle plants (13) showing damage from *G. solani* was examined for evidence of group movements. Eighty-five percent of the groups had moved upward on the plants from leaves containing the remains of egg masses. Moving up was significant at the 95% confidence level and closely matched the results obtained in the laboratory.

Alarm Response

The female's presence or absence made a significant difference when the aggregation was alarmed. When the female was present, 90% of the groups moved upward, and 10% moved downward; but none split and moved in both directions. When the female was absent, 67% of the groups moved either upward or downward; one-third of the groups split.

POSITION OF AGGREGATIONS FOLLOWING FEEDING MOVEMENTS OR ALARM RESPONSES

The results of experiments for both feeding and alarm movements were combined, and a comparison was made between female present and female absent.

Choice of Leaf

With a choice of 4 leaf positions above the one occupied by the aggregation, the probability of an aggregation's reassembling on any one of the leaves was 0.25. Using the binomial distribution (Eisenhart 1952), we compared the choice of leaf no. 1 with the choice of any other leaf (Table 3). Whether females were present or absent, the aggregations were more likely to move to leaf no. 1 than to any of the other leaves. If the aggregations split between leaves, the split usually included leaf no. 1. This behavioral pattern of the nymphs increased the likelihood that the group would remain together following movements on the host plant. When the female was present, the group was more likely to move as a unit to leave no. 1.

Choice of Single or Multiple Leaves

Movement to a single leaf was compared to movement to multiple leaves (Table 4). The probability associated with this choice was 0.5. When females were present, aggregations usually moved as a unit to a single leaf on the host plant but when females were absent, aggregations split up as often as they chose a single leaf.

WING FANNING BY THE FEMALE

Fink (1915) reported that on one occasion he saw an adult female *G. solani* chase a ladybeetle (*Hippodamia convergens* Guer.) away

Table 3. Choice of leaf position by *G. solani* aggregations following movements (1) on a host plant

	% of groups observed	
	<i>Female Present</i>	<i>Female Absent</i>
Leaf no. 1	56	36
Leaf no. 1 in combination with one or more leaves	17	36
Total positions including leaf no. 1	72* (2)	71* (3)

(1) Feeding movements and alarm responses combined

(2) 36 observations

(3) 14 observations

* Significant at the 95% confidence level

from an aggregation of feeding nymphs: the female "with outstretched, slightly raised wings suddenly darted toward the intruder, driving it from the leaf." In the laboratory, adult females of *G. solani* responded similarly (Fig. 3) to ladybeetles, anthocorids, ants, the tip of a brush, and a tomato pinworm caterpillar which was spinning a cocoon. Beamer (1930) and Wood (1976a, 1976b, 1977, and 1978) reported wing fanning in a total of 4 species of membracids. In each of these species, wing fanning was used by the adult female as a response to a predator (Beamer 1930; Wood 1976a, 1976b, 1977) or a threatening stimulus, such as a pencil used to prod the female (Wood 1978). Sheeley and Yonke (1977) observed wing fanning by the tingid *Corythucha bulbosa* when a jumping spider

Table 4. Choice of single or multiple leaves by *G. solani* aggregations following movements (1) on a host plant

	% of groups observed	
	<i>Female Present</i>	<i>Female Absent</i>
Choice		
Single leaf	81* (2)	50 (3)
Multiple leaves	19 (2)	50 (3)

(1) Feeding movements and alarm responses combined

(2) 36 observations

(3) 14 observations

* Significant at the 95% confidence level

approached, and they reported that the spider's response to touching the tingid suggested the presence of a defensive chemical.

Wing fanning in *G. solani* occurred not only in response to a predator, but also under other circumstances. It was often associated with alarm responses and was directed toward the nymphs as well as toward a possible predator. For 27 brooding females, 143 occurrences of fanning were recorded in 2 categories: deterring a predator (26%) and controlling the nymphs in one of several ways (74%).

Deterring Predators

The brooding female responded to predators quickly after she detected their presence. The relatively large coccinellids (*Hippodamia convergens*, *Olla abdominalis*) were detected more readily than smaller predators such as Pharaoh ants (*Monomorium pharaonis*) or the anthocorid, *Orius insidiosus*. Attacks by ants and anthocorids were observed with a dissecting microscope. Females



Figure 3. Adult female of *G. solani* fanning her wings.

and nymphs failed to respond when a single ant removed an egg or ate a newly hatched first instar nymph. Ants carried tiny nymphs away from the brood, and the release of alarm pheromone was apparently not detected. When two or more ants moved in front of a brooding female, she responded with wing fanning and moved her body over the egg mass. *Orius insidiosus* nymphs, which were about the size of second instar *G. solani* nymphs, attacked their victims by penetrating intersegmental membranes. *O. insidiosus* was not always detected by the brooding female or nymphs, perhaps because the site of penetration was often in the coxal area rather than on the abdomen. When an attack occurred in front of a brooding female, she responded by fanning her wings and prodding the anthocorid with her head. Anthocorids responded by remaining motionless for periods of up to 55 minutes in length.

An attendant female responded to a coccinellid by rushing at it, fanning her wings, and, occasionally, by prodding it with her head. In 5 experiments with the adult coccinellid *Hippodamia convergens*, first and second instar nymphs were killed each time. In 3 of those encounters, the adult female lace bug was successful in driving away the coccinellid, preventing further loss of nymphs. In 2 encounters with starved coccinellids, the female lace bug was not able to drive the attacker away. The remaining nymphs survived because they fled apparently in response to an alarm pheromone released by crushed nymphs. In 3 encounters with the coccinellid *Olla abdominalis*, the female lace bug chased the approaching beetle successfully (Fig. 4); however, the beetle did not attack any nymphs or show much interest in them.

Controlling Nymphs

Females used wing fanning in their interactions with the nymphs. On at least 6 occasions, the attendant female went ahead of the moving aggregation and waited on the new leaf for the nymphs to arrive. While waiting for the nymphs, the females fanned their wings repeatedly.

There were a number of instances in which wing fanning was used to quiet a restless aggregation or one which had recently dispersed to a new leaf. The adult female circled the group with rapid, jerky movements and stopped occasionally to fan her wings. For 2 different females and aggregations, the female backed up to the



Figure 4. Adult female of *G. solani* responding to coccinellid, *Olla abdominalis*.

nymphs and pointed the tip of her abdomen toward them as she fanned her wings. This behavior suggests that the fanning may be used to propel a pheromone toward the group. One female was observed to use wing fanning to prevent the movement of an aggregation. The female was oriented at the base of the leaf, headed toward the group of nymphs. When 2 nymphs left the group, moved down the mid-vein, and approached her, she fanned her wings. The nymphs' response was a retreat.

AGGREGATION

There is some indirect evidence for an aggregation pheromone or for the nymphs' need for physical contact with each other. Upon hatching, nymphs feed near the egg mass for a short period and then move away as an aggregation. Older nymphs wander away from their own aggregations and join others, stray fifth instars being particularly conspicuous when they join groups of first and second

instars. Following one experiment on the alarm response, 5 fifth instar nymphs from a second aggregation were released, one at a time, slightly above the leaf just vacated by the first aggregation. Four of the fifth instars moved directly up the stem and onto the newly occupied leaf, and the remaining nymph wandered about, first on higher leaves and then on the vacated leaf before moving to the occupied leaf. Other experiments showed that nymphs would reaggregate after they were separated by the experimenter. Need for physical contact might explain this adequately, but the presence of an aggregation pheromone should not be ruled out. Reaggregation is essential if the alarm response is to occur repeatedly.

FEMALE'S BEHAVIORAL MATURATION

Preliminary experiments (Kearns 1980) indicate that females undergo behavioral maturation from the time of oviposition through egg hatch and early development of the nymphs. Females at different stages of development were substituted for females which were attending aggregations of nymphs. Only those substitutes which had attended aggregations of their own behaved normally during an alarm response. When females which were still ovipositing were used as substitute mothers, they either avoided the alarmed nymphs or failed to interact with them.

CHLOROFORM EXTRACT

A chloroform extract of *G. solani* nymphs proved to be as effective in eliciting an alarm response as a fifth instar nymph squeezed with forceps or squashed on filter paper. Crushed adults also released the alarm pheromone, but the nymphal response was slower by a minute or less, to a crushed adult than to a crushed nymph. Preliminary attempts were made to test for alarm pheromones in 3 other tingids available locally: *Corythucha ciliata*, the sycamore lace bug; *Corythucha cydoniae*, the hawthorne lace bug; and *Corythucha marmorata*, the chrysanthemum lace bug. Nymphs of each species showed an alarm response to a crushed nymph of the same species. There were also cross responses between *G. solani* and each of the three species of *Corythucha*. Since not all three species of *Corythucha* overlap in time, it will be necessary to rear the insects in the laboratory or to make extracts of each for testing cross responses.

DISCUSSION

Gargaphia solani and some of the membracids (Wood 1974, 1976b) are unusual in having maternal care extend from the time of oviposition through the maturation period of the nymphs. This long brooding period appears to be an adaptation to environments in which predation is an important factor. The host plants of *G. solani* grow close to the ground, and ants appear to be the most numerous predators. Maternal care in this tingid may have evolved as a response to ants or to low-flying predators or to both. Sheeley and Yonke (1977) were unable to find predators for some of the 7 species of tingids studied, perhaps because the host plants of 6 species are trees rather than small annuals. *Gargaphia tiliae*, having maternal care, might be expected to live close to the ground, but it is a tree-dwelling species. Sheeley and Yonke found no natural enemies of this insect, but the predators could have included tiny anthocorid nymphs which escaped detection.

It seems worthwhile to compare *G. solani* with some of the membracid species since there are striking similarities, including wing fanning by the attendant female and the release of an alarm pheromone when the body wall is ruptured. If *G. solani* and the membracids represent examples of parallel evolution, they may be responding to similar environmental stresses.

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POLYMORPHISM AND DIVISION OF LABOR IN THE
DACETINE ANT *ORECTOGNATHUS VERSICOLOR*
(HYMENOPTERA: FORMICIDAE)*

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INTRODUCTION

The ants of the myrmicine tribe Dacetini exhibit a primary evolutionary trend from primitive epigaeic and subarboreal foragers to advanced cryptobiotic forms; in association with this trend are a number of secondary tendencies, including reduction in body size and mandible length, increasing specialization on collembolan prey, and loss of worker caste differentiation (Brown and Wilson 1959). The subarboreal and impressively long-mandibulate subtribe *Orectognathiti*, comprising the genera *Orectognathus* and *Arnoldidris*, occupies an intermediate position between the primitive polymorphic genus *Daceton* and the largely monomorphic higher subtribes *Epopostrumiti* and *Strumigeniti*. All but one of the twenty-nine known species of *Orectognathus* are monomorphic, the exception being *O. versicolor*, which possesses a distinctive major caste (Taylor 1977, 1979). Caste differentiation in this species is considered to have evolved secondarily, from the monomorphic generic stock (Brown and Wilson 1959).

The extreme polymorphism of *Daceton armigerum*, the only lower dacetine whose behavior has been studied, is put to work in an equally extreme division of labor (Wilson 1962). The minor workers are strictly limited to brood care tasks (in which they are aided by callows of larger castes), and to regurgitation with other adults. Small medias forage widely and actively, but larger medias and majors tend to rest in "way-stations" some distance from the nest. These large workers take prey away from returning smaller foragers, bringing it into the nest themselves, so that little prey is carried back by those that hunt for it. The species takes a broad variety of prey items; it has been suggested that the dietary specialization on collembolans seen in higher dacetines might account for their

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surrendering the polymorphism and polyethism of *Daceton* (Wilson 1971).

Orectognathus versicolor, as the sole polymorphic intermediate dacetine, is of special interest for polyethism analysis. The species is also an easy one to study, its slow-moving habits and small colony size making possible the recording of nearly every behavioral act performed by each individual worker. The minor workers possess the same long, slender mandibles, with pointed apical teeth, that their congeners bear. Majors, however, have massive, relatively short mandibles, with apical teeth thick, blunt and recessed; their large occipital lobes contain disproportionately developed mandible adductor muscles (figs. 1 and 2). In mandible allometry, at least, this species may be the most exaggeratedly polymorphic of all dacetines. The division of labor by which such morphologically divergent forms are utilized, particularly since the major caste is a secondary development, may shed light on the advantages of specialized castes in the context of dacetine evolution. To what use are the singular majors put? Does the polyethism of *O. versicolor* in any way resemble that of *Daceton*, or is it entirely independent? Has the return to polymorphism been accompanied by a return to the polyphagy of *Daceton*, or is *O. versicolor* a collembolan specialist, as the rest of its genus is thought to be (Brown 1953)? An opportunity to address these questions in the laboratory arose when Bert Hölldobler brought a live queenright colony of these ants from North Queensland, Australia; the results of observation of this colony are reported below.

MATERIALS AND METHODS

The *O. versicolor* colony was settled in a glass test tube (2 cm in diameter), with water trapped at its end behind a tight cotton plug. The tube was placed in a plaster-floored clear plastic container (18 cm by 12 cm by 6 cm), and a dissecting microscope was set over it on a moveable mount to permit viewing of ants both inside the nest tube and out on the container floor. A total of 45 hours of observation were made over a period of five weeks, during which 7,891 separate behavioral acts were recorded. Estimation of the completeness of caste behavior repertoires was made by fitting the data to a lognormal Poisson distribution, following the method of Fagen and Goldman (1977). The ants were offered various food



Figure 1: An *Orectognathus versicolor* colony. The queen is at the left; to her right are two major workers—note their mandibles and head size and shape. To their right are another major (top), minor (middle) and media (bottom) workers.

items; to examine their defensive behavior, small *Solenopsis invicta* workers were introduced into their container.

The two morphological castes were easily distinguished on the basis of mandible thickness. In order to record division of labor among individuals of different sizes, yet similar proportions—so critical in weakly allometric species such as *Daceton*—the minor workers were arbitrarily divided into small and medium size classes, also distinguishable by eye. For convenience, these subcastes will be referred to as “minors” and “medias”, as in Wilson 1978. By-eye assignment of caste to preserved specimens, subsequently measured, produced the following definitions of size classes and castes: minors, head width less than 1.12 mm; medias, head width between 1.13 and 1.64 mm; majors, head width greater than 1.65 mm. After some initial die-off, the colony contained fifty-two adults for the duration of the study: one queen, thirty minors, fifteen medias and six majors.

RESULTS

O. versicolor is in fact polyphagous. Live flightless *Drosophila* were readily accepted, and young were successfully raised on this diet. The ants also accepted *Drosophila* larvae, and, not surprisingly, collembolans. (Alternative foods were not offered simultaneously to test preferences; however, most collembolan specialist species would not touch other prey even if starving.) The same colony had been fed mealworm and cockroach fragments, various diptera and honey-water in Australia (B. Hölldobler, pers. comm.).

The ethogram or behavioral catalogue of workers and queen is presented in table 1, which gives both numbers of individual acts performed and the relative frequencies of acts in the total repertory of each caste. The colony repertory consisted of twenty-seven categories of behavior. (Worker regurgitation with the queen was added as a twenty-eighth because it was seen twice during preliminary observations, though never during the study.) The observed minor and media repertories both contained twenty-seven behavior categories; the observed major repertory contained twenty-four. Using the Fagen-Goldman statistical method, the estimated total repertory size for minors—the observed repertory plus an estimate of the number of categories not observed—was calculated to be twenty-nine, with a 95% confidence interval of (27,32) acts. The

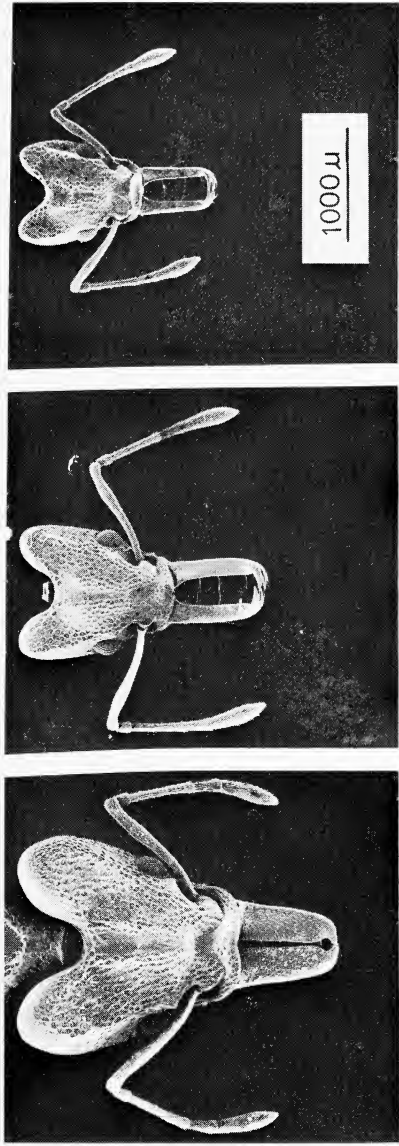


Figure 2: Heads of the worker castes of *O. versicolor*. Left, major; middle, media; right, minor.

Table 1: Ethogram of *Orectognathus versicolor*. The values given are numbers of individual acts performed by members of each caste. In parentheses are given relative frequencies of performance of each act in the total repertoire of the caste.

	Minor	Media	Major	Queen
Self-groom	1370 (.3481)	845 (.2996)	462 (.4306)	45 (.7258)
Allogroom minor	437 (.1110)	93 (.0330)	18 (.0168)	1 (.0161)
Allogroom media	144 (.0366)	224 (.0794)	16 (.0149)	0
Allogroom major	100 (.0254)	52 (.0184)	15 (.0140)	0
Allogroom queen	27 (.0069)	20 (.0071)	8 (.0075)	/
Regurgitation				
with minor	48 (.0122)	15 (.0053)	3 (.0028)	2 (.0323)
with media	10 (.0025)	21 (.0074)	7 (.0065)	0
with major	13 (.0033)	2 (.0007)	2 (.0019)	0
with queen	0	0	0	/
Carry or manipu-				
late egg	4 (.0010)	2 (.0007)	1 (.0009)	0
Lick egg	18 (.0046)	5 (.0018)	1 (.0009)	1 (.0161)
Carry or manipu-				
late larva	53 (.0135)	37 (.0131)	2 (.0019)	0
Lick larva	602 (.1529)	520 (.1844)	155 (.1445)	9 (.1425)
Regurgitate with				
larva	4 (.0010)	11 (.0039)	2 (.0019)	0
Feed larva solids	19 (.0048)	20 (.0071)	0	0
Carry or manipu-				
late pupa	7 (.0018)	9 (.0032)	6 (.0056)	0
Lick pupa	54 (.0137)	63 (.0223)	18 (.0168)	0
Forage	364 (.0925)	356 (.1262)	126 (.1174)	0
Capture prey	19 (.0048)	26 (.0092)	2 (.0019)	0
Return prey to				
nest	19 (.0048)	6 (.0021)	0	0
Process prey	45 (.0114)	25 (.0089)	4 (.0037)	0
Eat prey	132 (.0335)	109 (.0387)	19 (.0177)	2 (.0323)
Guard	313 (.0795)	280 (.0993)	186 (.1733)	0
Manipulate nest				
material	67 (.0170)	13 (.0046)	2 (.0019)	1 (.0161)
Lick tube wall	27 (.0069)	26 (.0092)	12 (.0112)	1 (.0161)
Remove refuse				
(in tube)	9 (.0023)	1 (.0004)	0	0
Remove refuse				
(out of tube)	12 (.0030)	19 (.0067)	4 (.0037)	0
Carry dead ant	19 (.0048)	20 (.0071)	2 (.0019)	0
Total # acts	3936 (1.0)	2820 (1.0)	1073 (1.0)	62 (1.0)
# categories	27	27	24	8
# individuals	30	15	6	1

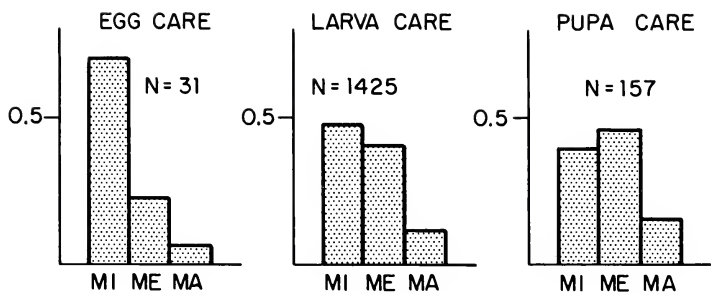
estimated total repertory size for medias was twenty-eight, the 95% confidence interval (27,33); for majors, twenty-seven, with a confidence interval of (24,37).

Minor and media workers engaged in the same tasks with essentially similar frequencies, while majors, with a smaller repertory, also performed certain acts with quite different frequencies. Self-grooming was the commonest act in all castes. Allogrooming and regurgitation occurred freely among all castes, with a tendency among minors and medias to interact with their own class. After self-grooming, brood care and foraging were the most frequently performed acts in the minor and media repertories. An ant was scored as "foraging" any time it left the nest tube - an act that does not necessarily signify hunting for food. Though majors did "forage" by this definition, they captured almost no prey and returned none to the nest. "Processing", in which workers tore at, dismembered and occasionally stung prey that had been brought inside the tube, was rarely performed by majors, despite the seeming usefulness of their heavy mandibles for such a task.

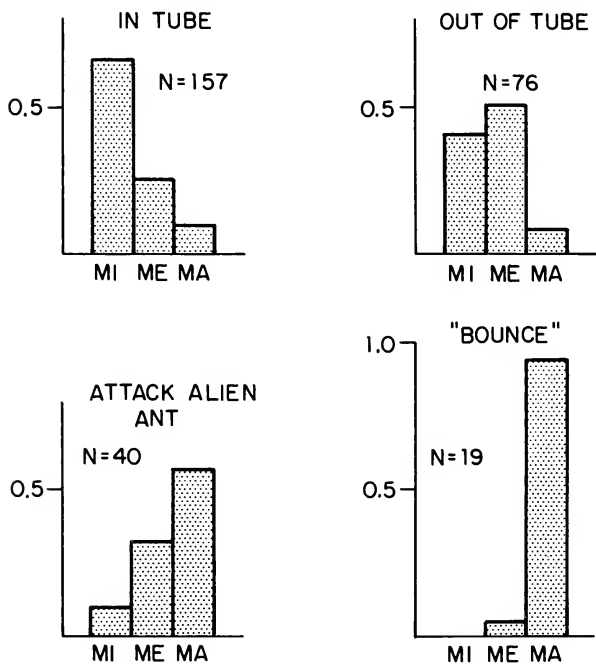
The province of the majors was "guarding": walking to the tube mouth and facing outward without setting foot on the container floor; after self-grooming, it was their most frequent act. A guarding ant might station itself at the opening for less than a minute or up to half an hour. That this is in fact a defensive behavior will be shown below. Minors and medias also guarded in large numbers, but less frequently than they foraged or attended brood.

Nest maintenance was undertaken almost exclusively by the small size classes. Carrying refuse down the tube, to be dropped inside or just outside the entrance, was defined as "in-tube refuse removal", while carrying trash out to corner refuse piles on the container floor (to which dead ants were also brought) was defined as "out-of-tube refuse removal." "Manipulation of nest material", that is, of the fibers of the cotton plug, may not be an actual maintenance behavior used in natural colony sites (under stones, in rotting wood); similarly, ants may lick the tube wall only to drink condensation on the glass, and not exhibit any such behavior in the wild.

The division of labor among minor and media size classes, and the role of the major caste, were better elucidated by constructing polyethism curves, depicting the percent contributions of each caste to the total colony performance of behaviors (figs. 3 and 4). For simplicity, certain behavioral categories from the ethogram were



NEST MAINTENANCE



combined, so that the polyethism curves indicated represent groups of tasks. There was a tendency to divide those tasks performed primarily by small workers among the size classes on the basis of size of objects handled and task location (fig. 3). Minors performed most in-nest maintenance; medias performed somewhat more out-of-nest maintenance than did minors. Minors contributed most to egg care. While both size classes attended larvae and pupae, minors contributed less to larva care than to egg care, still less to pupa care, medias compensating by putting more effort into care of larger brood.

On the introduction of *Solenopsis* workers, the function of the guarding majors became apparent. As an alien ant approached, they spread their mandibles about 120° apart. When the tip of the invader's head was within a major's gape, the mandibles snapped shut, pinching the invader's extremity with sufficient force to shoot it away like a squirted watermelon seed. This very effective defensive behavior, which was termed "bouncing", kept nearly all alien ants from gaining entrance to the nest. Only majors, with their large mandibles and powerful adductor muscles, are equipped to do this properly (fig. 3). Major bouncers, guarding the tube mouth, could propel invaders backward for up to 8 or 9 cm; a single large media was able to bounce an invader, but not for very far. The blunt apical teeth of majors pinched but did not penetrate—invaders were not injured at all, just repelled. Ants of all castes struck at invaders that managed to get past the bouncers, majors contributing most to these attacks (fig. 3). They did not attempt to bounce a successful invader, but instead grabbed it in their mandibles and dragged it out, unharmed, after which they resumed the guarding position.

Minor and media workers foraged in nearly equal numbers, but did not participate equally in predatory behavior. More prey was

Figure 3: Polyethism curves of nest-centered activities, showing the percent contribution of workers of each caste to the total colony performance of given tasks. MI = Minor worker; ME = media; MA = Major. Some tasks are composites of several behavior categories in the ethogram (table 1): Egg care = carry or manipulate egg + lick egg; larva care = carry or manipulate larva + lick larva + regurgitate with larva + feed larva solid food; pupa care = carry or manipulate pupa + lick pupa. In-tube nest maintenance = manipulate nest material + lick tube wall + remove refuse (in tube); out-of-tube maintenance = remove refuse (out of tube) + carry dead ant. Attacking alien ants and "bouncing" described in the text.

captured by medias, while most was returned to the nest by minors (fig. 4); minors also contributed most to processing, an in-nest activity. Medias brought back only about one-fifth of the prey they caught. It is possible that minors play a role similar to that of majors in *Daceton*, bringing in food captured by foragers of another caste, not themselves hunting as actively. However, minors were never observed to take prey away from medias. They simply retrieved prey that medias had dropped, a rather slipshod method of transferring

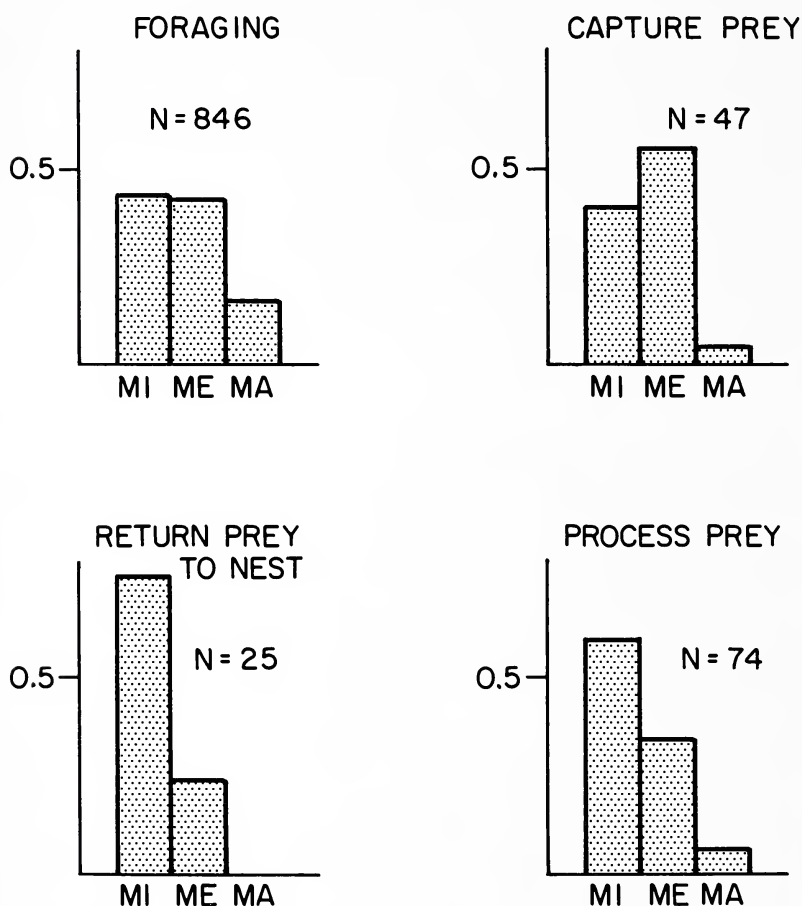


Figure 4: Polyethism curves of predatory behavior. Behavior categories are the same as in the ethogram (table 1).

food. Alternatively, the medias may have been killing flies as trespassers approaching the nest too closely, rather than as prey, whereupon minor foragers picked up the remains. Majors could not leave their post at the entrance to engage in defense of the nest vicinity without exposing the opening to invaders. Besides, the bouncing strategy would be less effective in the open; it requires an invader to walk directly into the defender's mandibles.

Callow workers being easily recognizable by their lighter body color, the repertoires of age groups within castes were examined for age polyethism. Callows exhibited fewer categories of behavior than older adults. As in *Daceton* and many other ant species (Wilson 1971) they tended to concentrate on safe, in-nest tasks. Callow majors were notably more involved in brood care than older majors.

As Brown (1957) had reported the genus to be nocturnal, observations were taken both during the day and, under red light, at night. Most foraging did indeed occur at night, but the ants engaged in a greater total number of acts, in more behavior categories, during the day, due to a diurnal rise in brood care and in-nest maintenance activity. This result suggests that more complete behavioral repertoires can be compiled in the laboratory by studying ants during their periods of "inactivity", when they are not investing so much of their effort in foraging.

DISCUSSION

Polymorphic workers of *Orectognathus versicolor* exhibit, all in all, a fairly elementary division of labor: Minor and media repertoires are predictably similar, while majors constitute a distinct caste on behavioral as well as morphological grounds. The minor size class contributes most to in- and near-nest activity, including prey retrieval; the medias have a somewhat greater tendency to perform out-of-nest tasks and care for large brood; and the majors defend.

Even if the medias are capturing prey and dropping it for minors to bring in, the resemblance to the polyethism pattern of *Daceton* is convergent at most. *Daceton* majors, not minors, return prey to the nest; *Orectognathus* majors are bouncers. *Daceton* minors are restricted to brood care, while medias perform in-nest processing and refuse disposal (Wilson 1962); *Orectognathus* minors attend all these tasks. The polyethism of *O. versicolor* is entirely unrelated to that of *Daceton*, having apparently arisen de novo along with its secondary polymorphism.

O. versicolor has also returned to polyphagy along with polymorphism, consistent with the general correlation seen in its tribe—the only higher dacetine to return secondarily to polymorphism, *Strumigenys loriae*, is also polyphagous (Brown and Wilson 1959). The degree of dietary specialization in the genus *Orectognathus* as a whole may have been overestimated: A colony of the monomorphic species *O. clarki*, collected by Hölldobler in New South Wales, Australia, was maintained at a subsistence level on a diet of cockroach and mealworm fragments and honey-water (Hölldobler, pers. comm.). However, this colony did not thrive, while the *O. versicolor* colony on the same diet flourished, raising many new workers and even males. Clearly *O. versicolor* does take non-collembolan prey more readily; what is not clear is the causality behind this correlation. The polyethism of *Daceton*, at least, is associated with predatory behavior. I had speculated that the *O. versicolor* majors might serve as “arthropod millers”, analogous to the seed-miller majors of *Solenopsis geminata* (Wilson 1978), their heavy mandibles used in processing a variety of prey with hard exoskeletons. Instead, they proved to be soldiers; perhaps in defending so efficiently, they somehow free smaller workers to forage for different prey items, which might require wandering further from the nest vicinity than would foraging for abundant collembolans. But this reasoning is vague at best and requires further investigation.

It is the major caste and its role that make this species noteworthy, among dacetines and among ants in general. “Bouncing” is a new kind of nest defense strategy, ideally suited for repelling enemies in a species whose modified mandibles, designed for impaling soft-bodied prey, are of no use in fighting. Minors and medias can be seriously injured, in attacking invaders they are unable to harm. Bouncing minimizes contact between defenders and invaders, expelling the latter without a fight. Presumably, large workers of the monomorphic species ancestral to *O. versicolor*, modifying slightly the prey-capturing strike to pinch an extremity rather than pierce, found themselves able to shoot enemies away for short distances. This defense was so advantageous that heavier mandibles with blunt, pinching teeth were strongly selected for, along with guarding behavior, eventually producing the modern majors. Generally, major castes in ants serve as soldiers. In a few species, they specialize in physically blocking the nest opening with their large heads

(certain *Camponotus* species, Wilson 1971; *Zacryptocerus texanus*, Creighton and Gregg 1954). In *Zacryptocerus varians*, which also has modified mandibles useless for fighting, majors use their saucer-shaped heads to actively "bulldoze" invaders out (Wilson 1976). Major bouncers of *O. versicolor* are unique in using their mandibles to expel invaders without injury.

To produce a caste so specialized for this form of defense, colonies must be under considerable pressure from ant species approximately the same size as *Solenopsis* (it would be hard to shoot a larger ant). When bouncing fails, majors do attack in a more conventional manner, as is seen in their response to successful invaders. (Bouncing might accidentally shoot these further into the nest.) It has recently been shown (Hölldobler 1982) that majors also respond to alarm-recruitment pheromones.

Other dacetines, including *O. clarki*, the monomorphic species most closely related to *O. versicolor*, often post "sentinels" at nest entrances (Brown 1953; he also observed occasional "retrosalience", an ant striking at a hard surface and shooting itself backward—the same motor act as bouncing, but apparently accidental). The *O. clarki* colony, when subjected to size class polyethism analysis, revealed a weak division of labor very similar to that of *O. versicolor* minors and medias. It is easy to conceive of these size classes as the "primitive caste" (Wilson 1980) typifying the monomorphic ancestor of both species, from which increasing defensive specialization turned the sentinels still seen in the former into the bouncers of the latter.

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TRAIL COMMUNICATION IN THE DACETINE ANT
ORECTOGNATHUS VERSICOLOR
(HYMENOPTERA: FORMICIDAE)*

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Although division of labor within two dacetine species has been studied at length (Wilson 1962; Carlin 1982), very little has hitherto been reported on social communication in the Dacetini, a myrmicine tribe of nearly 200 known species (Brown and Wilson 1959; Wilson 1962). Foraging habits have also been studied in several species (for review see Brown and Wilson 1959; Wilson 1962). As now known, the dacetines seem to be individual foragers; recruitment to food sources and cooperation during retrieval of prey have not been observed. It is therefore of some interest that we have recently discovered trail laying and trail following in the dacetine species *Orectognathus versicolor*. Experiments in the laboratory further indicate that trail communication may play an especially important role during nest emigrations.

Material and Methods:

A queenright colony of *O. versicolor* was collected from rotting wood near Eungella, North Queensland (Australia) and housed in a glass tube (ϕ 1 cm), with water trapped at its bottom behind a cotton plug. The nest tube was laced into an arena (45×30 cm) in which small pieces of cockroaches (*Nauphoeta cinerea*), chopped meal worms (*Tenebrio molitor*), several species of small flies and honey water were provided as food. The colony developed very well under these conditions, and when the experiments began (4 weeks after collection) it contained one queen, 80 workers (42 minors, 27 medias, 11 majors (see Carlin, 1982)), 14 freshly eclosed males, and brood of all stages.

For histological investigations live specimens were fixed in Carnoy (Romeis 1948), embedded in methyl-methacrylate and sectioned 8μ thick with a Jung Tetrander I microtome (Rathmayer 1962). The

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staining was Azan (Heidenhain). The SEM pictures were taken with an AMR 1000 A scanning electron microscope.

Additional methodological details will be given with the description of the individual experiments.

Results:

As demonstrated by Carlin (1982) most of the foraging in *O. versicolor* is conducted by the minor and medium worker castes; the majors function primarily or entirely as a defense caste, for which they have unique modifications in the form of the mandibles. Although workers of *O. versicolor* seem to forage individually, our observations in the laboratory indicate that some sort of social facilitation might be involved in stimulating foraging activity in the colony.

Often not more than 1-3 workers roamed the foraging arena. But when suddenly 30-50 flightless *Drosophila* flies were released into the arena, and the first one or two foragers had returned with captured prey to the nest, the number of workers leaving the nest tube and venturing into the foraging arena increased markedly. We did not, however, observe the foragers performing any motor display inside the nest, which might have stimulated the nestmates,

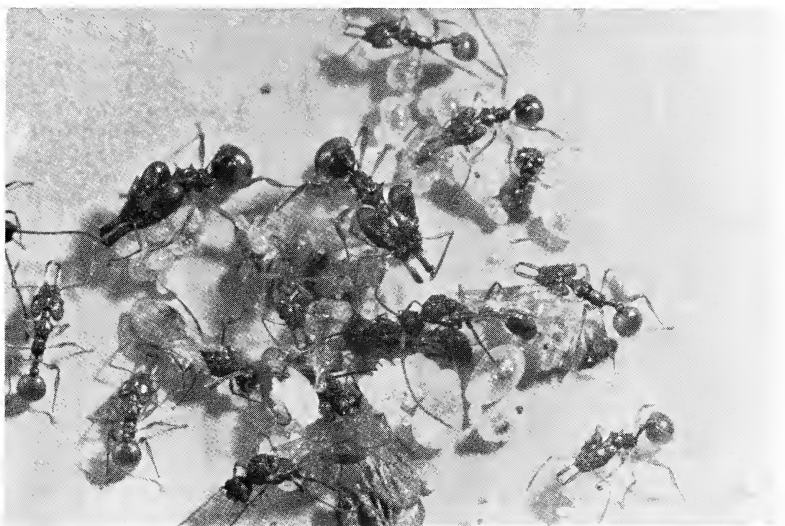


Fig. 1. Part of the colony of *Orectognathus versicolor*, the three worker castes (minors, medias, majors), males, and different developmental stages.

nor did it appear that workers leaving the nest followed chemical trails.

On the other hand, trail following was very obvious when the colony or fragments of the colony were forced to move to a new nest site. For example, when we shook the colony out of the nest tube into the arena, which had been provided with a new papered floor before each experiment, the "homeless" colony soon gathered at one spot, where it was closely guarded by members of the major worker caste (Fig. 1). After varying intervals (sometimes lasting more than one hour), some of the minors and medias began exploring the arena, and eventually they discovered a nest tube that had been provided at the edge of the arena (usually 30–35 cm away from the displaced colony). After exploring the nest tube, some of the ants returned to the colony, and after a while they often moved again to the nest tube to continue to explore it thoroughly.

Usually this procedure was repeated several times, before the first signs of a colony movement could be observed. It occurred when several additional minors and medias departed from the colony and traveled directly to the new nest. Their straight orientation and the fact that during running they kept the tips of their antennae close to the ground, suggested that these ants were following a chemical trail. Soon afterwards the traffic between the "homeless" colony and the newly discovered nest tube increased leading finally to a full-scale colony emigration.

All three worker castes were involved in transporting brood, callow workers, and males to the new nest, although the minors handled eggs and small larvae preferentially while the medias and majors concentrated on large larvae, pupae and adults (Fig. 2). Usually the queen moved during the early phase of the colony movement and always traveled on her own. On the other hand, the males were always carried by the workers (Fig. 2), usually not before most of the brood had already been moved. Only once did we see a fully pigmented worker being carried by a nestmate. The transported individual was grasped dorsally at the head and lifted upwards with gaster tip pointing forwards; it had the appendages folded in the pupal position. All ants traveled along a relatively narrow route between colony and new nest site. This strongly suggested that *O. versicolor* employs chemical trail communication during the process of colony migration. The following experiments

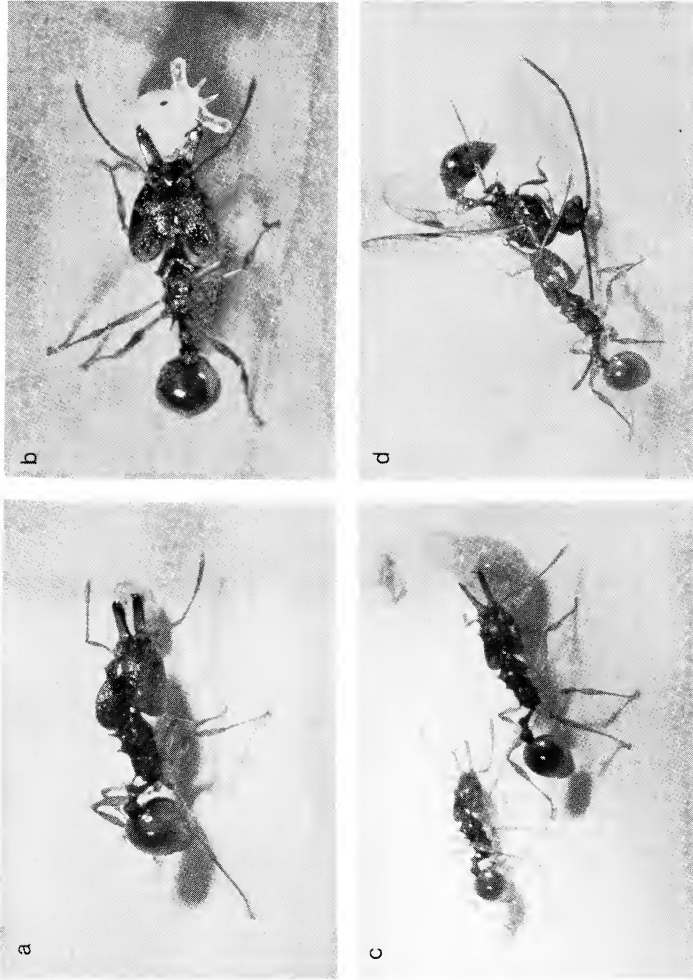


Fig. 2. Colony emigration in *Orectognathus versicolor*. (a) major transporting larva; (b) major transporting larva; (c) media transporting larva, accompanied by a minor; (d) media transporting male.

were designed to localize the anatomical source of a possible trail pheromone in *O. versicolor*.

Close-up cinematography and photography revealed that many *Orectognathus* workers, when moving back and forth between the displaced colony and the nest tube, touched their abdominal tips intermittently to the ground, presumably depositing droplets of trail pheromone. Three major exocrine glands open at or near the abdominal tip of *O. versicolor* workers: the poison gland and Dufour's gland, both of normal size, and a relatively large pygidial gland, which opens between the 6th and 7th abdominal tergites (Fig. 3).

Most myrmicine ants have a more or less well developed pygidial gland (Hölldobler et al. 1976, Hölldobler and Engel 1978; Kugler 1978), but in *O. versicolor* this gland is more complex than usually found in Myrmicinae. It more closely resembles the pygidial gland of some ponerine species, for example *Pachycondyla laevigata*, in which it serves as the source of a trail pheromone. The paired reservoir sacs (invaginations of the intersegmental membrane between the 6th and 7th tergites) are filled with a clear, lightly brownish liquid. Several ducts lead from paired clusters of glandular cells into the reservoir, penetrating the intersegmental membrane (Fig. 4). The cuticle of the 7th tergite has a grooved structure (Fig. 5), underneath of which is a large glandular epithelium (Fig. 4). *Orectognathus versicolor* workers, when engaged in trail laying behavior, usually hold their gaster in an almost vertical position. This brings the opening of the pygidial gland very close to the floor so that part of the grooved structure on the 7th tergite can be easily put in contact with the surface of the ground.

In the next series of experiments we tested the trail following response of *O. versicolor* to artificial trails drawn with glandular secretions of the poison gland, Dufour's gland and pygidial gland. The glands were dissected out of freshly killed workers and for each trail test one gland of a kind was crushed on the tip of a hardwood applicator stick and smeared once along a 20-cm-long pencil line. The trails were made to originate either from the entrance of the nest tube or from the periphery of the clustered colony, which had previously been shaken out of their nest tube into the test arena. As a control a second trail was offered simultaneously which was derived either from a droplet of water or from one of the other

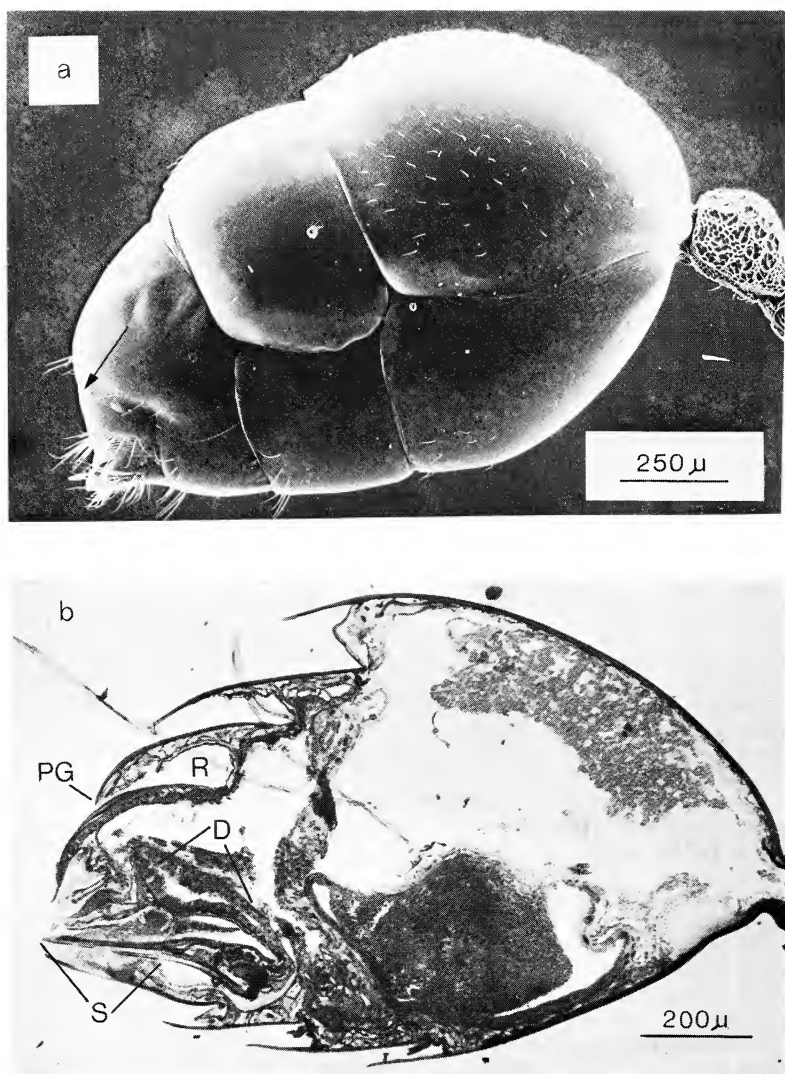


Fig. 3. Gaster of a media of *Orectognathus versicolor*. (a) SEM picture; arrow indicates opening of pygidial gland. (b) Sagittal section through gaster of a media. PG = pygidial gland; R = reservoir of pygidial gland; D = Dufour's gland; S = stinger.

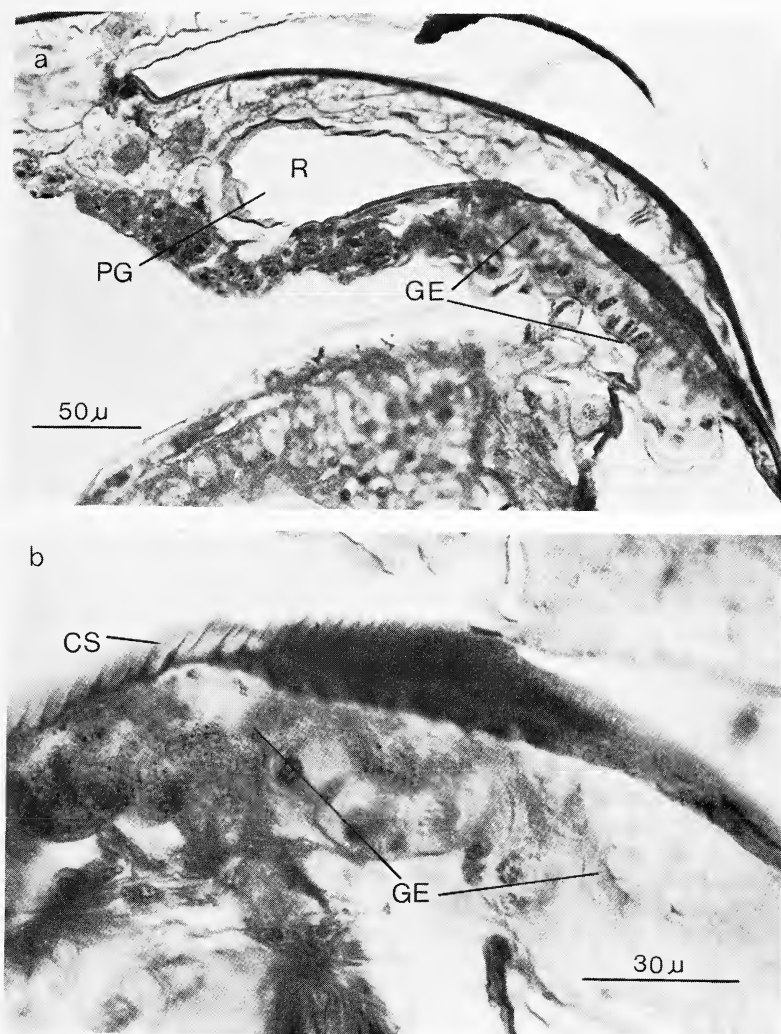


Fig. 4. (a) Sagittal section through pygidial gland of a media of *Orectognathus versicolor*. PG = pygidial gland; R = reservoir of pygidial gland; GE = glandular epithelium. (b) Close-up of glandular epithelium (GE) under the cuticular structure (CS) of pygidium.

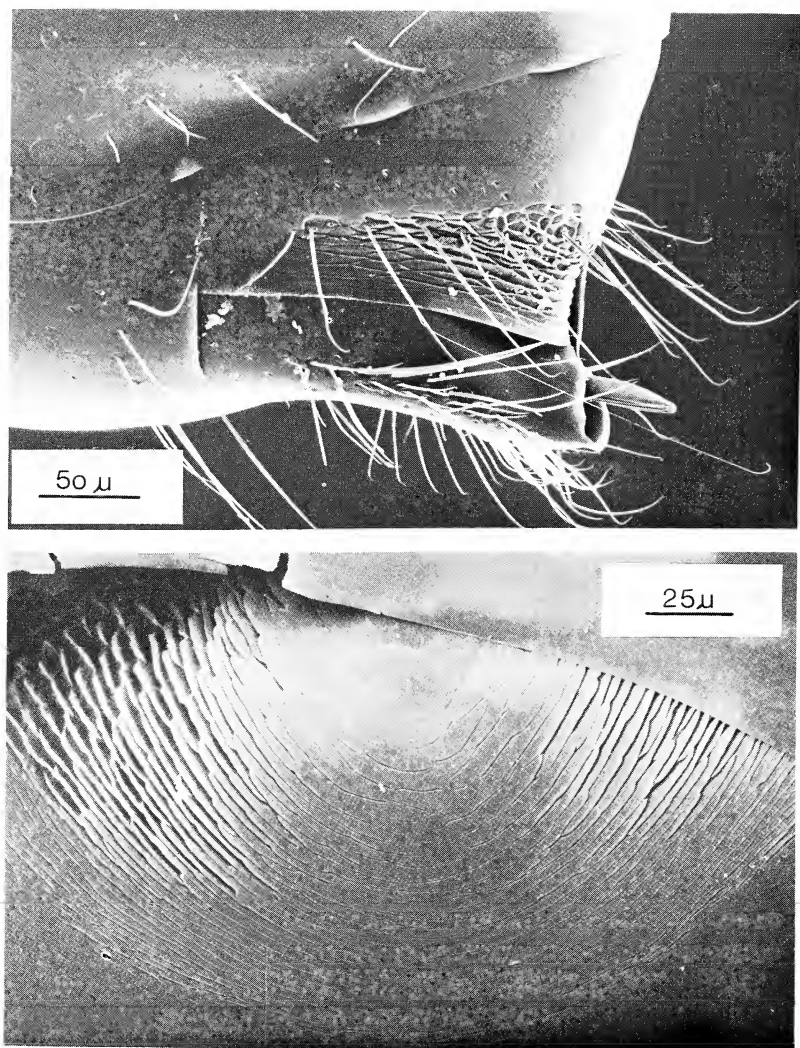


Fig. 5. Above: SEM pictures of the gaster tip of a media of *Orectognathus versicolor*. The slightly extruded stinger is visible. It is surrounded by long sensory setae (confirmed by histology; probably mechanoreceptors) on the edge of the pygidium and 7th sternum.

Below: Grooved cuticular structures on the pygidium associated with the pygidial gland. This structure is usually covered by the preceding 6th tergite.

glands. All ants following the trails to the end during a 5-minute period were counted.

As can be seen from table 1, trails drawn either with crushed pygidial glands or poison glands elicited a precise trail following behavior in all three worker castes (Fig. 6), but the ants did not respond to trails drawn with crushed Dufour's glands. We noticed, however, several differences in the reaction of the ants to poison gland trails and pygidial gland trails. (1) When both trails were offered simultaneously, starting at the periphery of a "homeless" colony, significantly more workers (Tab. 1) carrying brood moved along the poison gland trail. (2) In all tests the poison gland trail was the more effective one and lasted over a longer period of time. After 5 minutes the ants' response to pygidial gland trails had almost vanished, whereas they were still strongly following the trail drawn with poison gland material. In fact, poison gland trails presented to the ants 24 hours after they were drawn were still effective as orientation cues for emigrating *O. versicolor* workers. (3) Although we could not detect a preference for either trails drawn with poison glands or pygidial glands, ants moving along the pygidial gland trail seemed to gape their mandibles more frequently than ants moving along poison gland trails.

From these observations we conclude that the trail pheromones serve different functions. The poison gland trail is obviously employed during nest emigrations, where it serves as a stimulative recruitment signal as well as a longer lasting orientation cue. On the other hand, the pygidial gland trail probably functions as a relatively short lasting alarm-recruitment signal, channeling workers to areas of disturbance near the nest. It is also possible that the pygidial gland pheromone is discharged by successful foragers when they return to the nest, which might cause the social facilitation of the foraging activity mentioned above. In fact, when a crushed pygidial gland is presented inside the nest tube, it elicits more excitement in the workers than any other glandular secretions (mandibular gland, poison gland, Dufour's gland), causing several workers to move toward the nest entrance.

All three worker castes have the same glandular equipment and their secretions release the same behavioral responses.

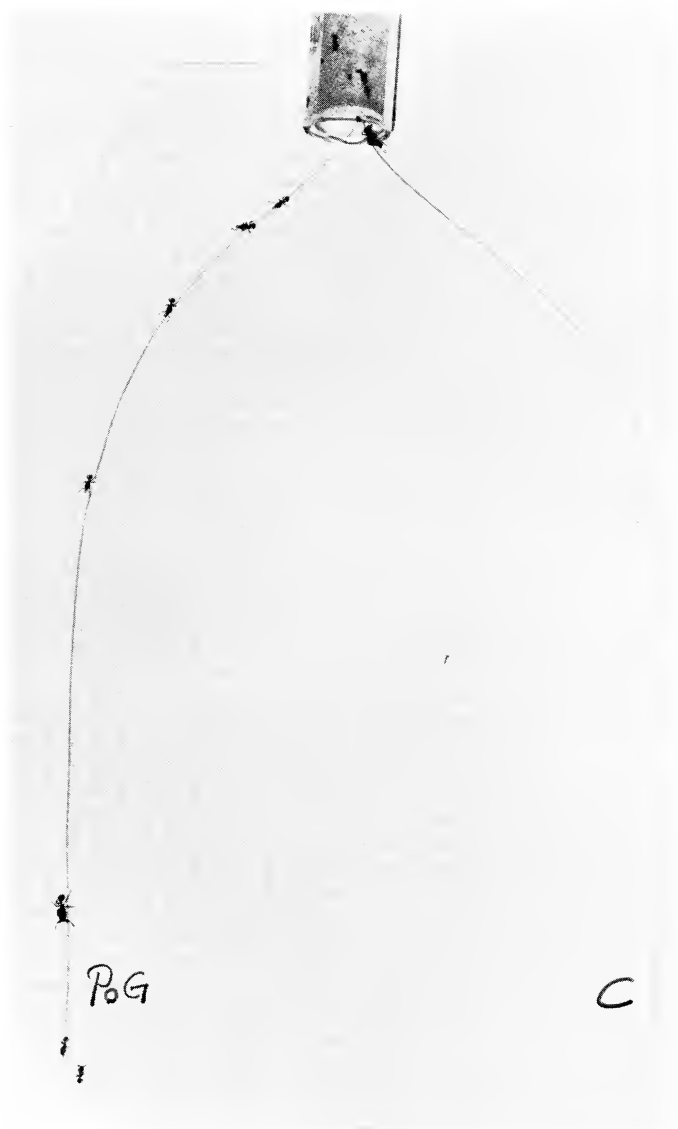


Fig. 6. Trail test with *Orectognathus versicolor*. Artificial trails drawn with secretions from the poison gland (PoG) and Dufour's gland (C), both originating at the opening of the nest tube, are offered simultaneously. All workers follow the poison gland trail.

Discussion:

It has been well documented that many species of the sub-family Myrmicinae employ secretions from the glands associated with the sting apparatus (poison gland, Dufour's gland) for chemical trail communication and orientation (for review see Wilson 1971; Hölldobler 1978). This paper presents the first evidence of the phenomenon in the myrmicine tribe Dacetini.*

In the dacetine species *Orectognathus versicolor* trails laid with poison gland secretions function both as recruitment and orientation signals during nest emigration. In fact, many dacetine species seem to construct relatively simple nests in soil or rotting wood and it is easily conceivable that colonies frequently abandon their nests and move to new nest sites. More surprising, however, was the discovery that this species possesses a pygidial gland whose structure closely resembles that of the pygidial gland of some ponerine species. The secretions of this gland can also function as a recruitment trail pheromone in *O. versicolor*.

Table 1. Number of workers following artificial trails within 5 min. periods. The means and standard deviations are given.

Trails presented at nest entrance (n = 4)					
Dufour's gland	water control	Poison gland	water control	Pygidial gland	water control
0	0	12.7 ± 3.8	0	8.3 ± 2.8	0
Trails presented simultaneously at periphery of clustered colony (n = 5)					
Dufour's gland		Poison gland		Pygidial gland	
with brood incl. males	without brood	with brood incl. males	without brood	with brood incl. males	without brood
0	0	7.8 ± 3.8	7.0 ± 2.2	2.0 ± 1.6	9.8 ± 3.1

*Blum and Portocarrero (1966) demonstrated that three attine ant genera follow trails drawn with poison gland secretions of *Daceton armigerum*, but they could not demonstrate trail following behavior in *Daceton*.

From recent investigations we know that the pygidial gland is quite common in the Myrmicinae (Kugler 1978; Hölldobler and Engel 1978). In at least two species its secretions serve as an alarm pheromone (Hölldobler et al. 1976; Kugler 1979). On the other hand, in several ponerine species the pygidial gland secretions have been demonstrated to function as a recruitment pheromone during tandem running (Hölldobler and Traniello 1980a) or trail communication (Maschwitz and Schönege 1977; Hölldobler and Traniello 1980b). From our findings in *O. versicolor* it appears now that this ponerine trait might have been preserved in the Dacetini, whose origin presumably dates back to early Tertiary times (Brown and Wilson 1959). If this speculation is right, we should expect that the most primitive dacetine species, *Daceton armigerum* (Brown and Wilson 1959; Wilson 1962), has a well developed pygidial gland, resembling closely that found in many ponerine ants, and its secretions presumably serve as an alarm-recruitment pheromone. In fact, Wilson (1962) observed that workers of *D. armigerum* often moved to areas of excitement and when a worker just had discovered prey it moved in "excited broken running patterns" by which other ants in the vicinity might be attracted. Wilson (1962, 1971) hypothesized that this running pattern might serve as a communicative signal of the kind of "Stäger's kinopsis", i.e. the large-eyed *Daceton* workers might respond to the visual stimuli produced by the excitedly moving nestmate. We have now to consider the possibility that a *Daceton* huntress which pursues a prey, discharges a short-range recruitment pheromone from the pygidial gland, and that consequently the attraction of other huntresses in the close vicinity is caused by this chemical signal.

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FRANCIS WALKER TYPES OF, AND NEW SYNONYMIES
FOR, NORTH AMERICAN *HYDROPSYCHE* SPECIES
(TRICHOPTERA, HYDROPSYCHIDAE)*

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INTRODUCTION

Recently, while assembling the manuscript of a handbook to the Arctopsychidae and Hydropsychidae of Canada, I had occasion to examine the female holotypes of three species of *Hydropsyche* described from North America by Francis Walker (1852). Betten & Mosely (1940) record these types, but in line with the still all too prevalent practice regarding unassociated female Trichoptera, they did not illustrate the genitalia. If they had provided figures for these types the true identities of at least two North American species of *Hydropsyche* would have been long since established. The genital segments of these types are illustrated here for the first time.

Hydropsyche confusa (Walker)

Philopotamus confusus Walker, 1852: 103.

Hydropsyche confusa: Milne, 1936: 61; Betten & Mosely, 1940: 21.

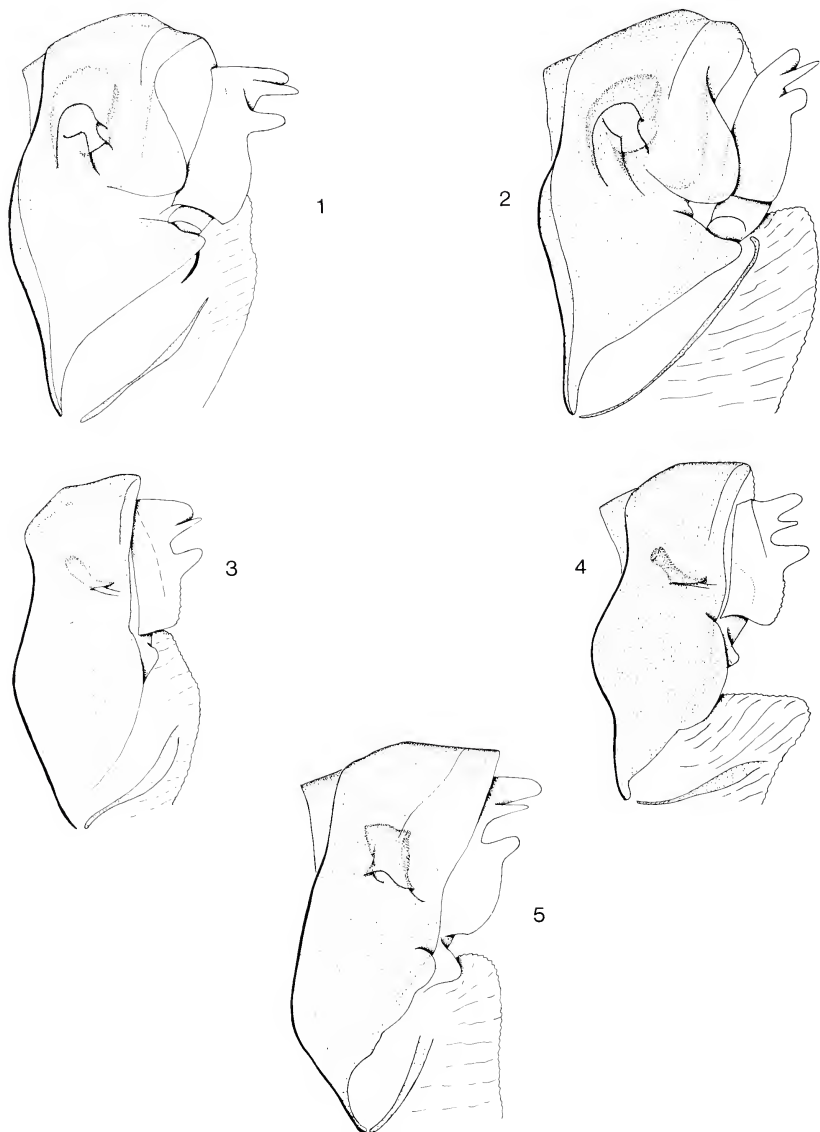
Hydropsyche separata Banks, 1936: 129; Ross & Spencer, 1952: 46
(as synonym of *H. guttata* Pictet); Smith, 1979: 10. NEW
SYNONYMY.

Hydropsyche guttata Pictet: Schuster & Etnier, 1978: 126.

Hydropsyche corbeti Nimmo, 1966: 688; Schuster & Etnier, 1978:
126 (as synonym of *H. guttata* Pictet). NEW SYNONYMY.

Fig. 2 depicts the genitalia of the female holotype of *H. confusa* (Walker). Fig. 1 is of the genitalia of a female which has been recognised as belonging to *H. separata* Banks. The rather obscure locality information recorded by Betten & Mosely (1940) indicates that the type of *confusa* was collected in the western Northwest Territories, adjacent to the northern boundary of Alberta. The female of *separata* was collected at Empress in southeastern Alberta.

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Figures 1-5. Fig. 1. *Hydropsyche separata* Banks [= *confusa* (Walker)]—genital segments of female, lateral aspect. Fig. 2. *H. confusa* (Walker)—genital segments of female holotype, lateral aspect. Fig. 3. *H. recurvata* Banks [= *alternans* (Walker)]—genital segments of female, lateral aspect. Fig. 4. *H. alternans* (Walker)—genital segments of female holotype, lateral aspect. Fig. 5. *H. reciproca* (Walker)—genital segments of female holotype, lateral aspect.

While not absolutely identical (the differences may be attributed to geographic variation, laboratory treatment, and observer variables), these two specimens are much more similar to each other than either is to the females of the most nearly related species (*H. betteni* Ross), and I judge them to be conspecific. *H. separata* is therefore synonymised with *H. confusa* which has clear priority.

Smith (1979) quotes me as considering the possibility that *H. corbeti* Nimmo may be a synonym of *separata*. Prior to my examination of the type of *confusa* I had decided that it was. However, it must now be entered as a synonym of *confusa*.

In view of the taxonomic history of this species Walker must be attributed with remarkable insight in naming it *confusa*.

Hydropsyche alternans (Walker)

Philopotamus alternans Walker, 1852: 104.

Hydropsyche alternans: Vorhies, 1909: 707 (sp.indet.); Betten, 1934: 185 (prob. *H. bifida*).

Philopotamus indecisis Walker, 1852: 104.

Hydropsyche indecisa: Betten & Mosely, 1940: 20 (as synonym of *H. alternans*).

Hydropsyche slossonae var. *recurvata* Banks, 1914: 253.

Hydropsyche recurvata: Betten, 1934: 190; Milne, 1936: 73 (as synonym of *H. slossonae*); Ross, 1944: 99. NEW SYNONYMY.

Symphitopsyche recurvata: Schuster & Etnier, 1978: 34.

Hydropsyche codona Betten, 1934: 187; Milne, 1936: 73 (as synonym of *H. slossonae*); Ross, 1938: 18 (as synonym of *H. recurvata*).

Fig. 4 depicts the genitalia of the holotype female of *H. alternans* (Walker) (from the Albany R., far northern Ontario). Fig. 3 depicts the genitalia of a female (from Wandering River, northeastern Alberta) which has been recognised as belonging to *H. recurvata* Banks. Again, these two females are not precisely identical, for possible reasons similar to those given under *H. confusa* above. I judge these two specimens to be conspecific. *H. recurvata* is therefore synonymised with *H. alternans* which has priority.

Hydropsyche reciproca (Walker)

Philopotamus reciprocus Walker, 1852: 104.

Hydropsyche reciproca: Betten & Mosely, 1940: 22.

The genitalia of the female holotype do not correspond to those of any other species known to me. They are illustrated here, for the first time, for the future reference of students of North American *Hydropsyche* species. The type locality is given simply as 'North America'.

SUMMARY

The female holotypes of *Hydropsyche confusa* (Walker), *H. alternans* (Walker), and *H. reciproca* (Walker), all from North America, were examined, and illustrations of the genitalia are provided for the first time. It is concluded that *H. separata* Banks is conspecific with *H. confusa* (Walker), and that *H. recurvata* Banks is conspecific with *H. alternans* (Walker). The Walker names have priority. *H. reciproca* (Walker) cannot yet be equated with any other known species.

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TERRITORIALITY, NEST DISPERSION, AND COMMUNITY STRUCTURE IN ANTS.

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INTRODUCTION

The dispersion patterns of ant colonies have been reported for a variety of species having very different ecological characteristics (Pontin 1961; Yasuno 1963, 1964a,b, 1965; Brian 1964; Brian *et al.* 1965, 1966; Greenslade 1971; Room 1971, 1975a,b; Bernstein and Gobbel 1979; Levings and Franks 1982), and typically, spacing studies involve discussions of territoriality. Recently, Hölldobler and Lumsden (1980), using a cost/benefit approach, examined the importance of the economic defensibility of territories and its influence on the use of space and dispersion patterns. Hölldobler (1974, 1976a, 1979a,b) demonstrated the relationship between resource distribution, territory shape and nest spacing. These studies also emphasize that in order to understand thoroughly territoriality and other intra- and interspecific relationships, it is necessary to comprehend the role of social design in the establishment and maintenance of territory. Without such a combined approach of behavior and ecology, it is difficult to assess accurately the significance of territoriality in social species such as ants.

In many studies there have been problems in the application of the term territoriality and discrepancies in the identification of territorial phenomena. Terms describing the use of foraging area such as territory and home range have been rather poorly defined and vary in meaning between authors. Territory to some authors denotes a defended area (Baroni-Urbani 1979; Hölldobler 1974, 1976a; Hölldobler and Wilson 1977a,b; Hölldobler and Lumsden 1980) whereas to others it is synonymous with home range or is casually used (Dobrzanska 1958, 1966). There are also problems with the application of information on territoriality in the interpretation of spacing patterns. For example, mathematical evidence of

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nest overdispersion is frequently confused with, or taken as evidence for, territoriality although crucial behavioral patterns are not considered. However, sufficient information is available in the literature to suggest some of the behavioral and ecological factors important in the regulation of nest distribution.

With the above cautions in mind, we here present a simple model of predicted spatial distributions of colonies under different ecological conditions. We then survey the literature to examine the fit of available data to our predictions. Finally we discuss the general problem of the form of interactions between colonies and some of the implications of this for both field and theoretical considerations.

THEORETICAL ASPECTS OF NEST DISTRIBUTION PATTERNS.

We would first like to develop a set of biologically realistic predicted spatial distributions of colonies. We begin by positing some simple assumptions about a hypothetical ant population:

1. Nest sites are unlimited.
 2. The habitat is homogenous and inhabited by a single species.
 3. Each colony forages symmetrically around the nest to some distance r , which forms the radius of a circle. Within this circle, no other colonies can forage or become established.
- Simberloff (1979) derives the maximum foraging distance, r , as

$$r = \frac{\sqrt{2}}{\sqrt[4]{3} \sqrt{p}}$$

where p is the density of nests. In this case, nests are hexagonally packed and the array of nests is overdispersed (more regularly spaced than expected if random; Figure 1, case 1). Nests are spaced $2r$ apart and have 6 equidistant nearest neighbors.

Under different ecological conditions, the expected spatial distribution of nests will change. In low density populations, nest distribution should reflect the best foraging or nest sites; nests may be dispersed in any way and should tend towards a random distribution (Figure 1, case 2). Internest distance should on the average be at least twice r and usually more; its variance should be high. If nest sites are not uniformly available, then nest spacing will

depend upon whether or not nest sites are farther apart or closer together than this distance. We predict one of 2 patterns: (1) nests will be more overdispersed than potential nest sites (Case 3a) or (2) although nests may be clumped in space, foraging ranges which are asymmetric and which partition foragers will develop (Case 3b). If potential nest sites are farther apart than twice r , then nests will be distributed only with respect to potential nest sites. The effects of habitat heterogeneity will depend upon the scale and extent of the patchiness in relation to the foraging range of a species. If patches hold several to many colonies, then clumps of nests which are overdispersed within the clump are predicted. Smaller patches in complex mosaics will not generate predictable nest distributions unless the arrays of patches are very regularly distributed.

The effect of adding more species to the system will depend upon the species. Generally, in multi-species systems, the level of repulsion observed between co-occurring species should be directly proportional to the amount of overlap in resource use. Species utilization curves can range in overlap from 0 to essentially complete ecological identity (100% overlap). Predicted spatial patterns will clearly depend on the actual distribution of species. If two or more species with identical requirements and foraging radii occur in the same area, interactions within and between species should be equally strong. In this case, the pattern of nest distribution predicted is random for any one species (Franks 1980; Levings and Franks 1982). Nests should be overdispersed, but each species is distributed with respect to every other species (i.e., nests of all species are treated as equivalents). In addition, there should be no pattern in the species identity of nearest neighbors (Case 4). Removal of any one species should have the effect of the removal of a nest at random from an overdispersed array; the degree of observed overdispersion should decrease. The spatial dispersion of any one species in such an array should tend to look like a low density nest population (Case 2), but the history of the area may cause any type of pattern under different conditions.

If two or more species have the same foraging radius but do not overlap 100% in resource requirements, intraspecific interactions should be stronger than interspecific interactions (Case 5). We predict that (1) the entire array will be overdispersed and (2) each species will also be overdispersed from itself. Franks (1980) and

FIGURE 1

Case 1 High density population

- Assumptions: 1. Single species
2. All nests have the same r
3. Unrestricted nest sites
- Predictions: 1. Overdispersed nest array
2. Nest to nest distance = $2r$

Case 2 Low density population

- Assumptions: 1, 2, 3
- Predictions: 1. Nest distribution will tend to randomness
2. Average nest to nest distance $> 2r$
3. High variance in nest to nest distance

Case 3 Limited nest sites

- a. Assumptions: 1, 2
- Predictions: 1. Nests more overdispersed than potential nest sites
2. Nest spacing will vary with nest site location, minimum nest to nest distance = $2r$, average nest to nest distance $> 2r$
3. High variance in nest to nest distance
- b. Assumptions: 1
- Predictions: 1. Nests distributed as nest sites
2. Asymmetric foraging ranges

Case 4 Intraspecific = interspecific interactions

- Assumptions: 2, 3
- Predictions: 1. Entire nest array overdispersed
2. Individual species are more randomly dispersed than the total array
3. No pattern in the identity of nearest neighbor
4. High variance in nest to nest distances within a species, average nest to nest distance $> 2r$
5. Low variance in nest to nest distances for the entire array, average nest to nest distance = $2r$

Case 5 Intraspecific interactions $>$ interspecific interactions

- Assumptions: 2, 3
- Predictions: 1. Entire nest array overdispersed
2. Individual species within the array are also overdispersed
3. Nearest neighbors tend to be members of other species
4. Low variance in nest to nest distances within species, average nest to nest distance $> 2r$
5. Low variance in internest distances for the entire array, average nest to nest distance = $2r$

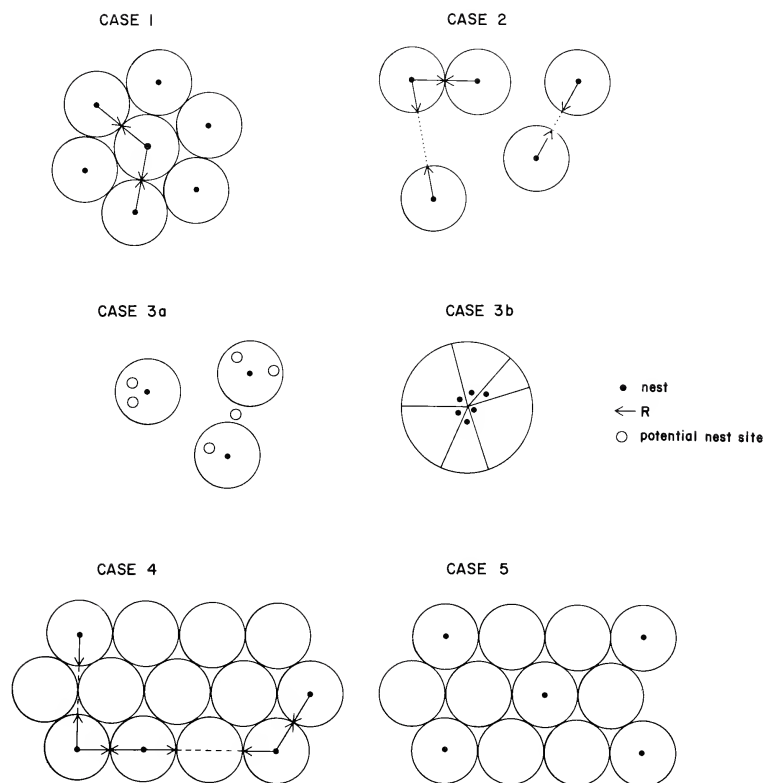


Figure 1. Theoretical nest dispersion patterns under different ecological conditions. Additional details in text.

Levings and Franks (1982) have reviewed the relevant statistical literature and give a suggested procedure for examining this problem.

In addition to changes in the observed spatial array of any one species, in multi-species populations, there should be correlated changes in expected internest distances under different competitive regimes. If intra- and interspecific interactions are equally strong, the average internest distance within any one species should be longer than twice the species' average r and the variance in between nest distances within any one species should be high (essentially a low density population, Case 2). If intraspecific interactions are more important than interspecific interactions, then internest distance within any one species should be greater than twice the species' average r and their variance should be relatively low. The exact predicted distance will be a function of the number of interacting species and their relative abundances. It may be possible to use the degree of departure from predicted intraspecific spacing patterns as a measure of competition between species in homogeneous habitats. If intranest distances within a species are $2r$, then it does not appear to be interacting significantly with sympatric species, at least not in ways which affect its spatial distribution.

DETECTION OF OVERDISPERSION AND METHODOLOGICAL PROBLEMS

There are certain methodological difficulties in applying any sort of spatial analysis to previously published data on nest distributions. In particular, the complicated structure of the nests of many species has confused workers, especially when many nest entrances are present. In *Lasius neoniger*, Headley (1941) assumed that the species was unicolonial, since he could only occasionally elicit aggression between adjacent nest entrances. In fact, *L. neoniger* colonies are distinct and well organized, but extensive field tests are required to delineate colony boundaries (Traniello 1980). Simple mapping of nest openings may reflect the distribution of colonies fairly well (as it does for many species in the ground ant community in Panama, Levings and Franks 1982; Levings, personal observations), but may lead to confusion unless sufficient data on the species are available (see, for example, Brough 1976). Whitford *et al.* (1980) assumed that workers of *Novomessor cockerelli* were entering an alien nest because they did not return to the same nest

entrance from which they departed. However, Hölldobler *et al.* (1978) and Davidson (1980) documented that this species has nests with multiple entrances.

Although there are several methods for the detection of overdispersion (Pielou 1977), we have chosen to apply Clark and Evans' (1954) nearest neighbor (NN) technique wherever possible. It is based upon the ratio between the observed mean nearest neighbor distance and the expected distance when a population is distributed at random. The index R can range from 0 (perfect aggregation) to 2.1491 (perfect hexagonal overdispersion). A value of 1 indicates a random dispersion pattern. The significance of R is tested using the z transformation. In an overdispersed population, the observed mean nearest neighbor distance is *larger* and the variance in nest to nest distance is *lower* than it would be in a randomly distributed population. Thus a population which is significantly overdispersed using this measure confirms 2 of our predictions (overdispersion and low variance in NN distance). Other methods do not have this property.

In our evaluation of spacing information in the literature, if we were unable to apply nearest neighbor methods, but complete quadrat counts were published, we calculated variance/mean ratios and tested them for significance using X^2 statistics (Pielou 1977). A V/M ratio of less than 1 indicates overdispersion while values greater than 1 indicate clumping. Cases are included in which data are not sufficient to test for statistical overdispersion, but information on partitioning of resources or area was published. We have organized the available data by geographic region, habitat and food types (Table 1). Methods used in gathering previously unpublished data will be described with the specific set of data. In testing our model and spatial predictions from the literature, we are limited by the previous interests and focus of other authors. We are able to test the spatial predictions far more thoroughly than the hypotheses about the actual expected distances between nests, but there is no empirical reason that they cannot be experimentally verified in the field (see discussion).

Data are discussed by subdividing reported cases into groups according to foraging type: (1) species which do not defend resources although they may or may not recruit to food, (2) species which defend randomly and unpredictably distributed resources (e.g., dead insects, which are patchy in both space and time), (3)

species which defend predictable and persistent resources (e.g., honeydew from aphids, resources which are patchy in space but not in time) and (4) truly territorial species which defend area which has potential food resources. These divisions mark some ecologically important foraging types within communities.

OBSERVED PATTERNS

1. Nest Defense

The data suggest that species which display only nest defense fall into 4 major groups, depending upon the details of their foraging biology. First, some species forage only as solitary individuals for food items which a single forager can subdue and retrieve (Group I foragers, Oster and Wilson, 1978). Examples of this group include most Dacetini, many Ponerinae, and some of the non-leaf cutting Attini (Brown and Wilson 1959, Wilson 1971, Oster and Wilson 1978).

There is very little applicable data on this group. The frequency of dacetine nests in extensive Berlese sampling of a tropical deciduous forest fit a Poisson distribution indicating a random distribution (Levings, unpublished data), but this sort of data does not differentiate between the suitability of the site or other important factors in the distribution of nests. Certainly there was no indication that nests were clumped. The maximum number of nests found was 6 in 84 0.25 m² samples. When a truncated Poisson was fit (0 class excluded), the distribution did not differ from Poisson expectation ($p > 0.5$, χ^2 test).

Second, some species may recruit nestmates to food resources, but make no attempt to defend them, decamping if another, more aggressive, species arrives before the food is retrieved (Group II, in part, Oster and Wilson 1978). These species specialize in the rapid location and removal of food. Examples include *Paratrechina longicornis* and *Tapinoma melanocephalum* (Wilson 1971). No data on their nest distribution is available, but many are known to form small fragmented colonies which move frequently between ephemeral nest sites.

The third set of species have developed mechanisms for feeding at the same resources as other, more aggressive ants, without eliciting defensive reactions (Groups I & II, in part, Oster and Wilson 1978, Wilson 1971). It is not known how much of a colony's food intake

results from such theft and how much is independently gathered. Examples include *Leptothorax acervorum* and various *Cardiocondyla* species (Brian 1955; Wilson 1959a, 1971). These species usually recruit few other workers to the food item; many of these species recruit only one other nestmate using tandem running (Wilson 1959a). No spacing information is available for these species.

The fourth set of species include the legionary ants (true group foragers) and most of the specialists on extremely difficult prey (Groups IV and V, Oster and Wilson 1978). These species defend only their nest sites (which may move often) and forage in various sized groups. The most spectacular examples of this type of foraging are the army ants (Schneirla 1971). Specialists on difficult prey occur in several genera (examples, *Pachycondyla* (= *Termitopone*), *Leptogenys*, *Gnamptogenys*); specialized retrieval methods may involve extensive cooperative foraging (Wilson 1971). Little nest spacing information is recorded about these groups. Army ants of several genera have been observed to avoid each other when they meet in the field, but no similar information is available for related groups (Schneirla 1971). Other legionary groups are relatively rare on BCI and, in 4 years of field work, no interactions were observed (Levings, personal observation).

In general, information on spacing patterns of ants which defend only their nests is extremely difficult to gather, since the investigator must usually depend upon luck to locate colonies and will never be certain that all colonies in an area have been found. Because information on foraging ranges for most species is unavailable, we are unable to test those aspects of our hypotheses. Many species which are now assumed to defend only their nest sites may well be found to defend either resources or a foraging territory.

2. Resource defense

a. short term

The defense of unpredictable resources occurs on varying time scales. Resources which persist for very short periods (i.e., minutes for most dead insects) are defended by many generalist or scavenging ants during the recruitment/retrieval process (Groups II & III, in part, Oster and Wilson 1978). Spatial overdispersion in densely populated areas has been shown in one complex tropical community (Levings and Franks 1982). It is probably typical of many

reported cases of overdispersion in temperate ground ant communities dominated by relatively few generalist species (most species of the genera *Myrmica*, *Tetramorium*, *Lasius*, *Aphaenogaster*, some *Formica*; Table 1). Some species are placed here somewhat arbitrarily because good foraging ecology data are not available.

In more complex (i.e., non-uniform) habitats, the pattern of nest spacing is reported to be directly related to environmental conditions. *Lasius flavus*, which has been intensively studied in several European habitats, displays different nest distributions between locations. Waloff and Blackith (1962; Table 1) found that nests were overdispersed in a high density population and tended toward randomness in a low density population. In a wet, low pasture with limited nest sites, nests were also overdispersed (Blackith *et al.*, 1963, Table 1). With *Myrmica rubra* present in a low density population, *L. flavus* was randomly distributed (Elmes 1974). However, the partial segregation of species indicated that both intra- and interspecific interactions were present; *M. rubra* nests were more overdispersed than potential nest sites (Table 1). Similar patterns have been noted in other species. Petal (1972) showed that the pattern of distribution in *Myrmica laevinodis* depended upon the scale with which the species was examined. Within the habitat, nests were clumped, but within clumps of nests on a small scale, nests were either overdispersed or randomly distributed. In another study, Petal (1977) linked observed nest distribution and the available food supply in *Myrmica lemanica*. In a year with low food abundance, nests were overdispersed; when food was abundant, nest distribution was random, tending to aggregation. Petal did not state if she distinguished between nests and nest openings by testing aggressive responses between colonies. However, overall nest density remained approximately the same. Most other studies have assumed but not demonstrated the correlation between food abundance and nest dispersion patterns.

Within colonies with multiple nest entrances, the distance between nest entrances should be approximately $2r$ and nest entrances should be overdispersed if avoiding redundant search is the underlying cause of polydomy. This appears to be the case in *Lasius neoniger*. Each nest is composed of a series of nest entrances which are overdispersed within a colony (Traniello 1980). *L. neoniger* is unable to retrieve prey effectively further than approximately 15 cm from any given nest opening due to interference from other species

or congeners (Traniello, 1980). Inter-opening distances are not statistically different from 30 cm in a set of 12 nests with varying numbers of nest openings ($P > 0.10$, t test, 11/12 cases; range 2–27 nest entrances), fitting our predictions quite well. The only nest with consistently closer inter-opening spacing was hemmed in by 3 larger nests; its openings occupied essentially the entire available area (18 cm between entrances, 4 entrances). Although this species fits our predictions, we are unable to test them further with other species, either within species between nest openings or between separate nests. Nest entrance patterns of *Paltothyreus tarsatus*, which is also a polydomous species, appear to be similar in function to those of *L. neoniger* (Hölldobler, personal communication). However, in polydomous species of *Camponotus*, *Atta* and *Pheidole*, nest entrances are often much less than 2 r apart (Yasuno 1964a; Hölldobler and Möglich 1980). Therefore, the association between foraging ecology and nest structure probably depends on the details of the biology of individual species.

When resources persist for slightly longer time periods (patches that can be exploited in a few days such as rotting fruit), we also expect overdispersion of nests. This pattern has been confirmed in several species. *Myrmecocystus mimicus* nests in desert areas and exploits patchy, unpredictable concentrations of termites which form a major part of its diet (Table 1, Hölldobler 1976b, 1979a, Hölldobler and Lumsden 1980). During the retrieval of these patches of food, a nest will defend the area by engaging surrounding nests in a complex ritualized display and battle ("tournamenting") which may result in the destruction of incipient colonies. Normally, the tournamenting behavior persists until the patch is exploited; searching in the area continues during this time. Nests are overdispersed (G. Alpert, personal communication). Nests of *Prenolepis imparis* are overdispersed (Table 1), and workers defend pieces of fruit for 1 or more days. This species has also been observed to tournament as *Myrmecocystus mimicus* does (Traniello, unpublished observations). It appears that in these species the cost of allocating a portion of the worker force to engage foragers from a neighboring nest in tournaments that prevent their access to a resource is less than the benefits obtained from these patchily distributed food sources (Hölldobler and Lumsden 1980).

b. persistent resources

Persistent resources vary in their importance to colonies, depend-

ing on their nutritional value, and can differ from a branch with a few aphids to a large homopteran population which provides most of a colony's food intake. The degree to which a colony depends upon persistent resources will approximately determine the intensity of their defense. *Formica fusca* tends only a very few aphids and can be chased from them relatively easily (Brian 1955), while *F. rufa* colonies regularly destroy each other in battles for the control of specific trees (Elton 1932, Skinner 1980). Therefore, the removal of persistent resources can affect colonies differently; some nests will die if they are deprived of them (Elton 1932). In this section we will only consider species which are dependent, at least in part, upon such resources (Groups II & III, in part, Oster and Wilson 1978).

Most studies on the defense of persistent resources concern the genera *Formica* and *Pogonomyrmex*. The patterns of their nest distribution depends upon colony structure, nest site requirements and habitat complexity. Most *Formica* nest distributions are the result of the interaction between the need for high insolation of the nest and the proximity of trees or bushes which are suitable for tending aphids. Many species nest along the ecotones between fields and forests, in forests, and in forest clearings (*F. lugubris*, *F. schaufussi*, *F. exsectoides*, *F. polycтена*, *F. rufa*, *F. ulkei*). These species will be found in overdispersed arrays only if habitat patches are found in rather predictable patterns. These are clearly special cases and explain some of the variation between authors for some species (see for example, *F. lugubris*, Table 1). We expect the linear distance along the ecotone to be relatively even in this case, but we have no data to test this hypothesis. Casual observations on *F. schaufussi* tend to support this (Traniello, personal observations). *Formica* species which nest in fields should be found in overdispersed arrays; the few reports that exist indicate that they are (*F. uralensis*, *F. opaciventris*, *F. fusca*, *F. pratensis*, Table 1). In addition, *Pogonomyrmex* species which defend patches of seeds are found in overdispersed arrays. These and other species that defend persistent resources and are not nest site limited are in general found in overdispersed arrays (*Atta* spp., *Acromyrmex octospinosus*, *Lasius niger*, etc., Table 1).

Colonies which depend upon persistent resources frequently organize resource defense and utilization with trunk trails. Trunk trails are long term routes which are marked with persistent trail

pheromones (Hölldobler, 1974, 1976a; Traniello, 1980; Group III, Oster and Wilson, 1978). Thus both the track to the resource and the resource itself constitute the defended area. These foraging ranges are highly asymmetric—foragers from different colonies are only likely to interact when trail systems overlap. Essentially all foragers follow these trails in some species (Hölldobler, 1976a), but this varies a great deal from group to group. In general, we expect that nest to nest distances will be shorter than the distance to the defended resource if colonies have highly skewed foraging. This prediction is born out in a study of three sympatric species of *Pogonomyrmex* (Hölldobler, 1976a). Between nest distances are shorter in the two interspecifically defending species which forage on trunk trails than between nests of the individually foraging *P. maricopa*.

3. Defense of area

We consider defense of space larger in area than nest yards or core areas (Hölldobler 1976a) to be true territoriality. This defense of area is, in essence, defense of potential foraging grounds. Only a few ant species, characterized by complex mechanisms of mass recruitment and high levels of intra- and interspecific aggression, are therefore truly territorial in our classification. Most dominant tropical canopy ants (some members of the genera *Azteca*, *Oecophylla*, *Crematogaster*, *Camponotus*, *Monacis*, *Polyrachis*, *Anoplolepis*, Table 1) and at least one member of the genus *Solenopsis* are truly territorial. We must point out that in some cases the distinction between true territoriality and resource defense is not perfectly clear, and that strategies of territorial defense and resource defense are at times difficult to distinguish.

Solenopsis invicta, an introduced species from South America, has been extensively studied in the southern United States where it may form monocultures in fields (Wilson *et al.* 1972). Extensive mapping of one population showed overdispersion of nests maintained over time despite frequent nest movement (Eisenberg 1972, Table 1).

Maps of intercolony dispersion have been published for a number of ant species in tree crops in tropical areas (Table 1). Individual colonies hold territories in the canopy both intra- and interspecifically. The distribution of the canopy mosaic of dominants can have a very complex structure (Way 1953; Greenslade 1971; Majer

1976a,b). Individual colonies are clearly separated from each other, frequently by a no ant's land between defended areas (Hölldobler 1979b).

However, the statistical dispersion of these colonies is difficult to assess. Territory size varies a great deal between species because population structure has very strong effects on colony size and organization. Only a few polydomous, polygynous colonies may occupy extensive areas (Steyn 1954, Greenslade 1971, Leston 1973, Majer 1976a,b). The dispersion of volumes in space is difficult to treat statistically from published data although 3-dimensional methods exist (Clark and Evans 1979, Simberloff 1979). Luckily, the biological evidence for dispersion and nonoverlap of area is overwhelming. Territorial battles are commonly observed and, in populations followed over a number of years, control of a given area shifts from colony to colony and species to species. Although we predict statistical overdispersion, we are unable, for both statistical and biological reasons, to test for it in these cases. There is, however, no question about the existence of true territorial defense and the spatial separation of colonies.

Ant plants are a special set of cases of true territoriality. Several tropical tree species (Table 1) are coevolved with certain species of ants (some members of the genera *Pseudomyrmex*, *Azteca* or *Pachysima*) which protect the tree from herbivores or overgrowth in return for food and nest sites. Few other animals of any species are tolerated on the plant; the ant species are characteristically extremely aggressive. The mutualism is sufficiently old than at least one species parasitizes it by using the plant without protecting it in return (Janzen 1975). These ant colonies are thus distributed with respect to the distribution of their host and form distinct territories within the canopy mosaic. They may also help "grow" new host plants by affecting the survival of nearby seedlings (Janzen 1967, 1973).

INTERCOLONY SPACING EFFECTS

Interspecific overdispersion is regularly reported in almost all habitats (Table 1). However, detailed ecological studies indicate that different mechanisms operate in different habitats. In part, this is due to the fact that the only necessary characteristic required to generate overdispersed arrays is the ability of a colony to interfere

with colony foundation of potential competitors. Few studies have examined the pattern of species mingling. Brian and his co-workers have shown that nest sites probably limit many species in England, which apparently is a rather poor habitat for ants. The pattern of dominance over nest sites determines the location and abundance of many species (Brian 1952, 1956b, Brian *et al.* 1965). Nest density could be increased by providing new nest sites, and once established, populations remained relatively stable over long periods (Brian *et al.* 1966). Competition between species where nest sites were not as limiting tended to restrict individual species to areas which were close to optimal species requirements (Brian *et al.* 1966, Elmes 1971, 1974). These studies indicate that the details of species biology and physical tolerances may be critical, even in very simple habitats like heath. However, even in these systems, species are definitely not distributed independently of their competitors.

Tropical canopy dominants are associated with certain canopy conditions, and tend to be found mostly in shade or under certain other limited environmental states (Majer 1976a). Removal experiments indicate that colony foraging areas are competitively compressed; when a dominant is removed, surrounding colonies expand to fill the available space. Species usually found in one kind of canopy may expand into other types of foliage if adjacent dominants are extirpated (Majer 1976a,b). This pattern is similar to that found in far simpler grassland communities.

In a complex tropical ground ant community with at least 16 ecologically similar species, Levings and Franks (1982) have shown that new nests are not added at random to the nest array. Grouping all species, nests are overdispersed from each other. Each common species considered independently was also overdispersed. This is interpreted as evidence that species are interacting more strongly intra- than interspecifically, but that interspecific effects were still important in determining nest distributions. Similar patterns in simpler communities indicate that this may be common (Table 1). The worst neighbor in a competitive sense should be identical to oneself. In any case, the simplifying assumption that species have identical requirements is almost infinitely unlikely to apply; even small differences in requirements or tolerances can be important in determining colony distributions. However, few adequate tests have been done and, in one published case, two closely related congeners,

Pogonomyrmex rugosus and *P. barbatus*, essentially act like exact ecological equivalents (Hölldobler 1976a). Davidson (1977a) has suggested that the distribution of several individually foraging *Pogonomyrmex* (*maricopa*, *californicus*, *desertorum* and *magnificanthus*) is consistent with the hypothesis that they replace each other between habitats. The pattern could also occur in some other, less completely documented cases, perhaps in *Atta* (Rockwood 1973).

POPULATION STRUCTURE AND ITS EFFECTS ON THE SPATIAL DISTRIBUTION OF COLONIES

Monogynous, queenright colonies are almost innavoidably aggressive to conspecific nests or foragers, regardless of how territorial they are (Hölldobler and Wilson 1977c). Polygynous colonies may or may not display internest aggression. Hölldobler and Wilson (1977c) point out the importance of queen number in the maintenance of clear territorial borders. Species which commonly have polygynous colonies and/or those which adopt newly fertilized females to augment or replace females already in the nest do not always have strong intraspecific interactions; some do not form distinct colonies (*Formica yessensis*, *F. lugubris*, Table 1). In these cases the location of nests should be predominantly determined by ecological factors, in particular the kind of resource defense the colony shows. Thus some species should retain overdispersed patterns of nest distribution while other show clumped or random patterns (see model and predictions).

Examining this issue is complicated by the lack of population structure data for many species. Several *Formica* species which form unicolonial populations, but depend upon randomly and unpredictably distributed resources, are found in overdispersed arrays [those species found in fields: *F. pratensis* (provisionally), *F. uralensis* (provisionally), *F. opaciventris*, *F. exsectoides*, Table 1]; those which nest along the margins of a habitat and/or which defend persistent resources tend to have more random or clumped distributions (*F. ulkei*, *F. rufa*, *F. lugubris*, Table 1). Territory size in some tropical tree ants is partially a result of population structure. Many dominant species are polygynous and are able to expand their territories almost indefinitely under good ecological conditions (Greenslade 1971, Majer 1976a,b). In some cases, single

queen species like *Oecophylla* may be at a disadvantage. Resistance to invasion or persistence of the nest may be limited by the female's egg production under some conditions, although this does not usually seem to be the case (Hölldobler and Wilson 1977c; Hölldobler and Lumsden 1980). We must emphasize that in populations with complex or variable structure it may be very difficult to determine the factors which are controlling distributions. Spacing may reflect foraging ecology as well as being an aspect of territoriality. More data are needed before good generalizations can be made.

BEHAVIORAL AND ECOLOGICAL ASPECTS OF SPACING

For the cases we have been able to examine statistically, 67 out of 80 show overdispersed nest distributions or tend toward overdispersed nest distributions. The other 80 cases, which cannot be treated statistically, mainly have either overdispersed nest distributions or tend toward overdispersed nest distributions. Thus the majority of species studied tend to have regular nest arrays. This pattern holds despite the large number of species, food types and habitats considered. Species which defend only their nests are too rare to consider in our sample.

Our basic assumption is that no colony can become established or forage within some radius r of another colony. There is a biological basis for this assumption in the patterns of interference with colony establishment and foraging patterns. Therefore, to understand nest spacing it is important to understand the different levels of competition in ant communities. Fertilized females or incipient colonies are usually destroyed when they are encountered by foragers from established colonies (Wilson 1971). The specificity of this behavior varies between species depending in part on population structure (Hölldobler and Wilson 1977c, DeVroey 1979). There is some evidence that workers are more likely to attack females from conspecific nests or closely related species, especially in monogynous, queenright colonies, as has been shown in *Pogonomyrmex* (Hölldobler 1976a) and *Myrmecocystus* (Hölldobler, personal communication). The studies of Pontin (1960) and others (reviewed in Wilson 1971) suggest that such behavior is more often directed toward queens of the same species as the attacking workers.

Another factor which may operate during this period is resource depletion mediated by either direct interference or exploitation.

Within the foraging radius of an established colony, there is likely to be less food available, even if the established colony ignores incipient colonies. The amount of depletion will depend on the amount of resource overlap. Because destruction of females and incipient colonies is frequently reported and resource depletion probably also affects colony persistence, the chance of a small colony becoming established is low. Wilson (1971) estimates that only 0.01% of all fertilized females survive to found successful nests. Therefore, established colonies tend to persist and interact over long periods, insofar as is known (Wilson 1971). Given this pattern, what is the form of the interaction and why are patterns of interspecific overdispersion so common?

According to current theory, species can segregate a habitat to avoid or lessen competition in several ways: microhabitat partitioning, food size or type, and activity period (Pianka 1978). Further, equilibrium theory generally asserts that only a limited amount of overlap is tolerated on any given niche axis (MacArthur and Levins 1967; Colwell and Futuyma 1971). Species which are too similar should not be able to coexist and, over a long enough period, the superior competitor in the overlapping pair will drive the other species extinct. Although there are many problems with the assumptions of this argument, we will use its basic divisions to examine the patterns of overlap between co-occurring ant species. Ant species may be specialized along these three major axes. We will consider each potential kind of specialization in turn and evaluate the evidence that segregation of species along that factor is usually sufficient to prevent strong competitive interactions.

Species may be considered specialized on food types in 3 major ways: (1) restricted prey types (i.e., only centipedes), (2) specific size ranges of prey (i.e., only prey 1–3 mm in length) or (3) some combination of (1) and (2) (i.e., centipedes between 5 and 8 mm long). Different kinds of specializations will have different effects on colony structure, nest size and foraging strategy. Resource restriction is frequently based on the matching of mandible or head size to food size or type (the trophic appendage, Schoener 1971, see below). Resources which are retrieved by individual workers, not by coordinated action, are especially likely to be treated in this manner (for example, seeds for desert ants, collembolans for dacetines). The resistance of the food item to recovery is also important; items

which do not resist (seeds) are more likely to be size matched than items which require more complex treatment from the ants. Nests of specialist species may be restricted to areas which contain concentration of suitable prey (and as such violate the assumptions of our model). If resource size is matched with worker size class, then size polymorphism is one way to expand the resource spectrum of the colony without any changes in individual retrieval patterns (Oster and Wilson 1978). The development of coordinated retrieval mechanisms can further expand the accessible resource spectrum.

Almost all specialists, by definition, have less harvestable energy available to them than generalists. Thorne and Sebens (1981) suggest that species with low habitat quality (i.e., low food density) will have smaller nests than species with high quality areas (high food density). We extend this argument to predict that once a species has broadened its diet, it will include essentially all retrievable food types encountered. Such an increase in diet breadth is needed to support large colony sizes, based on almost any simple foraging efficiency model. Although specific prey types, especially those with noxious chemical defenses, require special handling methods, many prey types may be captured and/or retrieved by species with a limited behavioral repertoire. Certainly scavenged material can be handled by all but the most specialized mandibular types. Since ant colonies persist over years, they more or less continually require resources. Resource distributions are highly variable over time; prey types appear and disappear seasonally (Mabelis 1979; Levings and Windsor 1982). It is a general consequence of this that once a species generalizes its diet, it is likely to overlap strongly with one or more sympatric species. The value of large colony size is reflected in reproductive output. Numbers of reproductives usually increase with colony size to some upper limit (Wilson 1971). Since the chance of success for any given reproductive is low, high production will be likely to correlate with the largest probability of leaving successful offspring. Colonies which bud will tend to have higher rates of success if the new buds have large worker forces; this is also a function of energy intake. Colonies almost all require protein to raise brood (usually from insect prey or seeds) and many accept or require sugar to maintain adult workers (usually from Homoptera, fruit or nectaries). In general, large colony size is strongly associated with the maintenance of sugar

resources. It appears that when adults can be fueled from sugar, more intensive foraging is possible and more brood and workers can be supported (Greenslade 1971; Leston 1973).

We do not deny that species which are specialized on prey types evolved resource segregation from competitive pressure. In fact, among specialized species which forage individually for prey, we expect some equilibrium co-existence theory to apply (see for example, Davidson 1980). We assert that there is no support for the contention that generalists segregate the resource spectrum to reduce competition (Wilson 1971). Available empirical studies indicate that high or essentially complete overlap in food type is frequent (Brian 1956a,b; Pontin 1961, 1963, 1969; Yasuno 1964a,b; Abe 1971; Hölldobler 1976a; Levieux 1977, Levings and Franks 1982). At best, partitioning of food type can account for only a small part of the observed pattern of species distribution in most habitats.

Habitat partitioning is a second possible method of limiting competitive interactions. Even in simple temperate grassland communities, co-occurring species forage at slightly different heights in the grass or tend to move more or less beneath the surface (Brian 1952, 1955, 1956b; Brian *et al.* 1966). However, all these species are usually described as being interspecifically territorial. Tropical faunas are well divided into arboreal and terrestrial components; many specialized species are further restricted to logs, rotting leaves or other microhabitats (Wilson 1959b, 1971; Carroll and Janzen 1973). Within these strata, high overlap between species resulting in intra- and interspecific aggression is frequently described (Carroll and Janzen 1973; Leston 1973; Greenslade 1975; Room 1975a,b).

Faunas may be further subdivided by time of foraging, if by foraging at different times, different resources are harvested. Time of foraging can differ daily (nocturnal vs. diurnal, Carroll and Janzen 1973), seasonally (*Prenolepis imparis* which forages in early spring and late fall, Talbot 1943, Lynch *et al.*, 1980) or may track environmental cues, such as desert species that forage after rains (Bernstein 1974, 1979). Although it has not been proven, it is probable that generalist and scavenging species forage on different resources if they forage at different times, if there are temporal components to food availability. Most dead or readily captured prey do not remain available for long periods, few probably persist even hours (Carroll and Janzen 1973, Culver 1974, Traniello 1980).

Other resources may be similarly affected—for example, winds may cover and uncover seeds in the desert (Reichman 1979). The option to forage at different times is not uniformly available to ant species; thermal tolerances may severely limit foraging time in both cold and hot climates or may affect the outcome of foraging contests (Hunt 1974; Davidson 1977a,b; Hölldobler and Möglich 1980). Many species change the time of their foraging in the presence of competitors (Hunt 1974, Swain 1977). Thus foraging times may separate some species, but as in the case of food or habitat, high overlap between sets of sympatric species in foraging time is the norm, not the exception, in ant communities. The evolution of intra- and interspecific behaviors including complex patterns of food retrieval and defensive strategies has resulted from such high overlap.

The form and outcome of interactions between species is determined in large part by the mechanisms of recruitment and communication within species. The subtleties of recruitment communication and their effects on foraging ecology and interference competition are not appreciated by most ecologists. Behavioral mechanisms are so critical that we suggest that when examining the diet of a species, an investigator first ask why more items are not included. For many years harvester ants were considered to forage individually for seeds, but the field and laboratory studies of Hölldobler (1976a), Hölldobler and Wilson (1970) and Hölldobler *et al.* (1978) unequivocally demonstrated that species of *Pogonomyrmex* and *Novomessor* rely on a sophisticated array of recruitment behaviors in foraging. In *Novomessor cockerelli*, short-range recruitment, mediated by both chemical and vibrational signals, allows workers to move food sources quickly and thereby enables them to compete with sympatric species (Hölldobler *et al.* 1978; Markl and Hölldobler 1978).

Behavioral interactions, not food choice, seem to partition food resources among generalists. Protein foods (arthropod prey) tend to be highly unpredictable in time, space and size; adaptations to this resource distribution among generalists may be behavioral rather than morphological. *Monomorium pharonis* and *Solenopsis fugax* employ a chemical interference technique both defensively and offensively during foraging (Hölldobler 1973). Adams and Traniello (1981) have documented the ecological effects of recruitment and resource defense in *Monomorium minimum*, a north temperate

open field ant. *Monomorium minimum* is a small (head width 0.47 mm), monomorphic species. Workers are successful at retrieving food particles which are either extremely small (less than 0.5 mg in weight) or large (greater than 450 mg in weight). Most items of intermediate size are lost due to either exploitative or interference competition from other species. Detailed laboratory and field experiments on the organization of foraging showed that *M. minimum* recruits other workers to food sources using trail pheromones. The quantity of pheromone determines the foraging response of the colony. As trail pheromone concentration increases, more workers are recruited. The amount of trail pheromone deposited is dependent upon resource quality (in this case, measured by the investigators as weight). Large food items induce trail laying by many workers and therefore result in strong recruitment. If there is interference from another species while prey is being dissected, workers display a specific posture (gaster flagging) while extruding the sting and discharging a droplet of poison gland secretion. This secretion has a repellent effect on intruding ants and causes them to recoil and vigorously groom. The effectiveness of this defensive behavior is dependent on the number of workers recruited. Therefore, large prey, which elicit strong trail pheromone deposition, induce strong recruitment responses and this results in a worker force which can successfully defend the item during retrieval. The result of this feedback between prey size, pheromone concentration and colony response is a diet composed of small individually retrieved items and large items recovered by recruitment and successful defense.

Perhaps the best evidence for the importance of behavioral parameters in species interactions is the phenomenon of alarm specification. Certain ant species which interact strongly with other species may respond specifically to the presence of the competitor. The best studied case is that of *Pheidole dentata* and *Solenopsis geminata* (Wilson 1975). *Pheidole dentata* colonies respond to the presence of *Solenopsis* by a strong recruitment of major workers. Major workers proceed to attack and kill all *Solenopsis* encountered and to search thoroughly the area near where the *Solenopsis* workers were found. They do not respond to the odors or presence of other species with major worker recruitment. A similar pattern of response is indicated in the interactions between *Oecophylla longi-*

noda and *Camponotus* sp. in Kenyan forest; alarm/recruitment specification may be the behavioral mechanism responsible for the structure and maintenance of the tropical canopy ant mosaic (Hölldobler 1979b).

In general, to defend any resource or area, including the nest, an ant must be able to summon her nestmates to a particular location. Within the nest, even quite primitive ants are able to communicate alarm and attract reinforcements (Robertson 1971; Traniello unpublished data). Outside the nest, recruitment is a necessary component of effective defense.

Ant species possess a wide diversity of recruitment communication techniques that are ecologically significant (see review by Hölldobler 1977). It is important to understand the ethology of social design to comprehend its role in ecological interaction. There are definite phylogenetic constraints and/or trends in the form of recruitment communication within the various subfamilies of ants (Hölldobler 1977). More primitive groups (some Ponerinae) usually recruit few workers to food sources; some group raiding species are exceptions. Mass recruitment is characteristic of some groups of Myrmicinae, Dolichoderinae and Formicinae. Each lineage has developed within certain paths involving specific glandular, physical and behavioral trends. These pathways are important in considering the evolution and development of ant community structure.

SUMMARY AND CONCLUSIONS

We have argued that a very simple hypothesis is sufficient to generate predictions of spatial distributions of colonies under a variety of ecological settings. The majority of cases in the literature (Table 1) support the hypothesis that most ant species are regularly distributed with respect to conspecifics and other co-occurring species. We assert that this is a natural outcome of high overlap in food utilization in many species, and in particular, among generalists. We have suggested that departures from expected spatial patterns be used as a measure of competition between species, but too little information on colony foraging radii in relation to spacing patterns exists to test our hypotheses critically. More field measurements of colony foraging distances in relation to intercolony spacing are needed. Measurements of potential foraging distances when

Table 1

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
OLD WORLD North Temperate grasslands: generalists						
Myrmicinae						
<i>Myrmica rubra</i>	A,B,C	b,c,e,f	II	o/+	Tested against the Poisson distribution	Brian (1952, 1955, 1956a,b)
<i>Myrmica rubra</i>	B	b,c,e,f	II	o/+	Nests more overdispersed than potential nest sites	Elmes (1974)
<i>Myrmica scabrinodis</i>	A,B,C	b,c,e,f	II	o/+	Tested against the Poisson distribution	Brian (1952, 1955, 1956a,b)
<i>Myrmica scabrinodis</i>	A	b,c,e,f	II	o/+	Nests distinctly spaced out	Pontin (1969)
<i>Myrmica laevinodis</i>	A	b,c,e	II	+	V/M test, significant overdispersion in suitable habitat	Petal (1972)
<i>Myrmica lemanica</i>	A	b,c,e	II	o/+	Overdispersed in bad year, random in good year	Petal (1977)
<i>Leptothorax acervorum</i>	A,B,C	a	II	o/+	Tested against the Poisson distribution	Brian (1952, 1955, 1956a)
<i>Tetramorium caespitum</i>	A	b,c?,e?,f?	II	o/+	Morisa's index, tend to overdispersion	Baroni-Urbani (1969)
<i>Tetramorium caespitum</i>	A,B	b,c,e,f	II	o/+	Intra- and interspecifically territorial	Brian et al. (1966)

Formicinae

<i>Lasius flavus</i>	A,B	b,c,e,f	II	o/+	R = 1.22-1.27, dense population overdispersed, low density population tends to randomness	Waloff and Blackith (1962)
<i>Lasius flavus</i>	A,B	b,c,e,f	II	o/+?	Spaced between <i>L. niger</i> nests	Pontin (1961, 1963)
<i>Lasius flavus</i>	A,B	b,c,e,f	II	o	$p > 0.05$, Clark and Evans' nearest neighbor analysis, low density population	Elmes (1974)
<i>Lasius flavus</i>	A,B	b,c,e,f	II	o/+	Nests distinctly spaced out	Pontin (1969)
<i>Lasius flavus</i>	A	b,c,e,f	II	+	Overdispersed even under extreme nest site limitation	Blackith et al. (1963)
<i>Lasius niger</i>	A,B	b,c,e,f	II	+	Overdispersed using Clark and Evans' nearest neighbor analysis	Pontin (1961, 1963)
<i>Lasius niger</i>	A,B	b,c,e,f	II	o/+	Nests distinctly spaced out	Pontin (1969)
<i>Lasius niger</i>	A,B,	b,c,e,f	II	o/+?	Intra- and interspecifically territorial	Brian et al. (1966)
<i>Lasius alienus</i>	A	b,c?,e?,f?	II	o/+	Morisita's index, tend to overdispersion	Baroni-Urbani (1969)
<i>Lasius alienus</i>	A,B	b,c,e,f	II	o/+	Intra- and interspecifically territorial	Brian et al. (1966)

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OLD WORLD North Temperate grasslands, generalists						
Myrmicinae						
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<i>Myrmica rubra</i>	B	b,c,e,f	II	o/+	Nests more overdispersed than potential nest sites	Elmes (1974)
<i>Myrmica scabrinodis</i>	A,B,C	b,c,e,f	II	o/+	Tested against the Poisson distribution	Brian (1952, 1955, 1956a,b)
<i>Myrmica scabrinodis</i>	A	b,c,e,f	II	o/+	Nests distinctly spaced out	Pontin (1969)
<i>Myrmica laevinodis</i>	A	b,c,e	II	+	V/M test, significant overdispersion in suitable habitat	Petal (1972)
<i>Myrmica lemanna</i>	A	b,c,e	II	o/+	Overdispersed in bad year, random in good year	Petal (1977)
<i>Leptothorax acervorum</i>	A,B,C	a	II	o/+	Tested against the Poisson distribution	Brian (1952, 1955, 1956a)
<i>Tetramorium caespitum</i>	A	b,c?,e?,f?	II	o/+	Morisita's index, tend to overdispersion	Baroni-Urbani (1969)
<i>Tetramorium caespitum</i>	A,B	b,c,e,f	II	o/+	Intra- and interspecifically territorial	Brian et al. (1966)
Formicinae						
<i>Lasius flavus</i>	A,B	b,c,e,f	II	o/+	$R = 1.22-1.27$, dense population overdispersed, low density population tends to randomness	Waloff and Blackith (1962)
<i>Lasius flavus</i>	A,B	b,c,e,f	II	o/+?	Spaced between <i>L. niger</i> nests	Pontin (1961, 1963)
<i>Lasius flavus</i>	A,B	b,c,e,f	II	o	$p > 0.05$, Clark and Evans' nearest neighbor analysis, low density population	Elmes (1974)
<i>Lasius flavus</i>	A,B	b,c,e,f	II	o/+	Nests distinctly spaced out	Pontin (1969)
<i>Lasius flavus</i>	A	b,c,e,f	II	+	Overdispersed even under extreme nest site limitation	Blackith et al. (1963)
<i>Lasius niger</i>	A,B	b,c,e,f	II	+	Overdispersed using Clark and Evans' nearest neighbor analysis	Pontin (1961, 1963)
<i>Lasius niger</i>	A,B	b,c,e,f	II	o/+	Nests distinctly spaced out	Pontin (1969)
<i>Lasius niger</i>	A,B	b,c,e,f	II	o/+?	Intra- and interspecifically territorial	Brian et al. (1966)
<i>Lasius alienus</i>	A	b,c?,e?,f?	II	o/+	Morisita's index, tend to overdispersion	Baroni-Urbani (1969)
<i>Lasius alienus</i>	A,B	b,c,e,f	II	o/+	Intra- and interspecifically territorial	Brian et al. (1966)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
<i>Formica fusca</i>	B, C	b, c, e, f	II	o/+	Tested against the Poisson distribution	Brian (1952, 1955, 1956a)
<i>Formica fusca</i>	A, B	b, c, e, f	II	o/+?	No food territory, can be aggressive over resources	Brian et al. (1966)
<i>Formica exsecta</i>	A	b, c, e, f	II?	o/+?	Intra- and interspecifically territorial	Pisarski (1972)
<i>Formica polyctena</i>	A	b, c, e, f?	III	o/+	Nests along edges of dunes, maintain distinct feeding areas	Mabelis (1979) (see note 6)
<i>Formica pratensis</i>	A	b, c?, e, f	II?	+?	Separated, intraspecifically aggressive nests	Stebaev and Resnikova (1972)
<i>Formica subpilosa</i>	A	b, c?, e	II?	o/+?	Nest between <i>F. pratensis</i> nests	Stebaev and Resnikova (1972)
<i>Formica uralensis</i>	A	b, c?, e, f	II?	+?	Separated intraspecifically aggressive nests	Stebaev and Resnikova (1972)
<i>Formica picea</i>	A	b, c?, e	II?	o/+?	Nest between <i>F. uralensis</i> nests	Stebaev and Resnikova (1972)
<i>Formica truncorum yessensis</i>	A	b, c, e, f?	III	+?	Negatively correlated with other species, mounds spaced out	Yasuno (1964a, 1965)

<i>Formica fusca japonica</i>	A	b,c?,e	II?	+	Clark and Evans' nearest neighbor analysis, where common are overdispersed	Yasuno (1964a, 1965)
<i>Formica yessensis</i>	A	b,c,e,f?	III	+?	Unicolonial, frequent budding, affect other species in habitat	Ito and Imamura (1974); Higashi and Yamuchi (1979)
<i>Camponotus herculeanus japonica</i>	A	b,c,e,f	III?	+?	Negatively correlated with other species, multiple nest openings	Yasuno (1964a)

OLD WORLD North Temperate grasslands: specialists

Formicinae						
<i>Polyergus samurai</i>	A	a?	II	+?	Nests about 300 m apart	Yasuno (1964b)

OLD WORLD North Temperate woodlands: generalists

Formicinae						
<i>Formica rufa</i>	A	b,c,e	III	+	Non-overlapping ranges, intra-nest aggression, colonies overdispersed	Elton (1932); Diver (1935); Skinner (1980)
<i>Formica lugubris</i>	A	b,c,e	III	o/+?	Unicolonial, surrounded by smaller colonies, all mutually aggressive	Cherix and Gris (1977)
<i>Formica lugubris</i>	A	b,c,e	III	+	$R = 1.32, p < 0.001$	Breen (1979)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
<i>Formica fusca</i>	B,C	b,c,e,f	II	o/+	Tested against the Poisson distribution	Brian (1952, 1955, 1956a)
<i>Formica fusca</i>	A,B	b,c,e,f	II	o/+?	No food territory, can be aggressive over resources	Brian et al. (1966)
<i>Formica exsecta</i>	A	b,c,e,f	II?	o/+?	Intra- and interspecifically territorial	Pisarski (1972)
<i>Formica polyctena</i>	A	b,c,e,f?	III	o/+	Nests along edges of dunes, maintain distinct feeding areas	Mabelis (1979) (see note 6)
<i>Formica pratensis</i>	A	b,c?,e,f	II?	+	Separated, intraspecifically aggressive nests	Stebaev and Reznikova (1972)
<i>Formica subpilosa</i>	A	b,c?,e	II?	o/+?	Nest between <i>F. pratensis</i> nests	Stebaev and Reznikova (1972)
<i>Formica uralensis</i>	A	b,c?,e,f	II?	+	Separated intraspecifically aggressive nests	Stebaev and Reznikova (1972)
<i>Formica picea</i>	A	b,c?,e	II?	o/+?	Nest between <i>F. uralensis</i> nests	Stebaev and Reznikova (1972)
<i>Formica truncorum yessensis</i>	A	b,c,e,f?	III	+	Negatively correlated with other species, mounds spaced out	Yasuno (1964a, 1965)
<i>Formica fusca japonica</i>	A	b,c?,e	II?	+	Clark and Evans' nearest neighbor analysis, where common are overdispersed	Yasuno (1964a, 1965)
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<i>Camponotus herculeanus japonica</i>	A	b,c,e,f	III?	+	Negatively correlated with other species, multiple nest openings	Yasuno (1964a)
OLD WORLD North Temperate grasslands: specialists						
Formicinae						
<i>Polyergus samurai</i>	A	a?	II	+	Nests about 300 m apart	Yasuno (1964b)
OLD WORLD North Temperate woodlands: generalists						
Formicinae						
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<i>Formica lugubris</i>	A	b,c,e	III	+	$R = 1.32, p < 0.001$	Breen (1979)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
<i>Formica lugubris</i>	A	b,c,e	III	o/-	Aggregations of nests	Sudd et al. (1977)
<i>Formica sanguinea</i>	A	b,c',e,f	II	o/+?	Mutually hostile nests, sub-divide and move frequently	Marikovsky (1963)
OLD WORLD Tropical deserts and savannahs: generalists and granivores						
Formicinae						
<i>Camponotus acvapimensis</i>	C	b,c,e,f	II?	o/+?	Intra- and interspecifically territorial	Lévieux (1971)
<i>Camponotus congolensis</i>	C	b,c,e,f	II?	o/+?	Intra- and interspecifically territorial	Lévieux (1971)
<i>Camponotus solon</i>	C	b,c,e,f	II?	o/+?	Intra- and interspecifically territorial	Lévieux and Lewis (1975)
<i>Camponotus vividus</i>	C	b,c,e,f	II?	o/+?	Intra- and interspecifically territorial	Lévieux and Lewis (1975)
<i>Camponotus maculatus</i>	C	b,c,e,f	II?	o/+?	Intra- and interspecifically territorial	Lévieux and Lewis (1975)

Myrmicinae					
<i>Messor barbatus</i>	A	b?,c?,e?,f	II?	o/+?	Nonoverlap of foraging trails, interspecific aggression Pickles (1944)
<i>Messor aegypticus</i>	A	b?,c?,e?,f	II?	o/+?	Nonoverlap of foraging trails, interspecific aggression Pickles (1944)
OLD WORLD Tropical forests: generalists					
Myrmicinae					
<i>Macromischoides aculeatus</i>	D	b,c,d,e,f	II,III?	o/+?	Nonoverlapping territories, also interspecifically aggressive Majer (1976a); Leston (1973)
<i>Crematogaster depressa</i>	D	b,c,d,e,f	II,III?	o/+?	Nonoverlapping territories, also interspecifically aggressive Majer (1976a); Leston (1973)
<i>Crematogaster striatula</i>	C	b,c,d,e,f	II,III?	o/+?	Nonoverlapping territories, also interspecifically aggressive Majer (1976a); Leston (1973)
<i>Crematogaster clariventris</i>	D	b,c,d,e,f	II,III?	o/+?	Nonoverlapping territories, also interspecifically aggressive Majer (1976a); Leston (1973)
<i>Crematogaster castanea</i>	?	b,c,d,e,f	II	o/+?	Intra- and interspecifically aggressive Steyn (1954)
<i>Pheidole megacephala</i>	A,C	b,c,d,e,f	II	o/+?	Nonoverlapping territories, also interspecifically aggressive Greenslade (1971)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
<i>Formica lugubris</i>	A	b,c,e	III	o/-	Aggregations of nests	Sudd et al. (1977)
<i>Formica sanguinea</i>	A	b,c?,e,f	II	o/+?	Mutually hostile nests, subdivide and move frequently	Marikovskiy (1963)
OLD WORLD Tropical deserts and savannas: generalists and granivores						
Formicinae						
<i>Camponotus acvapimensis</i>	C	b,c,e,f	II?	o/+?	Intra- and interspecifically territorial	Lévieux (1971)
<i>Camponotus congolensis</i>	C	b,c,e,f	II?	o/+?	Intra- and interspecifically territorial	Lévieux (1971)
<i>Camponotus solon</i>	C	b,c,e,f	II?	o/+?	Intra- and interspecifically territorial	Lévieux and Lewis (1975)
<i>Camponotus vividus</i>	C	b,c,e,f	II?	o/+?	Intra- and interspecifically territorial	Lévieux and Lewis (1975)
<i>Camponotus maculatus</i>	C	b,c,e,f	II?	o/+?	Intra- and interspecifically territorial	Lévieux and Lewis (1975)
Myrmecinae						
<i>Messor barbatus</i>	A	b?,c?,e?,f	II?	o/+?	Nonoverlap of foraging trails, interspecific aggression	Pickles (1944)
<i>Messor aegypticus</i>	A	b?,c?,e?,f	II?	o/+?	Nonoverlap of foraging trails, interspecific aggression	Pickles (1944)
OLD WORLD Tropical forests: generalists						
Myrmecinae						
<i>Macromischoides aculeatus</i>	D	b,c,d,e,f	II,III?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Majer (1976a); Leston (1973)
<i>Crematogaster depressa</i>	D	b,c,d,e,f	II,III?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Majer (1976a); Leston (1973)
<i>Crematogaster striatula</i>	C	b,c,d,e,f	II,III?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Majer (1976a); Leston (1973)
<i>Crematogaster clariventris</i>	D	b,c,d,e,f	II,III?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Majer (1976a); Leston (1973)
<i>Crematogaster castanea</i>	?	b,c,d,e,f	II	o/+?	Intra- and interspecifically aggressive	Steyn (1954)
<i>Phidole megacephala</i>	A,C	b,c,d,e,f	II	o/+?	Nonoverlapping territories, also interspecifically aggressive	Greenslade (1971)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
<i>Pheidole megacephala</i>	A,C	b,c,d,e,f	II	o/+?	Intra- and interspecifically aggressive	Steyn (1954)
<i>Pheidole megacephala</i>	A,C	b,c,d,e,f	II	o/+?	Intra- and interspecifically aggressive	Fluker and Beardsley (1970)
Dolichoderinae						
<i>Technomyrmex albipes</i>	A,C	b,c,d,e,f	II,III?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Room (1975a,b)
<i>Iridomyrmex cordatus</i>	C	b,c,d,e,f	II,III?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Greenslade (1971)
<i>Iridomyrmex humilis</i>	A,C	b,c,d,e,f	II	o/+?	Intra- and interspecifically aggressive	Fluker and Beardsley (1970)
Formicinae						
<i>Camponotus acvapimensis</i>	A	b,c,d,e,f	II?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Majer (1976a); Leston (1973)
<i>Polyrachis schiitacea</i>	?	b,c,d,e,f	II,III?	o/+?	Intra- and interspecifically aggressive	Steyn (1954)

<i>Anoplolepis longipes</i>	A,B	b,c,d,e,f	II,III?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Room (1975a,b)
<i>Anoplolepis longipes</i>	A,B	b,c,d,e,f	II,III?	o/+?	Intra- and interspecifically aggressive	Fluker and Beardsley (1970)
<i>Anoplolepis longipes</i>	A,B	b,c,d,e,f	II,III?	o/+?	Intra- and interspecifically aggressive	Greenslade (1971)
<i>Anoplolepis custodiens</i>	A	b,c,d,e,f	II,III?	o/+?	Interspecifically aggressive	Steyn (1954)
<i>Oecophylla longinoda</i>	D	b,c,d,e,f	II	o/+?	Nonoverlapping territories, also interspecifically aggressive	Hölldobler (1979b); Leston (1973); Majer (1976a)
<i>Oecophylla smaragdina</i>	D	b,c,d,e,f	II?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Greenslade (1971)
<i>Oecophylla smaragdina</i>	D	b,c,d,e,f	II?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Room (1975a,b)

OLD WORLD Tropical forests: ant plant species

Pseudomyrmecinae

<i>Pachysima aethiops</i>	C	b,c,d,e,f	II?	As plants	Restricted to <i>Barteria fiotulosa</i>	Janzen (1972)
<i>Pachysima latifrons</i>	C	b,c,d,e,f	II?	As plants	Restricted to <i>Barteria fiotulosa</i>	Janzen (1972)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
<i>Pheidole megacephala</i>	A,C	b,c,d,e,f	II	o/+?	Intra- and interspecifically aggressive	Steyn (1954)
<i>Pheidole megacephala</i>	A,C	b,c,d,e,f	II	o/+?	Intra- and interspecifically aggressive	Fluker and Beardsley (1970)
Dolichoderinae						
<i>Technomyrmex albipes</i>	A,C	b,c,d,e,f	II,III?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Room (1975a,b)
<i>Indomyrmex cordatus</i>	C	b,c,d,e,f	II,III?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Greenslade (1971)
<i>Indomyrmex humilis</i>	A,C	b,c,d,e,f	II	o/+?	Intra- and interspecifically aggressive	Fluker and Beardsley (1970)
Formicinae						
<i>Camponotus acvapimensis</i>	A	b,c,d,e,f	II?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Majer (1976a); Leston (1973)
<i>Polytrachis schitacea</i>	?	b,c,d,e,f	II,III?	o/+?	Intra- and interspecifically aggressive	Steyn (1954)
<i>Anoplolepis longipes</i>	A,B	b,c,d,e,f	II,III?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Room (1975a,b)
<i>Anoplolepis longipes</i>	A,B	b,c,d,e,f	II,III?	o/+?	Intra- and interspecifically aggressive	Fluker and Beardsley (1970)
<i>Anoplolepis longipes</i>	A,B	b,c,d,e,f	II,III?	o/+?	Intra- and interspecifically aggressive	Greenslade (1971)
<i>Anoplolepis custodiens</i>	A	b,c,d,e,f	II,III?	o/+?	Interspecifically aggressive	Steyn (1954)
<i>Oecophylla longinoda</i>	D	b,c,d,e,f	II	o/+?	Nonoverlapping territories, also interspecifically aggressive	Holldobler (1979b); Leston (1973); Majer (1976a)
<i>Oecophylla smaragdina</i>	D	b,c,d,e,f	II?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Greenslade (1971)
<i>Oecophylla smaragdina</i>	D	b,c,d,e,f	II?	o/+?	Nonoverlapping territories, also interspecifically aggressive	Room (1975a,b)
OLD WORLD Tropical forests: ant plant species						
Pseudomyrmecinae						
<i>Pachysima aethiops</i>	C	b,c,d,e,f	II?	As plants	Restricted to <i>Barteria foetida</i>	Janzen (1972)
<i>Pachysima latifrons</i>	C	b,c,d,e,f	II?	As plants	Restricted to <i>Barteria foetida</i>	Janzen (1972)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
Myrmicinae						
<i>Crematogaster</i> sp.	C	b, c, d, e, f	II	As plants	Restricted to <i>Macaranga</i> sp.	Janzen (1969)
NEW WORLD North Temperate grasslands: generalists						
Myrmicinae						
<i>Aphaenogaster treatae</i>	A	a	II	o/(+!)	V/M = 69, N.S., nest entrances at least 3 feet apart	Talbot (1954)
<i>Aphaenogaster rudis</i>	A, B	a	II	o/(+!)	When combined with <i>A. treatae</i> , V/M = 0.85, N.S.	Talbot (1954)
<i>Myrmica americana</i>	A	b, c?, f, e	II	+	Overdispersed	Traniello (unpublished)
<i>Solenopsis invicta</i>	A	b, c, d, e, f	II	+	R = 1.32, p < 0.001	Eisenberg (1972)
Formicinae						
<i>Formica ulkei</i>	A	b?, c, e, f?	III?	o	Mounds located along the edges of fields	Scherba (1958); Talbot (1961)
<i>Formica exsectoides</i>	A	b?, c, e, f?	III	o	Mounds located along the edges of fields	Nipson (1978)

<i>Formica opaciventris</i>	A	b?,c,e,f	III	+	R = 1.31, $p < 0.001$	Scherba (1964)
<i>Formica schaufussi</i>	A	b,c,e,f	III	+	R = 1.30, $p < 0.01$	Traniello (unpublished)
<i>Lasius neoniger</i>	A	b,c,e,f	III	+	Nest craters overdispersed (see text)	Traniello (unpublished)
NEW WORLD North Temperate grasslands: specialists						
Formicinae						
<i>Formica sanguinea subintegra</i>	A	a?,c?	II?	+?	Nests spread out on island, do not appear to raid the same <i>F. fusca</i> nests	Talbot and Kennedy (1940)
<i>Polyergus lucidus</i>	A	a?,c?	II?	+?	Colonies scattered widely over the fields	Talbot (1967)
NEW WORLD North Temperate woodlands: generalists						
Myrmicinae						
<i>Aphaenogaster rudis</i>	A,B	a	II	o/(+!)	V/M = 0.65, N.S., data from 9-5-50 to 10-26-50, N = 13	Talbot (1951, 1957)
<i>Aphaenogaster fulva</i>	A	b,e,f	II	o(!)	V/M = 1.46, N.S.	Headley (1952)
<i>Stenamma brevicorne</i>	A	b,e,f?	?	o/(+!)	V/M = 0.79, N.S.	Headley (1952)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
Myrmicinae						
<i>Crematogaster</i> sp.	C	b,c,d,e,f	II	As plants	Restricted to <i>Macaranga</i> sp.	Janzen (1969)
NEW WORLD North Temperate grasslands: generalists						
Myrmicinae						
<i>Aphaenogaster treatae</i>	A	a	II	o/(+!)	V/M = 69, N.S., nest entrances at least 3 feet apart	Talbot (1954)
<i>Aphaenogaster rudis</i>	A,B	a	II	o/(+!)	When combined with <i>A. treatae</i> , V/M = 0.85, N.S.	Talbot (1954)
<i>Myrmica americana</i>	A	b,c?,f,e	II	+	Overdispersed	Traniello (unpublished)
<i>Solenopsis invicta</i>	A	b,c,d,e,f	II	+	R = 1.32, p < 0.001	Eisenberg (1972)
Formicinae						
<i>Formica ulkei</i>	A	b?,c,e,f?	III?	o	Mounds located along the edges of fields	Scherba (1958); Talbot (1961)
<i>Formica exsectoides</i>	A	b?,c,e,f?	III	o	Mounds located along the edges of fields	Nipson (1978)
<i>Formica opaciventris</i>	A	b?,c,e,f	III	+	R = 1.31, p < 0.001	Scherba (1964)
<i>Formica schaufussi</i>	A	b,c,e,f	III	+	R = 1.30, p < 0.01	Traniello (unpublished)
<i>Lasius neoniger</i>	A	b,c,e,f	III	+	Nest craters overdispersed (see text)	Traniello (unpublished)
NEW WORLD North Temperate grasslands: specialists						
Formicinae						
<i>Formica sanguinea subintegra</i>	A	a?,c?	II?	+?	Nests spread out on island, do not appear to raid the same <i>F. fusca</i> nests	Talbot and Kennedy (1940)
<i>Polyergus lucidus</i>	A	a?,c?	II?	+?	Colonies scattered widely over the fields	Talbot (1967)
NEW WORLD North Temperate woodlands: generalists						
Myrmicinae						
<i>Aphaenogaster rudis</i>	A,B	a	II	o/(+!)	V/M = 0.65, N.S., data from 9-5-50 to 10-26-50, N = 13	Talbot (1951, 1957)
<i>Aphaenogaster fulva</i>	A	b,e,f	II	o(!)	V/M = 1.46, N.S.	Headley (1952)
<i>Stenamma brevicorne</i>	A	b,e,f?	?	o/(+!)	V/M = 0.79, N.S.	Headley (1952)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
<i>Leptothorax curvispinosus</i>	C	b,e,f	II	+	Intra- and interspecifically aggressive, raid and destroy nearby <i>Leptothorax</i> colonies	Alloway (1980)
<i>Leptothorax longispinosus</i>	C	b,e,f	II	+	Intra- and interspecifically aggressive, raid and destroy nearby <i>Leptothorax</i> colonies	Alloway (1980)
<i>Leptothorax ambiguus</i>	C	b,e,f	II	+	Intra- and interspecifically aggressive, raid and destroy nearby <i>Leptothorax</i> colonies	Alloway (1980)
Dolichoderinae						
<i>Dolichoderus taschenbergi</i>	A	b,c,e,f	III	+	Intraspecific aggression, nest movement away from competitors	Bradley (1972, 1973); Bradley and Hinks (1968)
Formicinae						
<i>Formica dakotensis</i>	A	b,c,e,f?	III?	o	$R \approx 0.9$, random dispersion, some parts of study site were unsuitable for nests	Francoeur and Pépin (1978)
<i>Formica obscuripes</i>	A	b,c,e,f	III	+	Intraspecific aggression; nest movement away from competitors	Bradley (1972, 1973); (1968) Bradley and Hinks (1968)

<i>Prenolepis imparis</i>	A	b,e,f	III	o/+ (?)	V/M = 0.54, N.S.	Headley (1952)
<i>Prenolepis imparis</i>	A	b,e,f	III	o/+ ?	Nests spaced out under fruit trees, aggression over food sources	Talbot (1943); Lynch et al. (1980)
<i>Camponotus noveboracensis</i>	C	b,c,e,f	III	o/+ ?	Nests spaced out where not nest site limited	Sanders (1970)
<i>Camponotus pennsylvanicus</i>	C	b,c,e,f	III	o/+ ?	Nests spaced out where not nest site limited	Sanders (1970)

NEW WORLD North Temperate woodlands: specialists

Ponerinae

<i>Ponera coarctata pennsylvanicus</i>	A	a	I	o(!)	V/M = a/1.60, N.S.	Headley (1952)
<i>Amblyopone pallipes</i>	B	a	I	o/-	Aggregated in habitat, possibly unicolonial	Traniello (unpublished)

NEW WORLD North Temperate deserts: granivores and omnivores

Myrmicinae

<i>Crematogaster emeryana</i>	C?	b?, c?, e?, f?	II?	o	R = 1.0	Bernstein and Gobbel (1979)
<i>Solenopsis xyloni</i>	A	b?, c?, e?, f?	II?	o	R = 0.6-2.1	Bernstein and Gobbel (1979)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
<i>Leptothorax curvispinosus</i>	C	b,e,f	II	+?	Intra- and interspecifically aggressive, raid and destroy nearby <i>Leptothorax</i> colonies	Alloway (1980)
<i>Leptothorax longispinosus</i>	C	b,e,f	II	+?	Intra- and interspecifically aggressive, raid and destroy nearby <i>Leptothorax</i> colonies	Alloway (1980)
<i>Leptothorax ambiguus</i>	C	b,e,f	II	+?	Intra- and interspecifically aggressive, raid and destroy nearby <i>Leptothorax</i> colonies	Alloway (1980)
Dolichoderinae						
<i>Dolichoderus taschenbergi</i>	A	b,c,e,f	III	+?	Intraspecific aggression, nest movement away from competitors	Bradley (1972, 1973); Bradley and Hinks (1968)
Formicinae						
<i>Formica dakotensis</i>	A	b,c,e,f?	III?	o	$R \approx 0.9$, random dispersion, some parts of study site were unsuitable for nests	Francoeur and Pèpin (1978)
<i>Formica obscuripes</i>	A	b,c,e,f	III	+?	Intraspecific aggression; nest movement away from competitors	Bradley (1972, 1973), (1968) Bradley and Hinks (1968)
<i>Prenolepis imparis</i>	A	b,e,f	III	o/+ (?)	$V/M = 0.54$, N.S.	Headley (1952)
<i>Prenolepis imparis</i>	A	b,e,f	III	o/+?	Nests spaced out under fruit trees, aggression over food sources	Talbot (1943); Lynch et al. (1980)
<i>Camponotus noveboracensis</i>	C	b,c,e,f	III	o/+?	Nests spaced out where not nest site limited	Sanders (1970)
<i>Camponotus pennsylvanicus</i>	C	b,c,e,f	III	o/+?	Nests spaced out where not nest site limited	Sanders (1970)
NEW WORLD North Temperate woodlands: specialists						
Ponerinae						
<i>Ponera coarctata pennsylvanicus</i>	A	a	I	o(!)	$V/M = a/1.60$, N.S.	Headley (1952)
<i>Amblyopone pallipes</i>	B	a	I	o/-	Aggregated in habitat, possibly unicolonial	Tranierlo (unpublished)
NEW WORLD North Temperate deserts: granivores and omnivores						
Myrmicinae						
<i>Crematogaster emeryana</i>	C?	b?,c?,e?,f?	II?	o	$R = 1.0$	Bernstein and Gobbel (1979)
<i>Solenopsis xyloni</i>	A	b?,c?,e?,f?	II?	o	$R = 0.6-2.1$	Bernstein and Gobbel (1979)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
<i>Veromessor andrei</i>	A	b?, c?, f?	II?	+	R = 1.2	Bernstein and Gobel (1979)
<i>Veromessor pergandei</i>	A	b, e, f	II	+	R = 1.0-1.6	Bernstein and Gobel (1979)
<i>Veromessor pergandei</i>	A	b, e, f	II	+	R = 1.5-1.6	Bernstein (1975) Byron et al. (1980)
<i>Novomessor cockerelli</i>	A	b, e, f	II	+?	Mapped quadrats	Davidson (1980)
<i>Novomessor cockerelli</i>	A	b, e, f	II	+	R = 1.7	Byron et al. (1980)
<i>Pheidole gilvaceus</i>	A	b?, c?, e?, f?	II?	o	R = 0.0-1.3, possibly did not separate colonies	Bernstein and Gobel (1979)
<i>Pheidole xerophilla</i>	A	b?, c?, e?, f?	II	-	R = 0.6-0.8, possibly did not separate colonies entrances	Bernstein and Gobel (1979)
<i>Pogonomymex californicus</i>	A	b, c?, e, f	II?	o/+	R = 0.8-1.3	Bernstein and Gobel (1979)
<i>Pogonomymex californicus</i>	A	b?, c?, e, f	II?	+	R, $p < 0.001$	DeVita (1979)
<i>Pogonomymex occidentalis</i>	A	b, c?, e?, f?	II?	+	R = 1.14	Bernstein and Gobel (1979)

<i>Pogonomyrmex</i> <i>owychii</i>	A	b, c?, e?, f?	II?	+	R = 1.14	Bernstein and Gobel (1979)
<i>Pogonomyrmex</i> <i>rugosus</i>	A	b, c, e, f	III	+	R = 1.1-1.3	Bernstein (1975); Bernstein and Gobel (1979)
<i>Pogonomyrmex</i> <i>rugosus</i>	A	b, c, e, f	III	o/+	Pielou's PD ² /ND ²	Whitford et al. (1976)
<i>Pogonomyrmex</i> <i>rugosus</i>	A	b, c, e, f	III	+	Intra- and interspecifically overdispersed	Hölldobler (1976a)
<i>Pogonomyrmex</i> <i>rugosus</i>	A	b, c, e, f	III	+	Intra- and interspecifically overdispersed	Davidson (1977a)
<i>Pogonomyrmex</i> <i>barbatus</i>	A	b, c, e, f	III	o/+	Pielou's PD ² /ND ²	Whitford et al. (1976)
<i>Pogonomyrmex</i> <i>barbatus</i>	A	b, c, e, f	III	+	Intra- and interspecifically overdispersed	Hölldobler (1976a)
<i>Pogonomyrmex</i> <i>barbatus</i>	A	b, c, e, f	III	+	Intra- and interspecifically overdispersed	Davidson (1977a)
<i>Pogonomyrmex</i> <i>desertorum</i>	A	b?, c?, e?, f?	II?	+	Intra- and interspecifically overdispersed	Davidson (1977a)
<i>Pogonomyrmex</i> <i>maricopa</i>	A	b, e, f	II	+	Intra- and interspecifically overdispersed	Hölldobler (1976a)
Dolichoderinae						
<i>Conomyrma</i> <i>insana</i>	A	b?, c?, f?	II?	o/+	R = 0.8-1.2	Bernstein and Gobel (1979)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
<i>Veromessor andrei</i>	A	b?, c?, f?	II?	+	R = 1.2	Bernstein and Gobbel (1979)
<i>Veromessor pergandei</i>	A	b, c, f	II	+	R = 1.0-1.6	Bernstein and Gobbel (1979)
<i>Veromessor pergandei</i>	A	b, c, f	II	+	R = 1.5-1.6	Bernstein (1975) Byron et al. (1980)
<i>Novomessor cockerelli</i>	A	b, c, f	II	+	Mapped quadrats	Davidson (1980)
<i>Novomessor cockerelli</i>	A	b, c, f	II	+	R = 1.7	Byron et al. (1980)
<i>Pheidole givescens</i>	A	b?, c?, e?, f?	II?	o	R = 0.0-1.3, possibly did not separate colonies	Bernstein and Gobbel (1979)
<i>Pheidole xerophilla</i>	A	b?, c?, e?, f?	II	-	R = 0.6-0.8, possibly did not separate colonies entrances	Bernstein and Gobbel (1979)
<i>Pogonomyrmex californicus</i>	A	b, c?, e, f	II?	o/+	R = 0.8-1.3	Bernstein and Gobbel (1979)
<i>Pogonomyrmex californicus</i>	A	b?, c?, e, f	II?	+	R, $p < 0.001$	DeVita (1979)
<i>Pogonomyrmex occidentalis</i>	A	b, c?, e?, f?	II?	+	R = 1.14	Bernstein and Gobbel (1979)
<i>Pogonomyrmex owyheei</i>	A	b, c?, e?, f?	II?	+	R = 1.14	Bernstein and Gobbel (1979)
<i>Pogonomyrmex rugosus</i>	A	b, c, e, f	III	+	R = 1.1-1.3	Bernstein (1975); Bernstein and Gobbel (1979)
<i>Pogonomyrmex rugosus</i>	A	b, c, e, f	III	o/+	Pielou's PD^2/ND^2	Whitford et al. (1976)
<i>Pogonomyrmex rugosus</i>	A	b, c, e, f	III	+	Intra- and interspecifically overdispersed	Hölldobler (1976a)
<i>Pogonomyrmex rugosus</i>	A	b, c, e, f	III	+	Intra- and interspecifically overdispersed	Davidson (1977a)
<i>Pogonomyrmex barbatus</i>	A	b, c, e, f	III	o/+	Pielou's PD^2/ND^2	Whitford et al. (1976)
<i>Pogonomyrmex barbatus</i>	A	b, c, e, f	III	+	Intra- and interspecifically overdispersed	Hölldobler (1976a)
<i>Pogonomyrmex barbatus</i>	A	b, c, e, f	III	+	Intra- and interspecifically overdispersed	Davidson (1977a)
<i>Pogonomyrmex desertorum</i>	A	b?, c?, e?, f?	II?	+	Intra- and interspecifically overdispersed	Davidson (1977a)
<i>Pogonomyrmex maricopa</i>	A	b, c, f	II	+	Intra- and interspecifically overdispersed	Hölldobler (1976a)
Dolichoderinae						
<i>Conomyrma insana</i>	A	b?, c?, f?	II?	o/+	R = 0.8-1.2	Bernstein and Gobbel (1979)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
<i>Conomyrma bicolor</i>	A	b?, c?, f	II	o/-	R = 0.3-0.8, did not separate nests	Bernstein and Gobel (1979)
<i>Conomyrma bicolor</i>	A	b, c, f	II	o/-	Multiple nest openings, possibly unicolonial	Möglich and Alpert (1979); Alpert (pers. communication)
<i>Iridomyrmex pruinosum</i>	A	b?, c?	II?	o/+	R = 0.9-2.1	Bernstein and Gobel (1979)
<i>Tapinoma sessile</i>	A?	b?, c?	II?	+	R = 1.2	Bernstein and Gobel (1979)
Formicinae						
<i>Camponotus vicinus</i>	B	?	II?	+	R = 1.3-1.6	Bernstein and Gobel (1979)
<i>Formica altipetens</i>	A	b?, c?	II, III?	o	R = 0.9	Bernstein and Gobel (1979)
<i>Formica planipilis</i>	A	b?, c?	II, III?	+	R = 1.2	Bernstein and Gobel (1979)
<i>Formica rorida</i>	A	b?, c?	II, III?	+	R = 1.4	Bernstein and Gobel (1979)
<i>Myrmecocystus kennedei</i>	A	b?, c?	II?	o/+	R = 0.9-1.6, depending upon density	Bernstein and Gobel (1979)

<i>Myrmecocystus mexicanus</i>	A	b,c	II	+	R = 1.3-1.7	Bernstein and Gobbel (1979)
<i>Myrmecocystus mexicanus</i>	A	b,c	II	+	R = 1.2	Alpert (unpublished)
<i>Myrmecocystus depilis</i>	A	b,c	II	+	R = 1.3	Alpert (unpublished)
<i>Myrmecocystus mimicus</i>	A	b,c,e	II	+	Intraspecific colony destruction	Hölldobler (1976b); Alpert (unpublished)

NEW WORLD Tropical forests: generalists

Ponerinae

<i>Ectatomma ruidum</i>	A	b,c,e,f	I	+	Clark and Evans' nearest neighbor analysis, nests overdispersed	Levings and Franks (1982)
<i>Odontomachus bauri</i>	A	b,c,e,f	I	+	Clark and Evans' nearest neighbor analysis, nests overdispersed	Levings and Franks (1982)

Myrmicinae

<i>Cephalotes atratus</i>	C	a,b,c?,e,f	II	o/+	Aggression between colonies, possibly nest site limited	Corn (1976, pers. communication)
<i>Pheidole biconstricta</i> group species (4+)	A,C	b,c?,e,f	II	+	Clark and Evans' nearest neighbor analysis, overdispersed	Levings and Franks (1981)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
<i>Conomyrma bicolor</i>	A	b?,c?,f	II	o/-	R = 0.3-0.8, did not separate nests	Bernstein and Gobbel (1979)
<i>Conomyrma bicolor</i>	A	b,c,f	II	o/-	Multiple nest openings, possibly unicolonial	Moglich and Alpert (1979); Alpert (pers. communication)
<i>Iridomyrmex pruinosum</i>	A	b?,c?	II?	o/+	R = 0.9-2.1	Bernstein and Gobbel (1979)
<i>Tapinoma sessile</i>	A?	b?,c?	II?	+	R = 1.2	Bernstein and Gobbel (1979)
Formicinae						
<i>Camponotus vicinus</i>	B	?	II?	+	R = 1.3-1.6	Bernstein and Gobbel (1979)
<i>Formica altipetens</i>	A	b?,c?	II,III?	o	R = 0.9	Bernstein and Gobbel (1979)
<i>Formica planipilis</i>	A	b?,c?	II,III?	+	R = 1.2	Bernstein and Gobbel (1979)
<i>Formica rorida</i>	A	b?,c?	II,III?	+	R = 1.4	Bernstein and Gobbel (1979)
<i>Myrmecocystus kennedei</i>	A	b?,c?	II?	o/+	R = 0.9-1.6, depending upon density	Bernstein and Gobbel (1979)
<i>Myrmecocystus mexicanus</i>	A	b,c	II	+	R = 1.3-1.7	Bernstein and Gobbel (1979)
<i>Myrmecocystus mexicanus</i>	A	b,c	II	+	R = 1.2	Alpert (unpublished)
<i>Myrmecocystus depilis</i>	A	b,c	II	+	R = 1.3	Alpert (unpublished)
<i>Myrmecocystus mimicus</i>	A	b,c,e	II	±?	Intraspecific colony destruction	Hölldobler (1976b); Alpert (unpublished)
NEW WORLD Tropical forests: generalists						
Ponerinae						
<i>Ectatomma ruidum</i>	A	b,c,e,f	I	+	Clark and Evans' nearest neighbor analysis, nests overdispersed	Levings and Franks (1982)
<i>Odontomachus bauri</i>	A	b,c,e,f	I	+	Clark and Evans' nearest neighbor analysis, nests overdispersed	Levings and Franks (1982)
Myrmicinae						
<i>Cephalotes atratus</i>	C	a,b,c?,e,f	II	o/+	Aggression between colonies, possibly nest site limited	Corn (1976, pers. communication)
<i>Pheidole biconstricta</i> group species (4+)	A,C	b,c?,e,f	II	+	Clark and Evans' nearest neighbor analysis, overdispersed	Levings and Franks (1981)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
<i>Wasmannia auropunctata</i>	C	b,c,e,f	II	+	Clark and Evans' nearest neighbor analysis, overdispersed	Levings and Franks (1982)
<i>Pheidole</i> misc. (3 species)	A,C	b,c,e,f	II	o/+	Clark and Evans' nearest neighbor analysis, overdispersed	Levings and Franks (1982)
Dolichoderinae						
<i>Monacis valida</i>	C	b,c,e,f	III	+?	Probably limited to nest sites, aggressive to other species as well as conspecifics (canopy dominant)	Swain (1977, pers. observation)
<i>Monacis omancantha</i>	C	b?,c?,e?,f?	III	+?	Probably similar to <i>M. valida</i>	Swain (1977)
<i>Monacis bispinosa</i>	C	b,c,e,f	III	+?	Canopy dominant with <i>Camponotus</i> , <i>Azteca</i> , etc., may be nest site limited as well	Swain (1977); pers. observation
NEW WORLD Tropical forests: army ants						
Dorylinae						
<i>Eciton burchelli</i>	D	a	V	o	Randomly distributed on Barro Colorado Island	Franks (1980)

NEW WORLD Tropics: leaf cutters (Attini)

Myrmicinae

<i>Acromyrmex octospinosus</i>	A	a,c?,e?	III	o/+	Overdispersed if in well drained areas, random or clumped if in waterlogged areas	Lewis (1975)
<i>Atta columbica</i>	A	a,c,e,f	III	+	Fight for trees in dry season—food limited	Rockwood (1973)
<i>Atta cephalotes</i>	A	a,c,e,f	III	+	Fight for trees in dry season—food limited	Rockwood (1973)
<i>Atta cephalotes</i>	A	a,c,e	III	+?	Larger nests have larger home ranges	Lewis et al. (1974)
<i>Atta sexdens</i>	A	a,c,e	III?	+?	Frequent internest conflicts in an expanding population	Autori (1941)

NEW WORLD Tropical forests: ant-plant species

Dolichoderinae

<i>Azteca alfari</i> (and <i>Azteca</i> spp.)	C	b,c,d,e,f	III?	As plants	Found only on <i>Cecropia</i> spp.	Janzen (1969)
<i>Azteca</i> spp.	C	b,c,d,e,f	III?	As plants	Found only on <i>Cordia</i> spp.	Janzen (1969)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
<i>Wasmannia auropunctata</i>	C	b,c,e,f	II	+	Clark and Evans' nearest neighbor analysis, over-dispersed	Levings and Franks (1982)
<i>Pheidole</i> misc. (3 species)	A,C	b,c,e,f	II	o/+	Clark and Evans' nearest neighbor analysis, over-dispersed	Levings and Franks (1982)
Dolichoderinae						
<i>Monacis valida</i>	C	b,c,e,f	III	+?	Probably limited to nest sites, aggressive to other species as well as conspecifics (canopy dominant)	Swain (1977, pers. observation)
<i>Monacis omanantha</i>	C	b?,c?,e?,f?	III	+?	Probably similar to <i>M. valida</i>	Swain (1977)
<i>Monacis bispinosa</i>	C	b,c,e,f	III	+?	Canopy dominant with <i>Camponotus. Azteca</i> , etc., may be nest site limited as well	Swain (1977); pers. observation
NEW WORLD Tropical forests: army ants						
Dorylinae						
<i>Eciton burchelli</i>	D	a	V	o	Randomly distributed on Barro Colorado Island	Franks (1980)

NEW WORLD Tropics: leaf cutters (Attini)**Myrmicinae**

<i>Acromyrmex octospinosus</i>	A	a,c?,e?	III	o/+	Overdispersed if in well drained areas, random or clumped if in waterlogged areas	Lewis (1975)
<i>Atta columbica</i>	A	a,c,e,f	III	+	Fight for trees in dry season—food limited	Rockwood (1973)
<i>Atta cephalotes</i>	A	a,c,e,f	III	+	Fight for trees in dry season—food limited	Rockwood (1973)
<i>Atta cephalotes</i>	A	a,c,e	III	+?	Larger nests have larger home ranges	Lewis et al. (1974)
<i>Atta sexdens</i>	A	a,c,e	III?	+?	Frequent internest conflicts in an expanding population	Autori (1941)

NEW WORLD Tropical forests: ant-plant species**Dolichoderinae**

<i>Azteca alfari</i> (and <i>Azteca</i> spp.)	C	b,c,d,e,f	III?	As plants	Found only on <i>Cecropia</i> spp.	Janzen (1969)
<i>Azteca</i> spp.	C	b,c,d,e,f	III?	As plants	Found only on <i>Cordia</i> spp.	Janzen (1969)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
<i>Pseudomyrmecinae</i>						
<i>Pseudomyrmex</i> sp.	C	b,c,d,e,f	I?	As plants	Found only on <i>Triplaris</i> sp.	Janzen (1969)
<i>Pseudomyrmex ferruginea</i> and related species (4+)	C	b,c,d,e,f	I?	As plants	Found in <i>Acacia</i> ssp. colonies intra- and interspecifically aggressive	Janzen (1973)
<i>Pseudomyrmex venefica</i> and related species (2+)	C	b,c,d,e,f	I?	As plants	Unicolonial, on <i>Acacia</i> spp.	Janzen (1973)
AUSTRALIAN Deserts and savannahs: generalists						
<i>Myrmicinae</i>						
<i>Nothomyrmecia macrops</i>	A	a?	I?	o	Randomly dispersed	Ward and Taylor (in prep.)
<i>Myrmecia tarsata</i>	A	b?,e	I	+	Intraspecifically territorial and overdispersed	Muir (1974)
<i>Myrmecia similima</i>	A	b?,e	I	+	Intraspecifically territorial and overdispersed	Muir (1974)

<i>Myrmecia</i> <i>decipiens</i>	A	b?,e	I	+	Intraspecifically territorial and overdispersed	Muir (1974)
<i>Myrmecia</i> <i>pilosula</i>	A	b?,e	I	+	Intraspecifically territorial and overdispersed	Muir (1974)
Dolichoderinae						
<i>Iridomyrmex</i> <i>detectus</i>	A	b?,c?,e	II,III?	+?	Internest aggression, trails from different nests do not overlap	Duncan-Weatherly (1953)
<i>Iridomyrmex</i> <i>purpureus</i>	A	b,c,e,	II,III?	+	Uniform distribution of nests, complete occupancy of area	Greenslade (1975)
Formicinae						
<i>Calomyrmex</i> <i>?splendidus</i>	A	b?,e?	II?	-	Clark and Evans' nearest neighbor analysis, did not separate nests, nest openings clumped (whole colony foraging areas actually overdispersed)	Brough (1976)

Table 1 (cont.)

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
Pseudomyrmecinae						
<i>Pseudomyrmex</i> sp.	C	b,c,d,e,f	I?	As plants	Found only on <i>Triplaris</i> sp.	Janzen (1969)
<i>Pseudomyrmex ferruginea</i> and related species (4+)	C	b,c,d,e,f	I?	As plants	Found in <i>Acacia</i> spp. colonies intra- and interspecifically aggressive	Janzen (1973)
<i>Pseudomyrmex venefica</i> and related species (2+)	C	b,c,d,e,f	I?	As plants	Unicolonial, on <i>Acacia</i> spp.	Janzen (1973)
AUSTRALIAN Deserts and savannahs: generalists						
Myrmeciinae						
<i>Nothomyrmecia macrops</i>	A	a?	I?	o	Randomly dispersed	Ward and Taylor (in prep.)
<i>Myrmecia tarsata</i>	A	b?,e	I	+	Intraspecifically territorial and overdispersed	Muir (1974)
<i>Myrmecia simillima</i>	A	b?,e	I	+	Intraspecifically territorial and overdispersed	Muir (1974)
Dolichoderinae						
<i>Iridomyrmex detectus</i>	A	b?,c?,e	II,III?	+	Internest aggression, trails from different nests do not overlap	Duncan-Weatherly (1953)
<i>Iridomyrmex purpureus</i>	A	b,c,e	II,III?	+	Uniform distribution of nests, complete occupancy of area	Greenslade (1975)
Formicinae						
<i>Calomyrmex splendidus</i>	A	b?,c?	II?	-	Clark and Evans' nearest neighbor analysis, did not separate nests, nest openings clumped (whole colony foraging areas actually overdispersed)	Brough (1976)

Table 1

Species	Nest site ¹	Defense type ²	Forager type ³	Nest spacing ⁴	Evidence ⁵	Source
AUSTRALIAN Forests: granivores						
Formicinae						
<i>Prolasius pallidus</i>	A	b?,c,e,f	II	o/+	V/M test, overdispersed in forest with bare floor	Ashton (1979)
<i>Prolasius bruneus</i>	A	b?,c	II	o/+	V/M test, overdispersed in forest with bare floor	Ashton (1979)
<i>Prolasius flavicornis</i>	A	b?,c?	II	o/+	V/M test, overdispersed in forest with bare floor	Ashton (1979)

¹A, ground or mound; B, under rock; C, preformed cavity (wood, etc.); D, constructed by ants (leaf nests, carton, etc.)
²a, nest defense only; b, short term resources; c, persistent resources; d, area (true territoriality); e, intraspecific defense; f, interspecific defense

³I, individual foragers for prey approximately the same size as the ant; II, recruit one or more nestmates to food; III, use trunk trails; IV, specialist on difficult prey; V, true group foragers (modified from Oster and Wilson, 1978)

⁴o, random; -, clumped; +, overdispersed; o/+, o/-, tends to overdispersion or clumping

⁵V/M, variance to mean ratio; !, our measurements or statistics based on published data; R, Clark and Evans' nearest neighbor analysis, $R = 1$, random dispersion, $R > 1$, overdispersed, $R < 1$, clumped

⁶Mabelis (1979) studied this species in dunes; it is usually found in woodland.

competitors are removed can provide additional evidence for competitive effects on spacing and foraging patterns.

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THE EFFECT OF FLOWER OCCUPANCY ON THE FORAGING OF FLOWER-VISITING INSECTS*

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INTRODUCTION

To locate flowers, insects use a variety of visual and olfactory cues such as flower color, shape, movement and scent (Faegri and van der Pijl 1971). In addition, other insects on the flowers may also serve as cues that either attract or repel prospective foragers. First, foragers might avoid occupied inflorescences because: 1) there is a high probability that other flowers on the inflorescence have been recently exploited (Pleasants and Zimmerman 1979, Zimmerman 1981); 2) of the potential loss of time and energy due to aggressive encounter with the occupant (Kikuchi 1963, Decelles and Laroca 1979); 3) the occupant might be an enemy (e.g., thomisids, phymatids, etc.). Thus, when flowers are abundant, unoccupied inflorescences may yield a greater quantity of energy and/or nutrients per unit effort. If so, the distribution of foragers across inflorescences should be regular or underdispersed, i.e., there should be more inflorescences with only one insect than expected on the assumption of a random distribution.

Existing evidence also suggests that a second hypothesis is tenable. Prospective foragers may be attracted by floral occupants because: 1) the presence of other foragers indicates that resources are available on the inflorescence; 2) the occupants themselves are sources of pollen to some foragers (Laroca and Winston 1978, Thorp and Briggs 1980). If insects are attracted to occupied inflorescences, then their distribution across inflorescences should be over-dispersed.

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In this paper we use data for insects foraging on plantings of commercial sunflowers (*Helianthus annuus* L.) and onions (*Allium cepa* L.) to test these hypotheses.

An additional question of interest is whether bee species differ in their distribution across flowers. For example, Benest (1976) has suggested that honeybees (*Apis mellifera* L.) are more tolerant of joint foraging than are bumblebees (*Bombus* sp.) and Kalmus (1954) reported that honeybees tend to form clusters at artificial feeding sites. Group foraging, leading to clumped distributions on flowers has also been reported for several tropical bee species (Frankie and Baker 1974). To ascertain if the distribution of the multispecies assemblage obscured differences among the component species, we compared the distributions of the more abundant species with the balance of other foraging individuals on the inflorescences.

METHODS

Five cultivars of sunflower and 2 of onions were grown at the Greenville Farm Agricultural Research Station in North Logan, Utah. Sunflowers were planted in 5 adjacent 40m rows, 1 row per cultivar. The 2 onion cultivars were planted alternately in 4 adjacent rows, 2 rows per cultivar.

Counts of floral visitors were made several times during the flowering period as 1 observer (FDP) walked along each row. A tape recorder facilitated observations. Only heads with some open flowers were censused.

The data were transcribed to number of flower heads with zero, one, two, etc. insects and then compared with values expected on the assumption of a Poisson distribution (Southwood 1978). The Poisson series describes a random distribution and is written $P_x(k) = e^{-\bar{x}}(\bar{x}^k/K!)$ where e = base of Napierian logarithms, and P_x is the expected number of flower heads with k insects ($k = 0, 1, 2, \dots$). The parameter \bar{x} is estimated by the mean number of insects per flower head. For the Poisson distribution, the mean and variance are equal, and an indication of the dispersion of insects across flowers is given by the coefficient of dispersion ($C.D. = s^2/\bar{x}$). When $C.D.$ is >1.0 the dispersion is clumped or contagious; and when <1.0 dispersion is regular or repulsed (Southwood 1978). The expected

and observed distributions were tested for significance using the χ^2 test (Zar 1974).

The distributions of more abundant species across sunflower heads was compared with the balance of the foraging assemblage as follows: each individual recorded was assigned to one of two mutually exclusive categories, according to whether it foraged alone or with at least one other insect (irrespective of species) on the inflorescence. A chi-square test of independence was used to compare each species represented by >10 individuals with the balance of the assemblage.

RESULTS

Bees were the predominant visitors to sunflowers; we recorded 15 species in 5 families (Appendix). The species were similar to that reported previously by Parker (1981) for the same study site. Onion visitors included many species of wasps and flies that did not forage on sunflowers. In contrast to sunflowers, there were more non-bee than bee visitors to onions.

For all sunflower censuses the distribution of total insects across flower heads did not differ significantly from a Poisson distribution, i.e., insects appeared to be foraging independently of other insects. The coefficients of dispersion were mostly around 1.0. There was no tendency for C.D.'s to be greater or less than 1; for 8 censuses C.D. was >1.0 and for 6 censuses C.D. <1.0 . (Table 1).

Only 2 of 7 censuses of onions deviated significantly from a random distribution (Table 1). Both deviations occurred on the same day and were in the direction of under-dispersion; more heads with single visitors were recorded than expected. There was a general tendency for insects visitors to be under-dispersed on onions; in all tests C.D. > 1.0 .

There was no indication that any particular species foraged other than randomly, with respect to other occupants of sunflower heads. The results of 34 comparisons of the distribution of individuals of abundant species with the balance of foragers for the single and joint foraging categories are shown in Table 2. Only one comparison yielded significant results; another closely approached significance (7/31 Peredovik, AM, *Halictus ligatus*, $P = 0.051$). It is likely that these two instances were due to chance.

Table 1. Total flower heads, mean insects per head, coefficient of dispersion ($C.D. = s^2/\bar{x}$) and probability levels (X^2 test) for insects visiting sunflower and onion heads. All counts made between 1000–1100 hrs except those with asterisks which were made between 1400–1500 hrs.

Sunflower	Total heads	Mean insects/head	C.D.	Prob	Onions	Total heads	Mean insects/head	C.D.	Prob
<i>Date/variety</i>					<i>Date/variety</i>				
7/25/Peredovik	47	1.21	1.00	>0.50	7/23/P54	772	0.18	0.98	>0.25
7/30/Peredovik	54	1.07	1.51	>0.25	7/25/P54	846	0.13	0.94	>0.10
/Sigo	30	1.53	1.12	>0.50	/P2	456	0.16	0.94	>0.05
7/31/Peredovik	83	0.92	0.83	>0.25	7/30/P54	610	0.19	0.91	<0.025
/Sigo	55	1.96	1.72	>0.25	/P2	326	0.16	0.84	<0.05
8/ 5/Sigo	210	0.84	0.99	>0.10	7/31/P54	456	0.09	0.96	>0.50
/Peredovik	100	0.45	0.91	>0.25	/P2	393	0.13	0.92	>0.10
/SW501	211	0.13	0.88	>0.05					
/254	148	0.64	1.02	>0.10					
/W501	194	0.46	0.91	>0.10					
/Sigo*	207	0.51	1.08	>0.25					
/Peredovik*	94	0.35	0.90	>0.50					
/SW501*	206	0.22	1.10	>0.10					
/254*	160	0.45	1.03	>0.25					
/W501*	195	0.61	1.04	>0.50					

DISCUSSION

In this study, foraging insects did not appear to react to the presence of other insects in choosing flowers. Only 2 of the censuses on onions and none of the censuses on sunflowers displayed a significant departure from a random distribution (Table 1). Sunflower foragers (*Apis*, *Perdita*, *Halictus*) frequently entered the flower by landing on the back of the petals or on the involucre bracts and then crawling onto the head. If occupancy by another insect were important, this would be an inefficient method of choosing a flower. In a similar study Waddington (1976) also concluded that halictid bees were foraging independently on bindweed (*Convolvulus arvensis*). None of the abundant species present appeared to forage other than randomly with respect to other flower occupants. This was especially surprising for honeybees which have been reported to more readily tolerate, or even form, clumped distributions (Kalmus 1954, Benest 1976). However, contagious distributions of honeybees may occur only under unusual circumstances; the data of Kalmus (1954) were gathered from a small number of feeding dishes and are quite artificial. Benest's (1976) suggestion that honeybees are more tolerant of joint foraging than bumblebees does not stand close examination. Additional study is required before such conclusions are warranted.

Instead of using the presence of insects on inflorescences as cues, some flower-visiting insects may make selections based on the number of open flowers or the amount of nectar or pollen available. Although all heads censused had some open flowers, some had more open flowers than others and insects may have been choosing those heads with more flowers irrespective of other visitors. Even if heads were equivalent in number of flowers, continuous removal of nectar and pollen by foragers would cause variation in resource availability between heads (e.g., Pleasants and Zimmerman 1979) and insects may be responsive to such variation prior to landing on a flower. For example, Thorp *et al.* (1975) have suggested that the fluorescent nectar (and perhaps pollen) of many species with open flowers may be used as a cue by foraging insects (see also Kevan 1976, Thorp *et al.* 1976); and onion nectar is intensely fluorescent (Thorp *et al.* 1975). Recently Heinrich (1979) has shown that bumblebee foragers reject many more nectar depleted (recently visited) white clover (*Trifolium repens*) heads than heads with abundant nectar. Rejec-

Table 2. Results of chi-square tests of individuals of abundant species vs. other foragers for single vs. joint occupancy. Asterisks as in Table 1.

Species	Chi-Square Values						
	<i>Melissodes agilis</i>	<i>Halictus ligatus</i>	<i>Halictus farinosus</i>	<i>Apis mellifera</i>	<i>Megachile pugnata</i>	<i>Bombus</i> spp.	<i>Syrphidae</i>
<i>Date/Variety</i>							
7/25 Peredovik	0.0	0.1	—	—	—	—	—
7/30 Peredovik	1.7	0.4	0.0	—	—	—	—
Sego	0.3	2.0	—	—	—	—	—
7/31 Peredovik	2.3	3.8	0.5	—	—	—	—
Sego	1.1	2.3	0.2	—	—	—	—
8/5 Sego	0.5	—	—	0.3	0.0	0.7	1.2
Peredovik	—	—	—	0.1	—	—	—
SW501	—	—	—	0.0	—	—	—
254	0.1	0.1	—	0.2	—	—	—
W501	0.2	—	—	1.3	—	—	—
Sego*	0.0	—	—	1.7	—	0.0	—
Peredovik*	5.2 α	—	—	0.6	—	—	—
SW501*	—	—	—	2.6	—	—	—
254*	0.4	—	—	0.3	—	—	—
W501*	—	—	—	0.0	—	—	—

$\alpha p < 0.025$

tion was accomplished without landing and the cue was probably scent of nectar (Heinrich 1979). Future field studies should explore the use of these more subtle cues by foraging insects.

ACKNOWLEDGMENTS

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APPENDIX

Insect taxa visiting sunflower and onion plantings.

Sunflowers

Hymenoptera: Bees—Andrenidae [*Andrena helianthi* Robertson, *Perdita* sp., *Pseudopanurgus* sp., *Pterosarus* sp.]; Anthophoridae [*Melissodes agilis* Cresson, *Svastra obliqua* (Say), *Triepeolus helianthi* (Robertson)]; Apidae [*Apis mellifera* Linnaeus, *Bombus* spp.]; Halictidae [*Agapostemon* sp., *Dialictus* sp., *Halictus farinosus* Smith, *Halictus ligatus* Say]; Megachilidae [*Megachile parallela* Smith, *Megachile pugnata* Say].

Diptera: Syrphidae

Lepidoptera: Hesperiiidae

Onions

Hymenoptera: Bees—Apidae [*Bombus* sp.]; Halictidae [*Evyaleus* sp, *Halictus farinosus* Smith, *Halictus ligatus* Say]; Megachilidae [*Hoplitis fulgida* (Cresson), *Megachile pacifica* (Panzer), *Megachile* sp.].

Wasps—Eumenidae [*Euodynerus* sp., *Pterocheilus* sp.]; Ichneumonidae; Sphecidae [*Amomphila* sp., *Astata* sp., *Cerceris* sp., *Philanthus* sp., *Podalonia* sp., *Sphex* sp., *Tachytes* sp.]

Diptera: Muscidae; Nemestrinidae; Sarcophagidae; Syrphidae; Tachinidae.

Lepidoptera: Hesperiiidae

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ABDOMINAL TROPHALLAXIS IN THE SLAVE-MAKING
ANT, *HARPAGOXENUS AMERICANUS*
(HYMENOPTERA: FORMICIDAE)*

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Abdominal trophallaxis refers to the passage of fluids from the abdominal tip of one individual to the mouthparts of another. It is common among lower termites (Kalotermitidae and Rhinotermitidae) where it functions in the vital transmission of intestinal flagellates to newly molted individuals. However, it has rarely been documented among ants (Wilson, 1971, 1976). By strict definition, the term abdominal trophallaxis should be applied only when alimentary fluid is being transmitted (Wilson, 1971). Nevertheless, in practice, the origin of the fluid is often unknown, at least initially. Indeed, in all cases where this behavior has been described in ants, the fluid is either suspected of being, or has since been shown to be, ovarian in nature. For example, workers of certain *Eciton* species (Dorylinae) readily feed from droplets secreted from the tip of the queen's abdomen, but this behavior has been observed only during egg-laying bouts (Schneirla, 1944; Rettenmeyer, 1963). So-called "proctodeal feeding" has also been described among the Dolichoderinae (*Dolichoderus quadripunctatus*, *Tapinoma erraticum* and *Iridomyrmex humilis*) (Torossian, 1958, 1959, 1960, 1961). However, at least in the case of *D. quadripunctatus*, the fluid has been identified as the yolky remnants of abortive trophic eggs (Torossian, 1978, 1979). Among the Myrmicinae, *Zacryptocerus varians* exhibits a similar behavior which is also thought to be associated with egg-laying (Wilson, 1976). This paper reports an unusual and interesting case of abdominal trophallaxis in colonies of the socially parasitic myrmicine ant, *Harpagoxenus americanus*. I have followed Wilson (1976) and tentatively applied the term abdominal trophallaxis, because the origin of the fluid is unknown.

H. americanus is an obligatory slave-maker and forms mixed colonies with members of certain *Leptothorax* species in eastern

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North America (Alloway, 1979). The observations reported here took place in artificial nests in the laboratory (Alloway, 1979) and utilized colonies of *H. americanus* containing one or both of its host species, *L. ambiguus* and *L. longispinosus*. The colonies were collected in the regional municipalities of Halton and Peel, Ontario.

Intermittent observations of activity inside *H. americanus* nests revealed that slave-maker queens and workers occasionally convey fluids to their slaves by means of abdominal trophallaxis. Donors characteristically raise their abdomens and assume a stereotyped posture, similar to that seen during "sexual calling" ("Locksterzeln") in other leptothoracine ants (Buschinger and Alloway, 1979). I was unable to ascertain whether the sting is exposed in the present context, as it is during "sexual calling" and "tandem calling", a similar behavior used during nest-mate recruitment in some leptothoracine ants (Möglich et al., 1974). While maintaining this posture, the donor secretes a droplet of clear fluid from the tip of her abdomen, and holds it there, at times for several minutes. Slaves do not seem to be attracted from any appreciable distance by this behavior, but those close by turn and antennate the donor's abdomen, apply their mouthparts to the tip, and consume the droplet. As many as three slaves have been observed to attend a donor simultaneously in this manner, clustered about her abdominal tip and attempting to consume the droplet. On one occasion, the droplet was removed from the donor's abdomen by three workers in concert, held between their mandibles momentarily, and then consumed. Once the droplet is removed, the donor lowers her abdomen, and both donor and recipients appear to resume normal activities. There is no indication that slaves ever solicit this fluid; and to date, the reverse, slaves donating to slave-makers, has not been observed. Similarly, this behavior has never been observed in laboratory colonies of the host species. The nature of the fluid transmitted is unknown. It may be ovarian in origin, since *H. americanus* workers will lay eggs, even in queenright colonies (Buschinger and Alloway, 1977). The frequency of this behavior is uncertain. It appears to be rare, since frequent observations of colonies for other purposes have seldom encountered it. However, no detailed behavioral repertoire study of this ant has been conducted.

The fact that *H. americanus* employs a characteristic posture during abdominal trophallaxis suggests that this behavior may have

important biological consequences. Furthermore, the apparent absence of this behavior in free-living lepto thoracic ants, and the fact that transmission is consistently from slave-maker to slave, suggests that abdominal trophallaxis may in some way contribute to this species' particular socially parasitic relationship. The discovery of this behavior in a slave-making ant opens a previously unknown avenue for consideration in discussions of the means by which slave-makers may affect the behavior of their slaves.

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NEW NAME FOR THE EXTINCT GENUS *MESAGYRTES* PONOMARENKO (COLEOPTERA: SILPHIDAE S.L.)

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Mesagyrtes communis Ponomarenko, a new beetle genus and species attributed to Silphidae, has recently been described from fossil-bearing beds of Jurassic age from the locality of Novospassk, USSR (Arnoldi et al., 1977: 117). Unfortunately the generic name is preoccupied by *Mesagyrtes* Broun (1895: 95), proposed for a Recent New Zealand species originally placed in Silphidae; this genus is now considered a subgenus of the genus *Colan* Herbst of the family Leiodidae (Szymczakowski 1964).

I have brought the homonymy to the attention of Dr. Ponomarenko, who has kindly allowed me to propose a replacement name for use in publications on the family Silphidae now in preparation. Accordingly, I propose **Mesecanus**, new name, to replace *Mesagyrtes* Ponomarenko (not Broun). The new name alludes to the resemblance in habitus between the extinct genus and the Recent agyrtine silphid genus *Ecanus* Stephens.

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HISTORICAL DEVELOPMENT OF BEE FORAGING PATTERNS IN CENTRAL NEW YORK STATE

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INTRODUCTION

The bee fauna of the northeastern United States has changed markedly in the past few centuries. The impetus for this change came largely from human activities, notably from introductions of foreign species and modifications of the regional flora. Several bee species, most notably the honey bee (*Apis mellifera*), were introduced into this region (Crane 1975; Linsley 1958). Honey bees can powerfully influence the foraging patterns of native bees (Pearson 1933; Eickwort and Ginsberg 1980). Replacement of forests over large areas by cities and farms (Ferguson and Mayer 1970; Vaughan 1929) and numerous introductions of alien plant species (Wiegand and Eames 1925) have resulted in major changes in northeastern plant communities.

How broad were these changes and how have they influenced the foraging ecology of northeastern bees? What was this area like before the European settlers arrived? The answers to these questions are vital to an understanding of contemporary bee foraging patterns and of community level interactions between flowers and their pollinators. The purpose of this paper is to describe some general trends in the foraging patterns of Apoidea in central New York State, and to interpret them in terms of the historical development of the flora and bee fauna of the region.

MATERIALS AND METHODS

The study site was a 5.8 hectare abandoned field (last cultivated about 1956) located near Ithaca, New York. It was bordered by

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wooded areas and cultivated fields. The soils were well-drained and flower bloom was profuse. More than 150 entomophilous species bloomed on the field. The most common woody plants were red maple (*Acer rubrum*), staghorn sumac (*Rhus typhina*), and various willows (*Salix* spp.), dogwoods (*Cornus* spp.), and brambles (*Rubus* spp.). The dominant herbaceous plants included several entomophilous species and the grasses timothy (*Phleum pratense*) and orchard grass (*Dactylis glomerata*).

I sampled Apoidea by walking transects and capturing bees from flowers. There were 10, 30 m transects randomly-placed on the field. I took transect samples during times of maximum foraging activity (1000–1600 hours) throughout the season (at least 3 samples in each 2-week period, late May–October, 1974 and 1975). I used all-day samples from randomly-selected patches of common flower species (throughout the growing season, 1975 and 1976) to confirm the results from the transect samples and to study spatial distributions of foraging bees. Voucher specimens of the bee species are placed in the Cornell University Insect Collection, lot number 1039.

I counted the number of flowers of each species at anthesis in 100, 1m² subquadrats. The subquadrats were arranged in groups of 10, randomly-placed within 30 m × 30 m quadrats (the bee transects were also within these quadrats). There were 10 quadrats randomly-placed on the field. Flowers were sampled once every 2 weeks throughout the season. Voucher specimens of the plant species are placed in the Bailey Hortorium Herbarium, Cornell University. Details of the field techniques are given by Ginsberg (1979).

I used the records of Fernald (1950) and Wiegand and Eames (1925) to determine whether flower species were native or were introduced into the area. Their determinations were based largely on the records of early botanical explorers (e.g. Pursh 1923) and on previous species lists for the area (e.g. Dudley 1886). Admittedly, there is some margin for error in these judgements, but because of the large number of entomophilous species on the sample site, mistakes about the points of origin of a few species should not influence the major arguments.

RESULTS

Red maple was the first abundant flower species to bloom on the field in spring. Several willows and rosaceous trees (*Prunus cerasus*,

Pyrus malus) bloomed soon after, as did several roadside weeds such as dandelion (*Taraxacum officinale*) and yellow rocket (*Barbarea vulgaris*). The spring species were typically clustered in distribution at roadsides and forest edges, and the woody species had relatively short blooming times. Of 16 species recorded on the field in spring (late April and early May in 1975) half were native and half were introduced. I do not include any of the several species that bloomed in the woods nearby.

Flower bloom increased on the field to a maximum in early summer (late June, early July). Most of the species in bloom at this time of the year were introduced (Fig. 1). Table I lists the most common of these species and gives their frequencies of occurrence in the subquadrats. Note that the most common flowers at this time were those of introduced herbaceous species. Most flowers of these species were past blooming by midsummer.

In August, goldenrods (*Solidago* spp.) predominated on the field. These late summer flowers are native to this region (Table I). *Aster*, another native genus of composites, predominated after goldenrod passed bloom in the fall. Late season flowers, therefore, were mostly native species (Fig. 1).

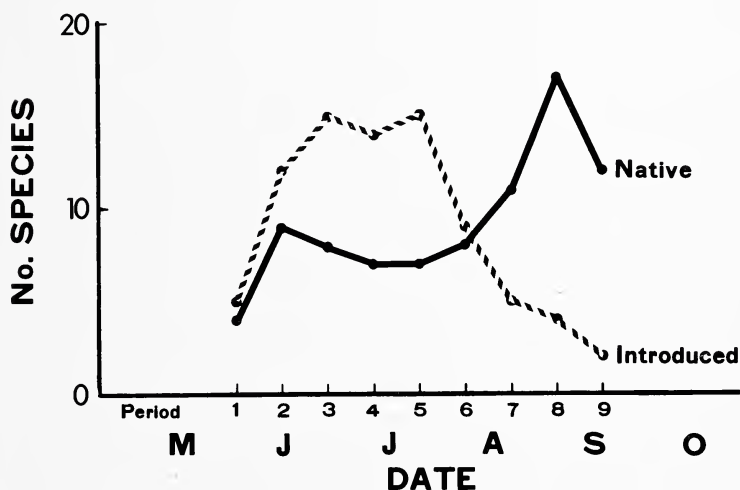


Fig. 1. Number of introduced and native flower species blooming over the summer, 1974, in an old field near Ithaca, New York.

Table 1. Frequencies of common flower species, 1974

Flower species	Origin ¹	Time of maximum bloom	Frequency ²	No. inflorescences/m ² ³
<i>Hieracium pratense</i>	I	mid June	70	12.55 \pm 2.06
<i>Chrysanthemum leucanthemum</i>	I	late June	54	2.21 \pm 0.32
<i>Cornus racemosa</i>	N	late June	12	2.10 \pm 1.10
<i>Satureja vulgaris</i>	N	late July	30	12.11 \pm 3.08
<i>Achillea millefolium</i>	I	late August	20	1.04 \pm 0.34
<i>Daucus carota</i>	I	late August	30	0.87 \pm 0.20
<i>Solidago juncea</i>	N	late August	60	12.86 \pm 2.08
<i>S. graminifolia</i>	N	early Sept.	54	9.16 \pm 1.85
<i>S. rugosa</i>	N	early Sept.	44	8.42 \pm 2.03
<i>S. altissima</i>	N	early Sept.	62	14.69 \pm 3.05

¹ N = native species; I = introduced species

² Number of 1 m² subquadrats (out of 100) in which species was flowering during period of maximum bloom.

³ Mean number of inflorescences (sprays for *Solidago*) per subquadrat during period of maximum bloom \pm standard error.

This flowering trend of early-summer introduced species and late-summer-fall native species probably holds for central New York as a whole. In Figure 2 I plotted the number of open-habitat, entomophilous species blooming in the entire Cayuga Lake Basin during each 2-week period over the season (compiled from Wiegand and Eames 1925). Again, introduced species predominate in early summer. Later in the summer, native and introduced species are about equal in number, but the tremendous abundance of goldenrod (Table I; also Ginsberg 1979, Hurlbert 1970) results in a preponderance of native flowers late in the season.

Foraging phenologies of the most common bee species indicate a partitioning of the season according to foraging times. Native wild bees (mostly primitively social halictines) predominated in early summer, while *Apis mellifera* predominated in late summer (Table II). This presents the interesting situation that native bees foraged primarily on introduced flowers in early summer, while the introduced honey bees foraged on native flowers in late summer and fall (Table III).

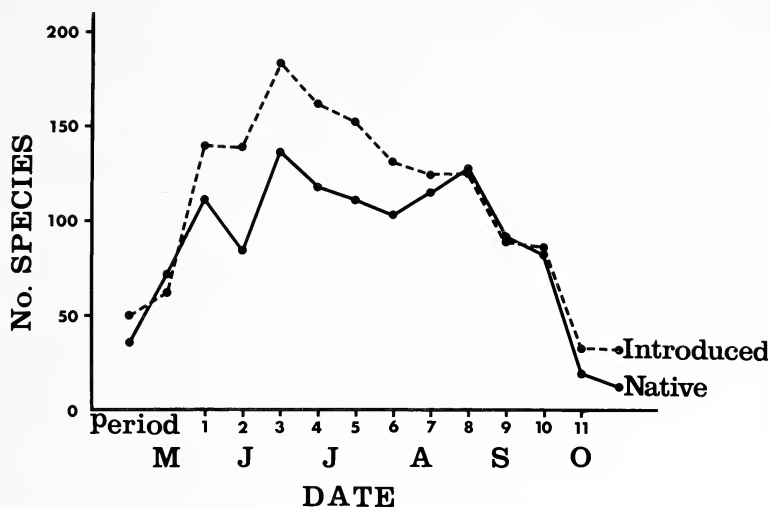


Fig. 2. Number of introduced and native flower species blooming in the Cayuga Lake Basin (compiled from Wiegand and Eames 1925).

Table II. Percent of honey bees in transect samples, 1974

Period	Dates	% honey bees ¹	N
1	22 May-4 June	2.1	48
2	5 June-18 June	1.9	52
3	19 June-2 July	9.0	67
4	3 July-16 July	7.6	79
5	17 July-30 July	13.8	29
6	31 July-13 August	15.9	44
7	14 Aug-27 August	79.8	119
8	28 Aug-10 September	95.2	230
9	11 Sept.-24 Sept.	89.7	78

¹ Percent of bees captured in transect samples that were *Apis mellifera*. Other bees in these samples were native wild bees (except for 3 individuals of *Andrena wilkella* captured on 28 May, 12 June, and 8 July—this species was probably introduced into the region).

Table III. Flower species most commonly visited by bees during the summer, 1974

Bee species ¹	Flower species ¹	% of visits ²	sample size ³
<i>Apis mellifera</i> (I)	<i>Solidago altissima</i> (N)	26.2	409
	<i>S. graminifolia</i> (N)	24.0	
	<i>S. juncea</i> (N)	18.8	
<i>Ceratina</i> ⁴ (N)	<i>Rubus allegheniensis</i> (N)	28.0	50
<i>Halictus ligatus</i> (N)	<i>Chrysanthemum leucanthemum</i> (I)	51.2	43
	<i>Potentilla recta</i> (I)	47.6	
<i>Halictus confusus</i> (N)	<i>Potentilla recta</i> (I)	47.6	21
<i>Auguchlorella striata</i> (N)	<i>Chrysanthemum leucanthemum</i> (I)	37.5	24
	<i>Potentilla recta</i> (I)	47.4	

¹ Point of origin given in parentheses; N = native to North America; I = introduced.

² Percent of individuals of that bee species in samples that were on named flower species.

³ Number of bees of that species in transect samples, 1974.

⁴ Includes *Ceratina dupla* and *C. calcarata*. Females of these species are indistinguishable at present.

Spring-flying bees were not included in Table II because they foraged on flowers that were most common off the field and could not be sampled by the transect technique. All-day samples from patches of common spring flowers revealed a great diversity of native bees, primarily solitary, univoltine species of *Andrena*, *Dialictus*, and *Ceratina*. Honey bees were also common in spring, especially on willows, rosaceous trees, and on large clusters of dandelion and yellow rocket.

DISCUSSION

The fact that native bees foraged on introduced flowers in early summer, while introduced bees predominated on native flowers in late summer, suggests that this type of old field association is quite recent in origin. Indeed, the development of this curious pattern can be clarified by tracing the recent biotic history of the Ithaca area.

Early explorers in the region (up until the early 1800's) reported extensive forested areas that were thickest near the head of Cayuga Lake and to the south of Ithaca (Dudley 1886). The Indians cleared considerable acreages for villages, corn fields, etc. (Day 1953) and kept corridors of land clear for stalking deer by annual burning

(Dudley 1886). These cleared areas were probably far less extensive than present-day open habitats. Also, the deer-stalking grounds differed from modern old fields because they were burned each year, and because they lacked many of the introduced flower species that are now common. Some of these species were introduced by 1807, when the explorer Frederick Pursh passed through Ithaca (Dudley 1886; Pursh 1923).

The first settlers arrived in Ithaca about 1789 (Dudley 1886). By the mid 1800's extensive areas of land had been cleared for farming and settlements. Total acreage used for farming reached a peak in New York State (approximately 23,780,754 acres) about 1880. Since then, gradual abandonment of farmland has given rise to many abandoned fields. By 1925, only 19,269,926 acres of farmland remained (Vaughan 1929). By the late 1960's the area of crop and pasture land in New York State totalled only about 8,771,800 acres (Ferguson and Mayer 1970). Much of this farm land was lost to villages and cities, but a considerable amount was left as abandoned fields. In the late 1800's and early 1900's several weedy species were introduced, and many others increased in abundance in central New York. Among the species that became common at this time were *Hieracium pratense* and *Potentilla recta* (Wiegand and Eames 1925), both important species at my sample site (Tables I and III). Taken together, these facts suggest that the current floral composition of old-field communities in central New York is on the order of 100 years old.

As a result of these changes in the local flora, at least three new classes of abundant flower forage have become available to bees. In spring, the introduced rosaceous trees and roadside weeds provide considerable forage. Second, the increased acreage of abandoned fields, along with introductions of several plant species, results in an historically novel flower bloom in early summer. Finally, the large acreage of open fields results in an unprecedented profuse bloom of goldenrod in late summer.

The honey bee was introduced into North America by the early colonists (Crane 1975). The Italian strain (*Apis mellifera ligustica*), which now predominates in New York State, was not introduced until 1859 (Ruttner 1975). Some more recent introductions into the Ithaca area include the megachilids *Megachile rotundata* (Mitchell 1962) and *Anthidium manicatum* (Pechuman 1967), and the andre-

nid *Andrena wilkella* (Linsley 1958). At my study site, the honey bee is far the most abundant of these species (Ginsberg 1979). In the 1950's, honey bee populations declined sharply in New York State due to the increased use of pesticides and the decline in farm acreage devoted to buckwheat, an important food source for honey bees (Morse 1975). Before 1950, therefore, honey bees were even more common than at present.

Apis mellifera is a high-density specialist in flower foraging. Its large colony size and recruitment capabilities facilitate this specialization (Eickwort and Ginsberg 1980; Sakagami 1959). In spring, honey bees forage on high-density resources such as rosaceous trees, willows, and clusters of roadside herbs. In late summer, honey bees forage on the super-abundant goldenrods, also high-density resources.

In early summer, honey bees are relatively rare on the old field (Table II). At this time of season they forage primarily off the field on high-density resource species in forests and on cultivated fields (Farrar 1944; Ginsberg 1979). The introduced herbs that bloom at this time are exploited by primitively social halictines (Table III). The multivoltine seasonal cycles of these bees allow them to build up their populations over the season, thus they can exploit the recently introduced flower species that are now abundant in early summer. *Ceratina*, which is probably univoltine in the Ithaca area, is also common in early summer, but it forages somewhat earlier than the halictine bees, and is most common on native flowers such as *Rubus* spp. (Table III).

An interesting result of this analysis is that each of the major historically novel instances of resource abundance is exploited by social bees. Honey bees forage on rosaceous trees and roadside weeds in spring, and on goldenrods in late summer. Native bees forage on these flowers also, but honey bees predominate because of their high populations and recruitment ability, both features related to their social behavior. Social halictines predominate on introduced herbs in early summer because of their broad host ranges and their multivoltine seasonal cycles, also related to their sociality. Apparently, the ability to adapt to landscape-level changes in resource availability is an important advantage that accompanies social behavior in bees. This does not mean that only social insect species can adapt rapidly to changes in resource levels. It does suggest that in bees, sociality facilitates this rapid adaptability.

CONCLUSIONS

In an abandoned field in central New York State, native bees foraged predominantly on introduced flower species in early summer, while the introduced honey bee predominated on native goldenrods in late summer. This situation results from recent changes in the flora and fauna of the region.

The activities of European settlers have caused large-scale changes in the flora of the northeastern United States. These changes result primarily from introductions of alien species, and from clearing of land for farming with subsequent abandonment. At present, there are at least three instances of profuse flowering over the season that are historically novel to this area. These are the abundant bloom of introduced trees and roadside weeds in spring, the flowering peak of introduced weeds in early summer, and the profuse flowering of native goldenrods in late summer. In all three of these cases, the predominant foragers are social bees; honey bees in spring and late summer, and social halictines in early summer. The ability of these bees to exploit historically novel pulses of flowering results from features related to their social behavior; large colony size and recruitment ability in *Apis mellifera*, and the multivoltine seasonal cycle in the social halictines.

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MYRMECOPHILIC RELATIONSHIP OF *PELLA*
(COLEOPTERA: STAPHYLINIDAE) TO
LASIUS FULIGINOSUS (HYMENOPTERA: FORMICIDAE)

BY B. HÖLLDOLBER*, M. MÖGLICH**, U. MASCHWITZ***

INTRODUCTION

A large number of staphylinid beetles are closely associated with ants and termites (for review see Wilson 1971, Kistner 1979). Those species living with ants are commonly called myrmecophiles. At least a few (*Atemeles*, *Lomechusa*) have "broken" the communication code of their host species and are thereby able to become completely integrated in the social system of the ants (Hölldobler 1967, 1970, 1971). In an attempt to understand the evolutionary pathways of this highly specialized social parasitic behavior, we studied closely related staphylinid species that do not live within the ant society but instead occupy the foraging trails and garbage dumps of an ant nest.

Many of such myrmecophilous staphylinids can be found with the formicine ant *Lasius fuliginosus* and most of them belong to the genus *Pella*. Apparently these beetles are not endowed with the behavioral repertory that would enable them to live within the ant colony, although they seem to have a close ecological association with ants (Hölldobler 1972).

Kistner (1971) redefined the genus *Zyras* and raised the former subgenus *Pella* to generic rank. The first behavioral observations concerning *Pella* (= *Zyras*, *Myrmedonia*) were published by Wasmann (1886, 1930). He stated that these beetles feed on dead or disabled ants, but that they also lie in wait near the entrance and hunt ants returning to the nest. Furthermore, Wasmann pointed out that because of their generalized and primitive structure these beetles can be regarded as close to the ancestral forms from which some of the more specialized staphylinid myrmecophiles were derived.

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MATERIAL AND METHODS

At our major study sites near Ochsenfurt, Riederau (both Bavaria, W.-Germany) and Gravenbruch (Hessen, W.-Germany) we found 12 staphylinid species associated with *Lasius fuliginosus* (Tab. 1). Our investigations concentrated on the genus *Pella* (mainly *P. funesta*, *P. laticollis* and *P. cognata*). Since the myrmecophilous behavior of these species was found to be very similar we will refer to the individual species only where necessary. In fact, when observing the beetles in the field it was usually not possible to identify the species precisely. We made additional observations with *Pella humeralis*, which can be found with *L. fuliginosus*, but which often also occurs near the nests of *Formica polyctena* (Wasmann 1920; Kolbe 1971).

The field observations were conducted throughout the years 1967–1969, and sporadically in 1970–1973. In an attempt to follow the life cycle of the beetles in the laboratory we set up a large colony of *Lasius fuliginosus* in a laboratory nest. The culture and maintenance of these ants over a longer period of time was particularly difficult, because *L. fuliginosus* constructs carton nests with the aid of a special symbiotic fungus (*Cladosporium myrmecophilum*). A detailed description of the nest building behavior of *L. fuliginosus* and of the laboratory nest is given in Maschwitz and Hölldobler (1970).

In order to measure quantitatively possible trophallactic feeding of the myrmecophiles by their host ants, tracer experiments were carried out using the radioisotope ^{32}P mixed with honey-water. The quantity of marked food taken up by the ants was reflected in the counts per minute which were determined with a standard Geiger-

Table 1
Staphylinids found near one nest of *Lasius fuliginosus*.

<i>Pella laticollis</i>	<i>Oxydopa vittata</i>
<i>Pella lugens</i>	<i>Rugilus rufipes</i>
<i>Pella cognata</i>	<i>Thiasophila inquilina</i>
<i>Pella funesta</i>	<i>Homoeusa acuminata</i>
<i>Pella humeralis</i>	<i>Sipalia circellaris</i>
	<i>Atheta fungi</i>
	<i>Atheta sodalis</i>

Müller counter combined with an automatic sample changer (Philips). For further information concerning the tracer techniques applied in this study see Gösswald and Kloft 1958; Kloft 1959.

For histological investigations live specimens were fixed in alcoholic Bouin (Dubosq Brasil) or Carnoy (Romeis 1948), embedded in Methyl Methacrylate, and sectioned 5-8 μ thick with a Jung Tet-rander microtome (Rathmayer 1962). The staining was Azan (Heidenhain).

For the chemical analysis of the defensive secretions of *Pella*, liquid material was collected with glass capillaries from the dissected glandular reservoirs or washed with water from the surface of the irritated beetles. The quinones were identified by thinlayer chromatography as 2,4 - dinitrophenylhydrazine in 2 N hydrochloric acid or by reduction with sulphurous acid. The dinitrophenylhydrazones were separated on alumina F 254 (Merck) with chloroform methanol (19:1) as mobile phase and on silica gel F 254 (Merck) with benzene-ethyl acetate (4:1) as mobile phase (Moore 1968). The hydroquinones were separated on silica gel F254 with benzene dioxane (3:1) as mobile phase and then sprayed with a solution of 0.5% hydrogen peroxide and a solution of peroxidase. The newly formed quinones were made visible by spraying with DNP and treating with ammonia vapour (Schildknecht and Krämer 1962). Hydrocarbons, terpenes and carbonic acids were analyzed by GLC. We used a Perkin Elmer chromatograph, model 300, equipped with a flame ionization detector. Columns: 1.8m \times 2.7mm stainless steel, packed with a) 4% polypropylene glucol on Chromosorb G (100°C column temperature); b) 4% polyethyleneglycol 1500 on Chromosorb G (70°C); c) 25% diethylhexyl sebacinate plus sebacinic acid on Kieselgur 60-100 (140°C) (30 ml N₂/min; FID).

RESULTS

The life cycle of *Pella funesta*

The following description of the life cycle of *Pella funesta* is based on field observations and on data obtained from laboratory cultures. *Pella laticollis* appears to have a similar life cycle, but our observational data are not as complete as for *P. funesta*.

In late March and early April a large number of *P. funesta* beetles were typically found in the excavation material on the base of the trunks of *L. fuliginosus* nest trees. At this time most of the beetles

were lying motionless in the loose material and showed a kind of "dormance posture": the abdomen was bent over its back, with the legs and antennae folded tightly to the body. On warmer days, however, the beetles exhibited high locomotory and flight activity, and in the laboratory they showed a strong positive phototaxis. During this period we frequently observed beetles copulating in the laboratory nests. Toward the end of April the sexual behavior and flight activities ceased. In the laboratory as well as in the field the beetles were now active primarily during the night, while during the daytime they clustered under shelters near the *Lasius fuliginosus* nest. Only occasionally were we able to spot a beetle outside the shelters at daytime.

Also near the end of April we found the first beetle eggs in the "garbage dumps" of the laboratory nest of *L. fuliginosus*, and by early May the first *Pella* larvae had hatched. The larvae developed quite rapidly, so that in mid-May we found the first pupae in the "garbage dumps" of the ant nests, even though larvae could still be found throughout the months of June and July. In June the mortality of adult beetles in our laboratory nest increased markedly and in late July and August the first young beetles eclosed from their pupae. These beetles, as well as those collected in the field in early August, exhibited strong positive phototaxis and high flight activity for a few days. After this short period, however, the beetles were primarily active at night and during the day they stayed in shelters. Finally, in October, the number of beetles found outside the ant nest declined markedly and by November no more beetles could be found outside the nest. In December we excavated to *L. fuliginosus* nests. In both nests we found several *Pella* beetles in "dormance position" covered by loose nest material of the peripheral nest chambers and on the ground inside the nest tree trunk. Presumably these beetles were overwintering within the *Lasius fuliginosus* nest until their activity period would start again in early spring the coming year.

From these observations we propose the following life cycle for *Pella funesta*: in early spring the adult beetles deposit eggs near the ants' "garbage dump" area. The larvae develop in the "garbage dump", pupate during the period from May to July and between July-August the adult beetles eclose. After eclosion the young beetles apparently migrate, as indicated by the short period of high diurnal locomotory and flight activity. After this period the beetles

forage near the *L. fuliginosus* nest during the night and stay in shelters during the day. They overwinter in dormancy inside the *L. fuliginosus* nest. With the end of winter the beetles enter a second diurnal activity phase during which mating takes place. After reproduction the beetles die, normally a few weeks before the new beetle generation ecloses in June.

The behavior of the larvae of *Pella*

The description of the behavior of the larvae is primarily based on observations in the laboratory. In the field and in the laboratory nest, the larvae were almost exclusively found near or in the "garbage dumps" of the *L. fuliginosus* nests. We frequently observed the larvae feeding on dead ants (Fig. 1B). During feeding the larvae always attempted to stay "out of sight" either by remaining entirely beneath the booty and devouring it from below or by crawling inside the dead ant's body. Occasionally 2-4 larvae could be observed feeding on the same ant cadaver. But when they became too crowded they frequently attacked each other, sometimes resulting in one larvae eating the other (Fig. 1C).

When ants encountered the larvae they usually attacked them. Almost invariably the larvae reacted with a typical defense behavior. They raised their abdominal tip towards the head of the ants. Usually the ant responded by stopping the attack and palpating the larva's tip (Fig. 1A). In most cases this short interruption was enough to allow the larvae to escape. We observed hundreds of such encounters between ants and *Pella* larvae; only a few ended fatally for the larvae.

Histological investigations revealed that the *Pella* larvae have a complex dorsal glandular structure with a reservoir near the abdominal tip in the second last segment. In addition we found single cell glands positioned dorso-laterally in each segment. Similar glandular structures had previously been found in larvae of the myrmecophile staphylinids *Atemeles* and *Lomechusa*, and circumstantial evidence strongly indicated that in these species the glands produce so-called pseudopheromones which release adoption behavior in the host ants (Hölldobler 1967). We have no evidence to suggest that these glands have a similar function in *Pella*. However, it is possible that the more complex glandular structure at the abdominal tip, produces an appeasement secretion by which the aggressiveness of attacking ants can be briefly blunted.

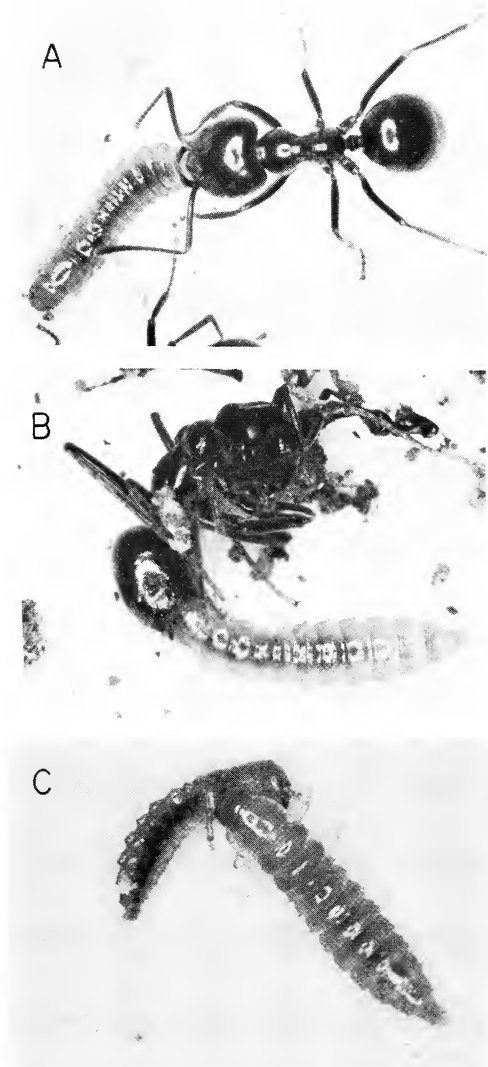


Fig. 1 Behavior of the larvae of *Pella*. A) Larva presenting abdominal tip to an attacking worker of *Lasius fuliginosus*. The ant interrupts attack and licks at the larva. B) Larva feeds on dead ant. C) Cannibalistic behavior of *Pella* larvae.

In any case, *Pella* larvae are able to come into close contact to workers of *L. fuliginosus* without being attacked, especially when the temperature is low (14–17°C). Under those circumstances we have seen the beetle larvae licking the cuticle of live ants, including even the mandibles and mouthparts. This led us to the question of whether the beetle larvae occasionally solicit regurgitation in ants. In order to investigate this possibility ants were fed with honey-water labeled with the isotope ^{32}P and then housed together with beetle larvae. For each sample we kept 30 radioactive ants with 5 beetle larvae in plastic containers (10 × 15 cm) with a moist gypsum bottom. One experimental series was conducted in a temperature range of 14.5–16.5°C, the other in 20–23°C. After 24 hours we measured the amount of radioactivity in each individual ant and larva. No significant amount of radioactivity had been transferred from the ants to the larvae, except in container 6, where one ant was found dead and obviously partly eaten by the larvae. Since the amount of radioactivity carried by some of the larvae was only very slightly above the background activity, we concluded that it was transferred by contamination. From this experiment it appears that the *Pella* larvae do not solicit regurgitation in ants. Their main food source seems to be dead ants or debris of the ants. In fact, they can easily be raised by keeping them entirely separated from living ants, just by feeding them regularly with dead ants.

Predatory behavior of adult beetles

Since Wasmann's early observations (1886, 1920, 1925) very little has been reported concerning the biology of the myrmecophilous *Pella*. Wasmann reported that all species he had studied (*P. humeralis*, *P. funesta*, *P. cognata*, *P. similis*, *P. lugens* and *P. laticollis*) live with *Lasius fuliginosus*, and only *P. humeralis* can also be found with species of the *Formica rufa* group. According to Wasmann all these *Pella* species prey on ants, concentrating especially on disabled ants. In addition Wasmann observed that the beetles are active primarily during the night. In a more recent publication Kolbe (1971) failed to find a predatorial behavior in *P. humeralis* and concluded that this species primarily feeds on dead ants. Similar observations were made with *Pella japonicus*, which lives with *Lasius spathepus* (= *L. fuliginosus* var. *spathepus* Wheeler) (Yasumatsu 1937; Kistner 1971). Kistner also observed that these beetles "ate small insects that are being transported by the

ants". However, he could not "see the *Pella* eating live ants or fighting any of the ants on the trail".

Our observations of *Pella funesta*, *P. laticollis* and *P. humeralis* confirmed that these species live as scavengers, feeding on dead or disabled ants and debris discarded by the ants. However, we also observed these beetles acting as very effective predators on the ants. Most of the following studies were made with *P. laticollis* and *P. funesta*.

During the main foraging season from May to October *Lasius fuliginosus* is active day and night. Foragers travel along well established trunk trails to feeding sites which are sometimes more than 40 m distant. At daytime we only occasionally saw *Pella* beetles moving along or nearby the trail. However, when we watched the trunk trails with a flash light at night many *Pella* were seen running along the ants' foraging routes. Although most beetles were found within a range of 5 m from the nest tree of *L. fuliginosus*, we also found beetles on the trunk trail as far as 22 m away from the nest.

On 6 different occasions we witnessed *Pella* beetles hunting *L. fuliginosus* workers at night on the foraging trail. When an ant was killed it was dragged a few centimeters away from the trail and eaten under a shelter, sometimes by several beetles simultaneously.

More detailed observations on the behavioral interactions of *Pella* and *L. fuliginosus* were made in the laboratory. As long as enough dead ants were available at the ants' nest midden, the beetles showed no predatory behavior at all, limiting themselves to a diet of ant cadavers (Fig. 2A). But when the beetles were starved for a few days and then placed together with ants in an observation arena, the predation by *Pella* became strikingly prominent, although the time of onset was often very unpredictable. We saw the beetles hunting during the daytime, but we observed such activity most frequently in the evening or at night. The beetles chased after individual ants and pursued them through approximately 2-6 cm (very rarely through longer distances than that). When the beetle moved directly behind the ant it attempted to mount it and insert its head between the ant's head and thorax. When attacked the ant usually reacted by suddenly stopping and pressing the femur rapidly and tightly to its body (Fig. 5). Often this reaction threw the beetle off the back of the ant, allowing the ant to escape. In one series of observations we counted 178 beetle onslaughts on *L. fuliginosus* workers within a period of 3 hours; of these, only 9 attempts (5%) were successful.

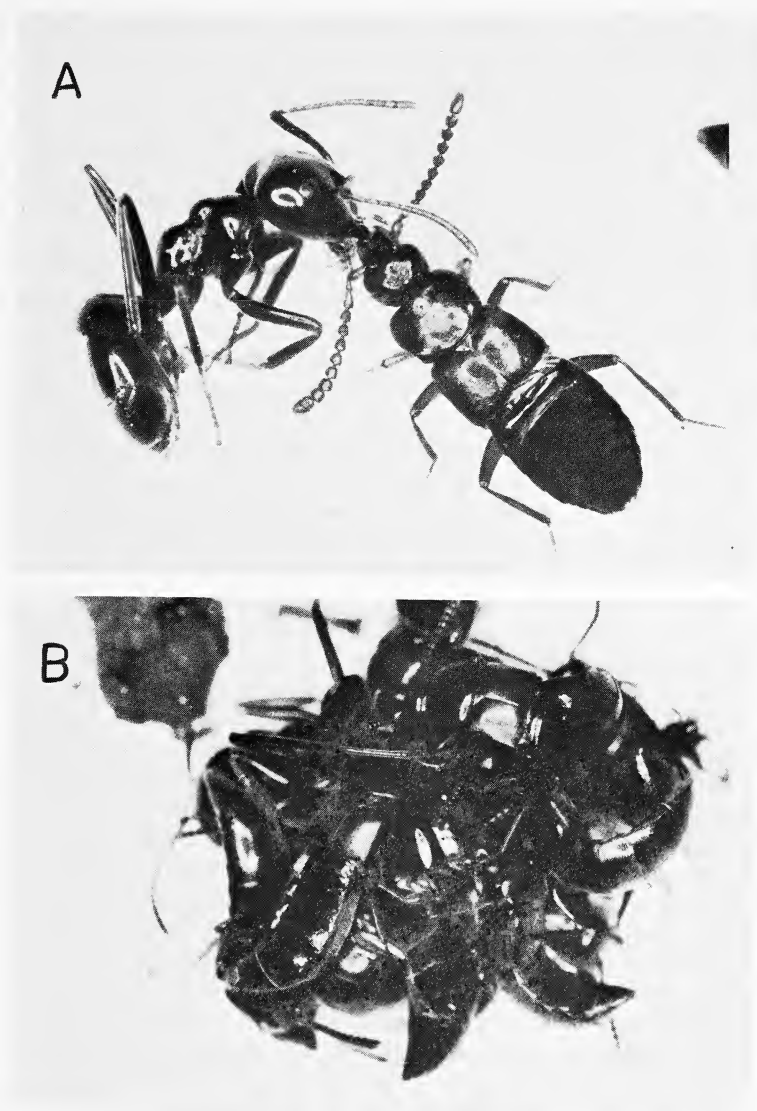


Fig. 2 A) *Pella* beetle feeding on dead *L. fuliginosus* worker. Frequently the beetles lick first the mouth parts of the ants, before tearing the cadavers apart. They might be attracted to mouthparts by sweet remainders of honeydew. B) Cluster of *Pella* beetles around a prey object.

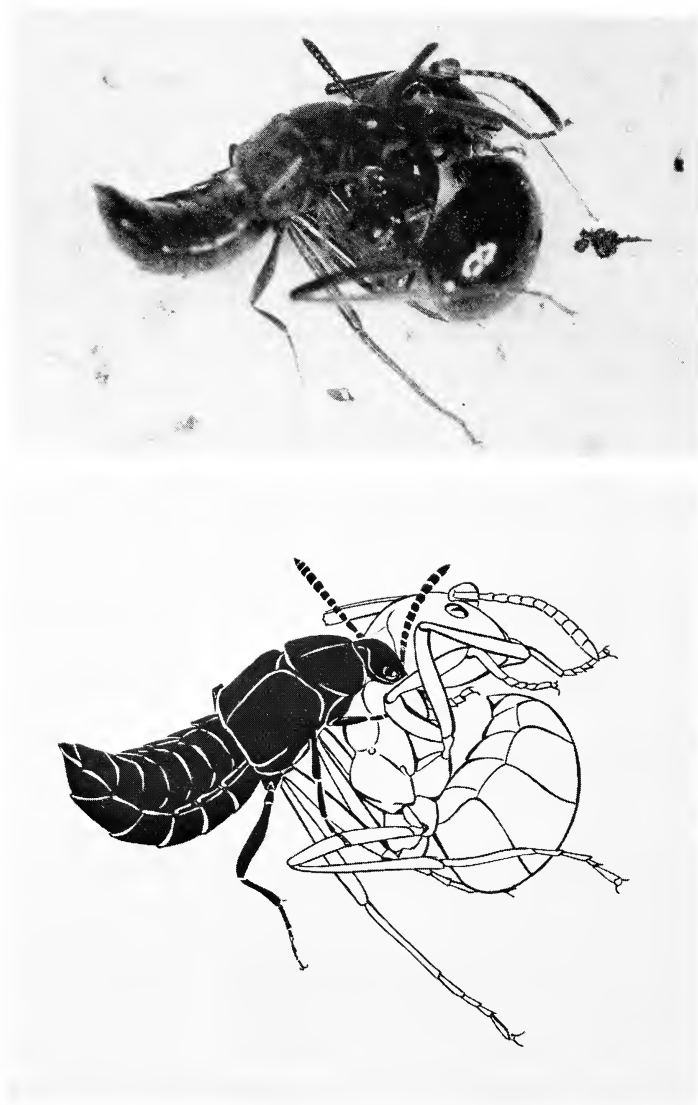


Fig. 3 Photograph and drawing of *Pella* attacking live worker of *L. fuliginosus*.

The hunting behavior of the beetles was always the same in *P. laticollis*, *P. funesta* and *P. humeralis*: the beetle attacked from behind and always attempted to insert its head between the head and thorax of the ant. We inspected several ants which had just been immobilized by an attack of a beetle and found that in most cases the pronotum was widely separated from the head and usually the oesophagus and connectives of the nervous system were cut.

Occasionally we observed 2–3 beetles chasing behind one ant (Fig. 4). Once the ant was caught by a beetle the other beetles joined in subduing and killing the ant. Although individual beetles often tried to drag the prey away from the rest of the “hunting pack”, usually several beetles fed on the prey simultaneously. No aggression among the beetles was observed in this situation. However, when the beetles were starved for several days and were kept without ants, they occasionally chased each other, jumping on each other’s back as they normally did when hunting ants. But we never saw cannibalistic behavior among the adult beetles, even when the beetles were densely crowded around a prey object (Fig. 2B).

Defense and appeasement behavior in adult beetles

Defense with tergal gland secretion:

Usually the *Pella* beetles run around with their abdomen curved slightly upwards. When encountering an ant, the beetles flex the abdomen even more strongly. This is a typical and frequently described behavior of many staphylinid myrmecophiles and is commonly considered a defense response (Wasmann 1886, 1920; Jordan 1913; Patrizi 1948; Koblick and Kistner 1965; Pasteels 1968; Hölldobler 1970, 1972; Kolbe 1971). It has been suggested that during this abdominal flexing the beetles discharge secretions from their tergal gland (Jordan 1913; Kistner and Blum 1971).

The tergal gland is located between the sixth and seventh abdominal tergites (Fig. 6), and is unique to the subfamily Aleocharinae (Jordan 1913; Pasteels 1968). The chemistry of the tergal gland secretions of several species has been investigated and found to be extraordinarily diverse (Blum et al. 1971; Brand et al. 1973; Kolbe and Proske 1973).

Kistner and Blum (1971) suggested that *Pella japonicus* and possibly also *P. comes*, both of which live with *Lasius spathepus*, produce citronellal in their tergal glands. This substance is also a

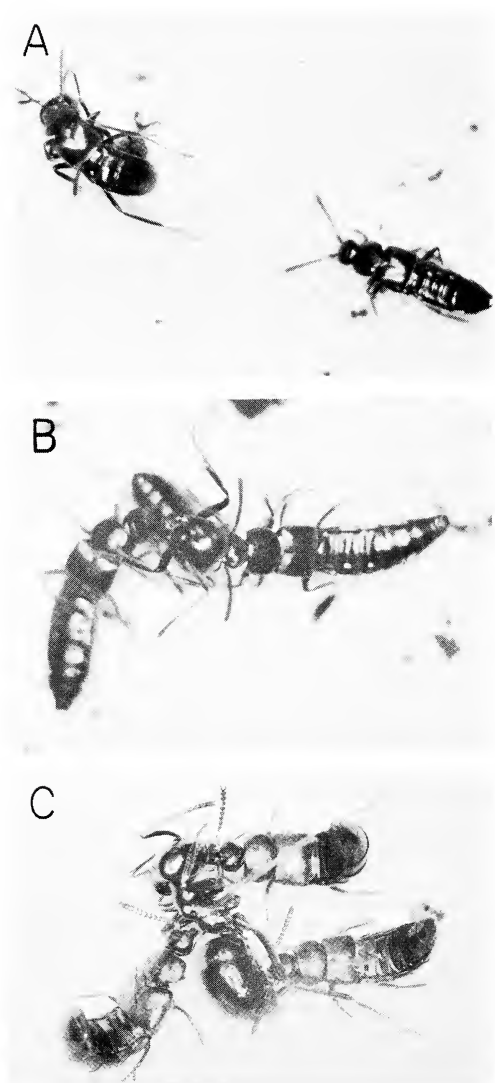


Fig. 4 Sequence of group hunting behavior of *Pella*. A) Two beetles chase a forager of *L. fuliginosus*. One of the beetles is jumping on the back of the ant. B) The ant has been captured and subdued by both beetles. C) A third beetle is joining the hunting group.

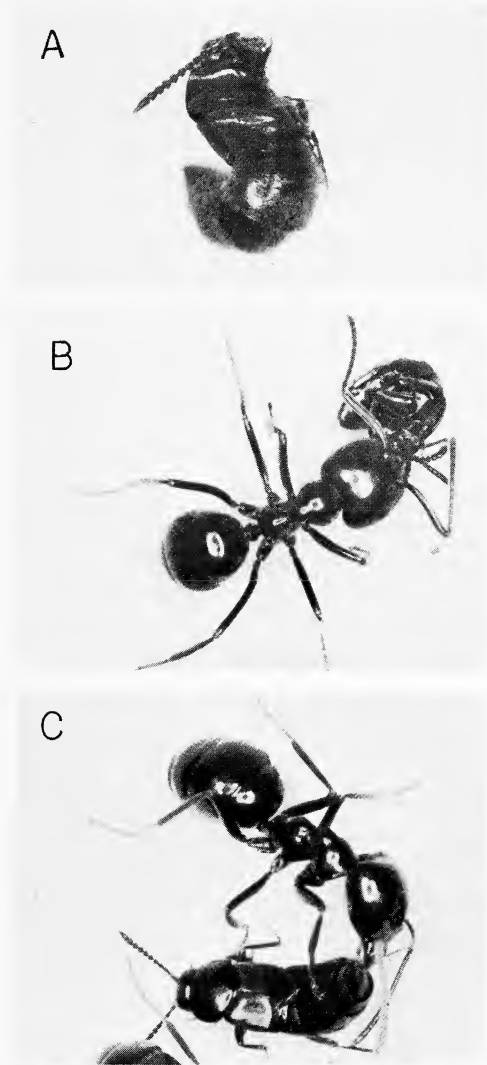


Fig. 5 A) *Pella* in "death feigning" position. B) A "death feigning" beetle is carried around by a *L. fuliginosus* worker. C) *Pella* presents abdominal tip to attacking *L. fuliginosus* worker. The ant licks at the abdominal tip.

major compound of the mandibular gland secretions of their host ants, for which it functions as an alarm pheromone. Although no *Pella* tergal gland contents were available for chemical analysis, because irritated beetles seemed to smell like the ants' mandibular gland secretion, Kistner and Blum speculated that *Pella* produce in their tergal glands citronellal and thereby mimic the alarm pheromone of their host ants. They suggested that in this way the beetles can "cause the ants to reverse their direction; a reaction which allows the myrmecophiles to escape".

Our investigations of the defensive strategy employed by the European *Pella* towards their host ants *Lasius fuliginosus* led to

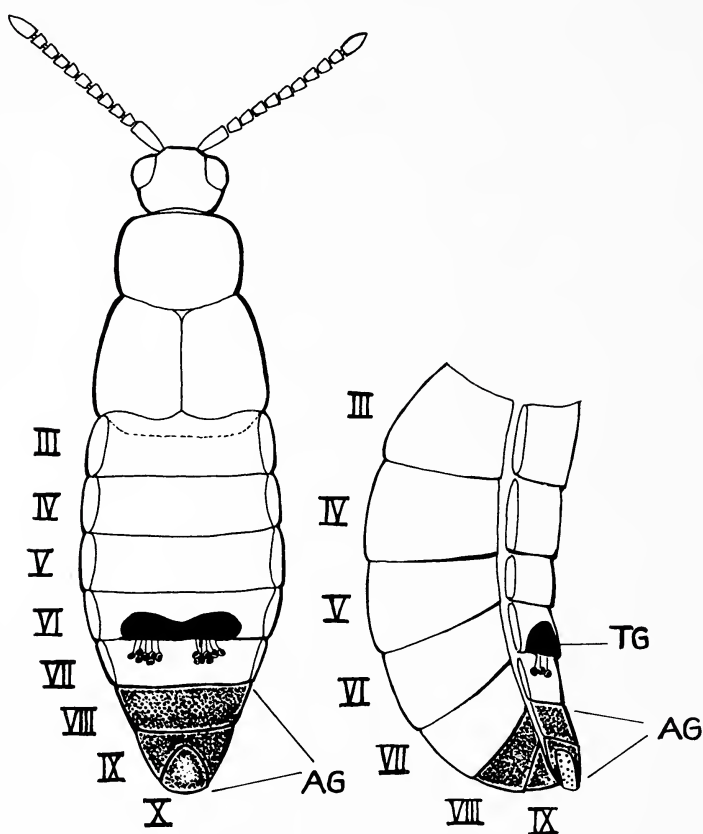


Fig. 6 Schematic drawing of a *Pella* beetle indicating the position of the exocrine glandular complexes. TG: tergal gland; AG: appeasement gland complex.

different results. *Pella laticollis*, when irritated mechanically discharges a pungent smelling brownish secretion from its tergal gland that shows acidic reactions. Only when the beetles were severely attacked and firmly grasped on their appendages by the ants, could we smell the tergal gland secretion. We never observed the beetles employing tergal gland secretion when they were attacking ants. Ants contaminated with tergal gland secretion usually exhibited a repellent reaction, releasing the grip on the beetles and grooming and wiping their mouth parts and antennae on the substrate. But the beetles had to escape quickly, because other ants close by became alerted and were rapidly approaching the scene, apparently alarmed by the ants' alarm pheromone. We noticed that beetles that were attacked by *L. fuliginosus* workers often smelled somewhat like the ants' mandibular secretions, but the beetles' tergal gland secretions clearly smelled differently. Conceivably, some of the attacked beetles were contaminated with the ants' strongly smelling mandibular gland secretions.

Our chemical analysis of the tergal gland secretions of *P. laticollis* did not reveal a resemblance to the mandibular gland secretions of *L. fuliginosus*, whose major compounds are farnesal, 6-methyl-5-hepten-2-one; perillene and dendrolasin, a furan (Quilico et al 1957; Bernardi et al 1967). When we treated the tergal gland section with 2,4—dinitrophenyl-hydrazine, we obtained an orange-yellowish precipitate. This was subjected to thinlayer chromatography in two separate systems. In each system we obtained two spots. The R_f values and the color reaction, when treated with ammonia vapour, identified them as dinitrophenylhydrazones of p-benzoquinone and p-toluquinone. Furthermore, the chromatography of the hydroquinones obtained from the secretion by reduction with SO₂ also demonstrated the presence of p-benzo- and p-toluquinone in the tergal gland secretion.

For comparison we used thinlayer chromatography to analyze the dinitrophenylhydrazones of the tergal gland secretion of several other aleocharine staphylinids found near the nests of *L. fuliginosus*. *Pella humeralis*, *Atheta fungi* and *Sipalia circellaris* also produce benzo- and toluquinone; in *Oxypoda vittata* we found only toluquinone.

In addition Kolbe and Proske (1973) identified isovaleric acid in the tergal gland secretion of *P. humeralis*, and with the aid of gas chromatography we detected saturated hydrocarbons and short

Table 2
GLC analysis of the secretion of *Pella laticollis*

		+ = present; - = absent; ? = not tested					
	n-decane (main peak)	n-undecane	n-tridecane	isovaleric acid (3- methylbu- tyric acid)	isobutyric acid	n-butyric n-valeric 2-methylbu- tyric acid	citronellal
column a	+	+	+	+	+	-	-
column b	+	+	+	?	?	?	-
column c	+	+	+	+	+	-	?

chained fatty acids in the secretion of *P. laticollis* (Tab. 2). However, in none of the species could we find citronellal.

The common presence of quinones in the tergal gland secretions of *Pella* and the related aleocharine species agree with the previous findings by Blum et al (1971), who found the tergal gland secretion of *Lomechusa strumosa* to contain benzoquinone, methyl-benzoquinone, ethyl-benzoquinone and n-tridecane, the latter substance accounting for more than 80% of the volatiles detected in the secretion. In addition Brand et al. (1973) analyzed the tergal gland secretion of *Drusilla canaliculata*, also an aleocharine beetle, finding quinones and hydroquinones together with alkanes, saturated and unsaturated aliphatic aldehydes. Pasteels (1968) demonstrated that *D. canaliculata* effectively employs the tergal gland secretion as a repellent-defense weapon against ants in a similar fashion as we described it for *Pella*.

Although we could not find any resemblance of the *Pella* tergal gland secretions to the mandibular gland secretions of *Lasius fuliginosus*, it was noteworthy that the *Pella* secretions contained undecane, a hydrocarbon commonly found in the Dufour's glands of formicine ants (for review see Blum and Hermann 1978) and considered to be an alarm pheromone in *L. fuliginosus* (Dumpeert 1972). However, isolated tergal gland secretions of *P. laticollis* elicited a repellent reaction rather than an alarm response in *L. fuliginosus*. Apparently the repellent effect of the quinones in the secretions is stronger than a possible alarming effect released by undecane. In fact, when the ant's antennae were directly contaminated with the beetles' tergal gland secretions the antennae were hanging almost motionless and flabby and the ant appeared disoriented for several minutes. From all our laboratory tests it appears obvious that the tergal gland secretions of *Pella* functions as a powerful chemical defense weapon against attacks by ants.

Appeasement behavior:

When foraging on the ants' "garbage dumps" or running along the ants' trails, *Pella* frequently encounter ants. Yet we were impressed by the scarcity of their application of the tergal gland defensive system. Much more frequently the beetles employed an appeasing defensive strategy, and the repellent defense seemed to be employed only as a last resort.

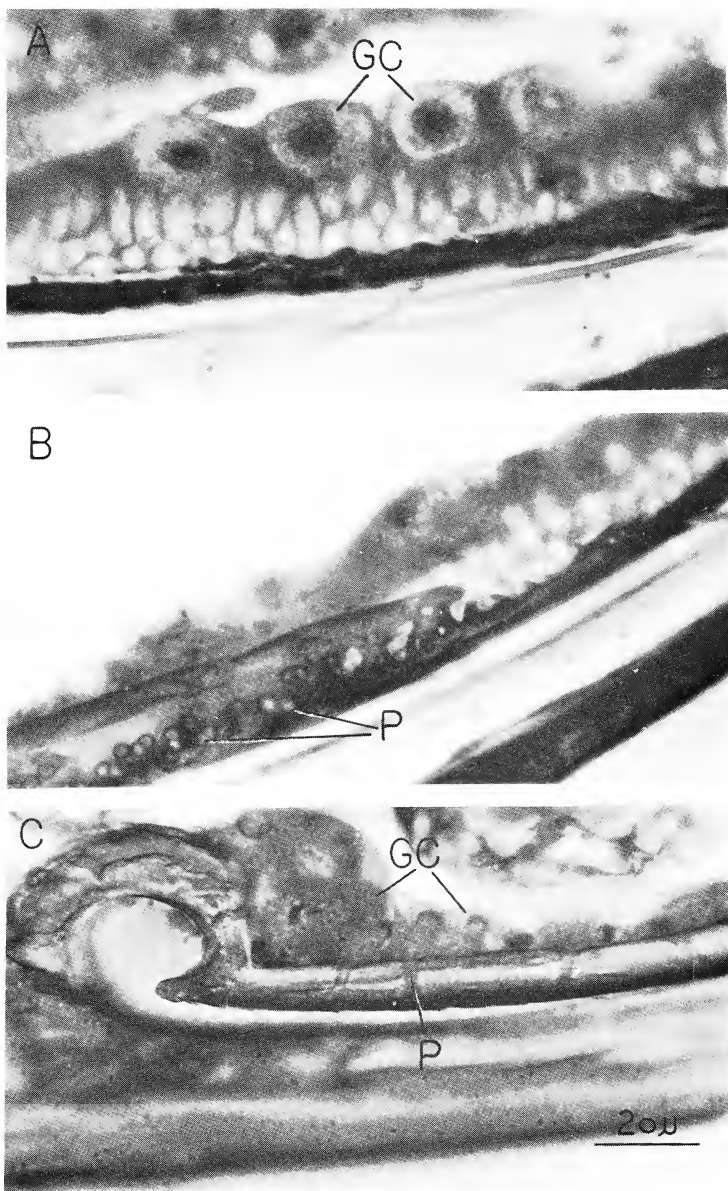


Fig. 7 A,B) Transversal section through glandular epithelium in 9th sternum of *P. humeralis*. C) Sagittal section through sternal gland in 7th sternum of *P. humeralis*. GC: glandular cell; P: pore in cuticle.

It was especially common in early spring, when most of the beetles were found close to the entrance of the ants' nest, that the beetles showed "death feigning" behavior, when attacked by ants. They fell to the side, the legs and antennae folded tightly to the body and the abdomen curved upwards (Fig. 5A). The ants either ignored these motionless beetles or carried them around and finally discarded them on the "garbage dump". But only rarely did they injure the beetles (Fig. 5B).

Later in the year, when the activity of ants and beetles was much higher, the beetles employed a different appeasement technique. As mentioned before, we only very rarely saw the discharge of tergal gland secretions by the beetles, although every time they encountered ants they flexed their abdomen and pointed with the abdominal tip toward the head of their adversaries. Usually the ants responded by antennating the tip and briefly licking it (Fig. 5C). This ordinarily slowed down the ants' aggression and the beetles used the ants' distraction to escape. Occasionally, when the ants remained very persistent, a white, viscous droplet appeared at the abdominal tip, whereupon the ants usually very eagerly licked it up. This appeasing defensive behavior was much more common during the interactions between *Pella* and *Lasius fuliginosus* than the repellent defense. For a series of simulation experiments we cut off the last 3 segments of the abdomen of freshly killed *P. laticollis*, sealed the cut with wax, pinned the segments on dissecting needles and presented these "dummies" to the ants. In a total of 60 tests (using 3 different dummies) the ants interrupted their run in 47 cases (78%) and licked the abdominal tip briefly.

Histological investigations revealed that the abdominal tips of *Pella* are batteries of exocrine glandular structures, all of which together we call the appeasement gland complex. In the following section we give a brief description of the glands which could be involved in the appeasement behavior.

The most comprehensive study of the glandular morphology of some termitophilous and myrmecophilous aleocharine beetles has been published by Pasteels (1968). From this work we learned that these beetles possess a surprising variety of exocrine glandular structures and that various species can differ considerably in their glandular systems. In the four species of *Pella* (*P. cognata*, *P. funesta*, *P. humeralis*, *P. laticollis*) we investigated, we did not find major differences, although *P. humeralis* appeared to be somewhat

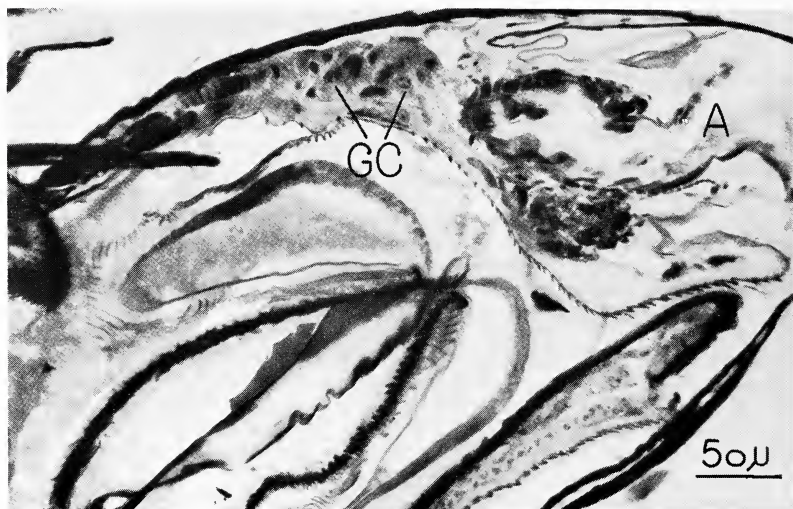


Fig. 8 Sagittal section through abdominal tip of *P. humeralis*. GC: glandular cells under 10th tergite near anus. A: anus.

more richly endowed with hypodermal glandular cells, especially in the area of the paratergites.

In staphylinid beetles the first fully developed abdominal segmental ring (tergite plus sternite) is usually considered to be the 3rd abdominal segment (Blackwelder 1936). All *Pella* species have a well developed compound tergal gland between the 6th and 7th tergites (Fig. 6) as described by Jordan (1913), Pasteels (1968) and Hölldobler (1970). We have also detected glandular cells located primarily in the 7th segment, which Pasteels (1968) calls postpleural glands. According to Pasteels the glandular channels associated with these cells open dorsolaterally through the pleural membrane between the 7th and 8th segments. Pasteels could clearly see these openings in several species (for example in *Gyrophanaena affinis*), but not in *Pella* (Zyras) *humeralis*. In a series of longitudinal, transverse and frontal sections, we too were unable to detect the external openings of these glandular cells.

At the anterior edge of the 4th, 5th, 6th and 7th sternites are found clusters of glandular cells that open through pores in the cuticle (Fig. 7A). They are especially well developed in the 7th sternite. Pasteels (1968) assumes that the secretions of these glands

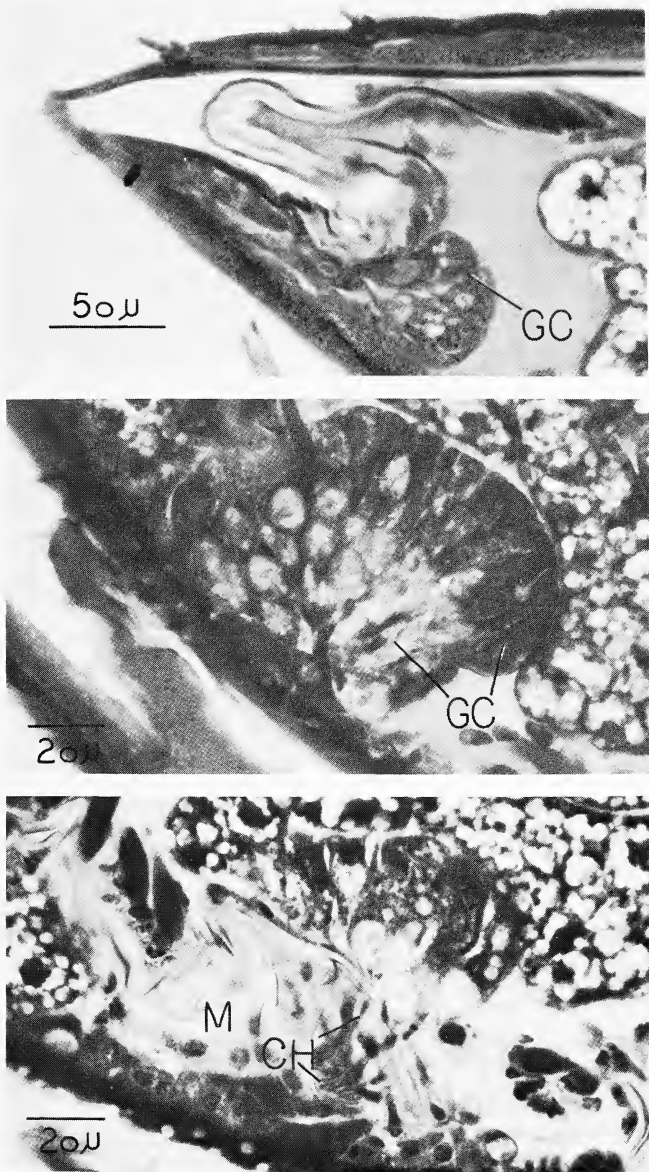


Fig. 9 Sagittal sections through abdominal tip of *Pella laticollis* female. GC: glandular cell clusters; M: membrane; CH: glandular channels.

serve primarily for lubrication to alleviate friction between the sternal sclerites when the beetles flex their abdomen. But more than any other of the abdominal segments the last 3 tergites (VII, IX, X) (Fig. 6) and the 8th and 9th sternites are richly endowed with glandular epithelia, the individual cells of which open through pores in the cuticle (Fig. 1B, 1C). The last two segments can be telescoped with especial ease into the preceding segments, and during the appeasement process the beetles often move them slightly back and forth. Furthermore, there are clusters of glandular cells with longer channels under the 10th tergite near the anus (Fig. 8). They resemble the type of cells that Hölldobler (1971) located in the same position in *Atemeles* and called pygidial glands. We have, however, abandoned this term, because it is very confusing, especially in the Aleocharinae, where the last visible tergite is usually not the 8th tergite (often called pygidium in the Coleoptera) but the 10th tergite.

In addition to these hypodermal glandular structures, females and males possess special exocrine glandular complexes that might be involved in the reproductive processes but which could also play a role in the myrmecophilous behavior of the beetles. In the 9th sternite of females there are several clusters of glandular cells, the channels of which open through the intersegmental membrane at the tip of the abdomen and near the oviduct (Fig. 9). Males have similar glands in the 9th sternite which also open through the intersegmental membrane near the posterior part of the genital chamber (Fig. 10). Furthermore, males possess a very large glandular complex, consisting of numerous tightly packed glandular cells each connected with a long channel that open dorsally in bundles through a membrane at the genital chamber (Fig. 11). We assume that the secretions of this gland flow into the genital chamber. Females do not have this gland, but the spermathecal gland has a very similar appearance.

Finally, the hindgut might also be involved in the appeasement process. On several occasions we observed that beetles, upon presenting their abdominal tip to the ants, released a droplet at the anus that was licked up by the ants.

DISCUSSION:

Some of the most advanced myrmecophilic relationships are found in the aleocharine beetles *Lomechusa* and *Atemeles*. We

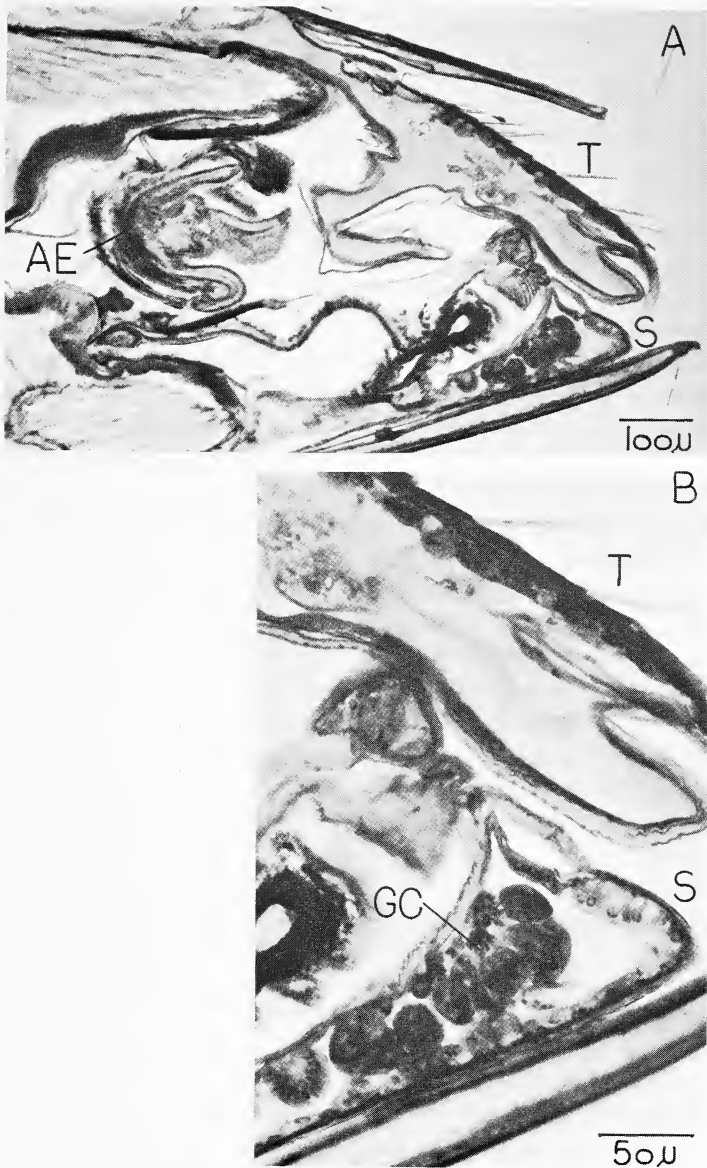


Fig. 10 A) Sagittal sections through the abdominal tip of *P. humeralis* male. T: 9th and 10th tergite; S: 9th sternite; AE: aedeagus. B) Close-up of sagittal section through 10th tergite and 9th sternite. GC: glandular cell clusters.

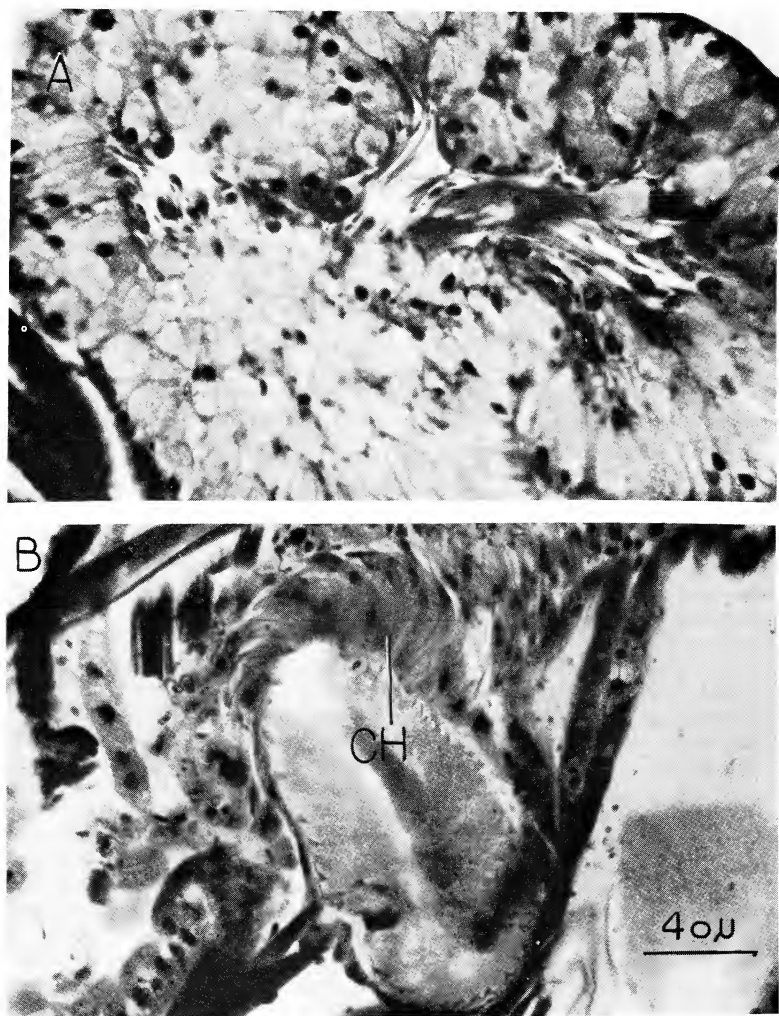


Fig. 11 A) Glandular complex in males of *Pella humeralis*, located dorsally of the genital chamber. B) Opening of the bundles of glandular channels through membrane; presumably into the genital chamber.

know from observations by Wasmann, made more than 60 years ago, that these beetles are both fed and reared by their host ants. Both chemical and mechanical interspecific communication is involved in these unusual relationships. These aleocharines have broken the communication code of their host ants and are thereby able to live as parasites within the social system of the ant colony (Hölldobler 1967, 1970, 1971, 1972).

Species of the genus *Pella* are less advanced in their myrmecophilic relationships. Rather than occupy the brood chambers of the ant nest, they live as scavengers and predators in the peripheral zones around the nest, at the garbage dumps, and on the trunk routes. Some of the behavioral features of *Pella*, however, seem to be very similar to those of *Atemeles* and *Lomechusa*. In fact, these behavioral patterns might be preadaptations for the evolution of a highly advanced myrmecophilic relationship in the aleocharine beetles. In particular, the appeasement behavior appears to be an important prerequisite for living closely with ants. This "gentle" defense technique does not cause excitement in the ants, as a repellent defense would do.

Indeed, our observations indicate that *Pella* only rarely employ their strongly smelling tergal gland secretions when they are near the host ant colony. This defense system might be used more during the migration phase, when the beetles can be attacked by individual foraging ants. Similar results were previously obtained with *Atemeles* (Hölldobler 1970) and *Lomechusa* (Hölldobler unpublished). In the presence of their host ants these species use the appeasement defense almost exclusively.

The appeasement behavior also plays an important role during the adoption of *Atemeles* by their host ants. When encountering a worker of the host species near the ant's nest, the beetle first offers the appeasement gland complex (at the abdominal tip) to the ant. This apparently suppresses aggressive behavior in the ant; only then does the beetle lower its abdomen to permit the ant access to the adoption glands, which are located in the paratergites. The glandular openings are surrounded by bristles. These are grasped and used by the ant to carry the beetle into the brood chamber. While being carried, *Atemeles* adopts the same posture as that used by *Pella* during the "death feigning" behavior. As we have noted, the initially aggressive ants respond by either ignoring the beetles or else picking

them up and carrying them around until they eventually discard them, usually unharmed, at the garbage dump. It is conceivable that the carrying posture of *Atemeles* has evolved from a defensive "death feigning" behavior employed by less advanced ancestral species.

Finally, *Pella* beetles do not have adoption glands associated with trichrome bristles. It is most likely, however, that the small clusters of glandular cells in the paratergites (for example in *P. humeralis*) represent morphological precursors of the massively developed adoption glands in *Atemeles* and *Lomechusa*.

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BEHAVIORAL ORIGIN OF TREMULATION,
AND POSSIBLE STRIDULATION,
IN GREEN LACEWINGS
(NEUROPTERA: CHRYSOPIDAE)¹

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Introduction

Abdominal vibration or "jerking" in connection with courtship behavior has been described for several green lacewing species (e.g. Smith 1922; Toschi 1965; Tauber 1969; Sheldon and MacLeod 1974) and explored in detail by Henry (1979, 1980a, b, c). In *Chrysoperla carnea* (Stephens) isolated individuals produce long, patterned sequences of discrete short bursts of rhythmic vibration of the abdomen in the vertical plane. The wings may also vibrate. Sexually receptive pairs establish duets of reciprocal abdominal jerking. Actual drumming of the abdomen on the substrate does not occur. It had been assumed that abdominal vibration produces high-frequency sounds by stridulation (Adams 1962, Riek 1967, Eichele and Villiger 1974, Henry 1979) and acoustical communication was discussed in connection with the tympanal ultrasound receptor organ described by Miller (1970, 1971). Courtship and copulation take place on the vegetation, usually on the underside of leaves. Henry (1980a, c) in his work with *Chrysoperla* spp. demonstrated that communication is performed via low-frequency substrate vibration and not by airborne sound. Males were able to establish duets with females within a range of 15 cm. According to Henry (1980a, b, c), differences in the vibration patterns of *Chry-*

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soperla rufilabris (Burmeister), *C. downesi* (Banks) and *C. carnea* suggest that "acoustical" communication may help to reproductively isolate sympatric lacewing species.

Since the vibration produced by abdominal jerking in lacewings seems to be propagated in a transverse wave (perpendicular to the plane of the substrate) we prefer to call this type of communication "tremulation", following Busnel et al. (1956), Henry (1980c) and Morris (1980). On the other hand, sound in the form of longitudinal waves, is produced by stridulation and percussion. Possible stridulatory structures in lacewings were first described for the chrysopid *Meleoma schwarzi* (Banks) by Adams (1962) and later for other Neuroptera (Riek 1967). However, to date, there is no reported record of any sound produced by these organs (Henry 1980c). In *M. schwarzi*, sound may be produced when the second abdominal sternite, with its regular striae of microtrichia, is rubbed against the femora by abdominal vibration (Adams 1962). *C. carnea* and some other species of Chrysopidae may stridulate using microtrichia on the venter of the anal lobe of the forewings and dorsolaterad on the metanotum (Riek 1967; Henry 1979). Alternatively, these paired areas of microtrichia may function to hold the wings in place when at rest (Henry 1980c). Thus, tremulation and possible stridulation are both produced by vibrating the wings and abdomen.

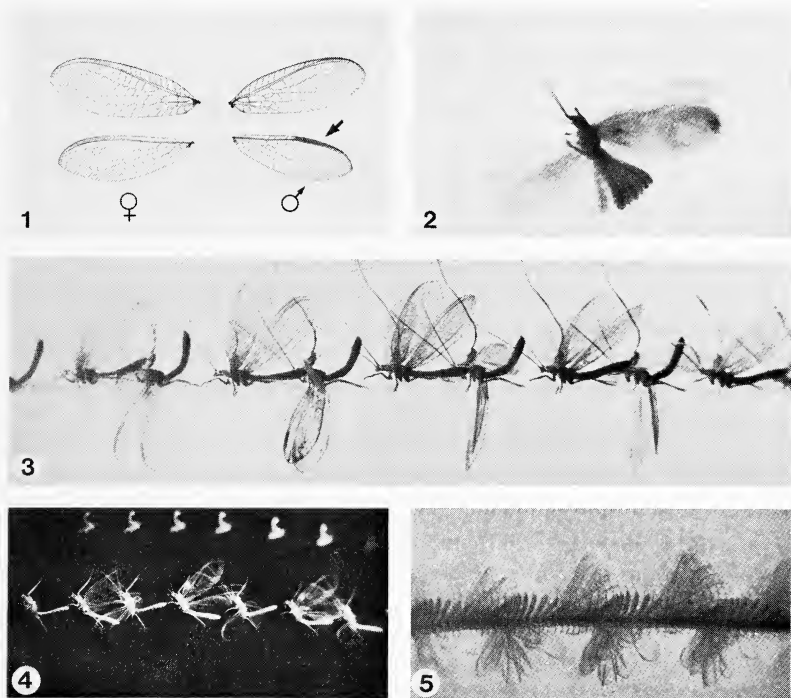
Methods and Materials

Observations of free flight and mating behavior were made on the following species: *C. carnea*, *Eremochrysa punctinervis* McLachlan, *E. tibialis* Banks, *Mallada basalis* (Walker), *Meleoma hageni* Banks and *Nodita* n. sp. The only specialized technique required for this study was the use of a strobe light to illuminate lacewings on a flight mill (Duelli 1980). By varying the frequency of the strobe flashes, it was possible to determine the rate of the wing beats and other body movements, as the highest flash frequency at which the motion appeared to be "frozen" and each structure was seen in only one position. A multiple of this frequency again produces a frozen image, but the body is seen in multiple positions. *C. carnea* and *M. basalis* were examined in this manner.

Results

Among the species observed, there appeared to be great variation in the patterns and intensities of vibration of the wings and abdomen during courtship, but this was not quantified. The beha-

vior was strongly developed in species of the genera *Meleoma* and *Eremochrysa*, but was even more conspicuous in the Indo-Pacific lacewing *M. basalis*, as observed on the island of American Samoa. In this species, the males flapped their wings so vigorously that they hit the substrate and produced sounds easily perceptible to the human ear. Heavily developed pterostigmata in the hind wings of the male may enhance substrate vibration and protect the wings from damage (Fig. 1). During courtship, the males moved forward



Figures 1-5. Fig. 1. Forewing and hind wing of female (left) and male (right) *Mallada basalis*. The arrow indicates the heavily developed pterostigma in the hindwing of the male. Fig. 2. Stationary flight of a tethered *Chrysoperla carnea* male. Strobe flashes (60 Hz, exposure 0.25 sec) show the extent of the abdominal motion. Fig. 3. *Chrysoperla carnea* male mounted horizontally on a flight mill. Strobe flashes (54 Hz) show the exact antiphase of abdominal and wing vibration. Fig. 4. *Chrysoperla carnea* male mounted on a flight mill in "natural" flight position as shown in figure 2. Any forced deviation from the "natural" body angle leads to an increased amplitude of the abdominal vibration (See figure 3 for comparison). Fig. 5. Same specimen and same position as in Fig. 3. 400 Hz strobe flashes show the full flow of the movements of wings and abdomen.

and backward in front of the female, and sometimes even sideways. Especially vigorous males were seen to perform small jumps, reminiscent of take-off behavior.

A chrysopid usually flies with its head higher than its abdomen. If the insect is mounted on a flight mill and illuminated with a strobe light, the abdomen can be seen moving up and down in the same way as described for the courtship behavior (Fig. 2). When mounted horizontally, the abdominal movements were exaggerated (Fig. 3). In both orientations the strobe flashes revealed that the frequencies of the wing beat and of the abdominal vibration were the same. With each down-stroke of the wings the abdomen was lifted (Figs. 3 and 4). The flow of the movements can be seen in Fig. 5.

Observations made during this study indicate that the wing beat frequency was positively correlated with temperature and, in general, negatively correlated with wing length. At 23°C, a wing beat frequency of 27 Hz (strokes/sec) was recorded for *C. carnea* and 38 Hz for the smaller *M. basalis*. Miller (1975) reported similar results, 25 Hz at 21–24°C in tethered flying *C. carnea*.

Discussion

The frequencies of abdominal vibration during courtship have been reported for three species of *Chrysoperla*. For *C. rufilabrus* the rates were 14–18 Hz (Henry 1980a). No temperature data were given. In *C. carnea* the frequencies varied from 30 to 100 Hz at 24–28°C (Henry 1980c), while the courtship behavior of *C. downesi* included volleys of abdominal vibration with a frequency of 60–80 Hz, with a mean of approximately 73 Hz, at 24–29°C (Henry 1980b).

The greater variability in the frequencies of abdominal vibration during courtship, relative to flight, is probably related to two factors. First, there is no minimum rate of wing beats necessary to maintain flight. Second, the maximum possible rate is increased, since the wings merely vibrate rather than making full strokes. These would open a wide range of frequencies for chrysopids to use in tremulation. If character displacement occurred, as hypothesized by Henry (1980b), this would tend to expand the range of frequencies actually used by chrysopids.

Tremulation has also been reported in the courtship behavior of other groups of insects. Plecoptera communicate via the substrate by drumming with their abdomens (Rupprecht 1968). Similar

drumming and/or abdominal vibration is known from certain Psocoptera (Pearman 1928), Orthoptera (refs. in Rupperecht 1968 and Morris 1980), Megaloptera (Rupperecht 1975) and Mecoptera (Rupperecht 1974). Wing fluttering is also involved in courtship of *Panorpa* spp. (Mecoptera) (Rupperecht 1974) and three genera of Coniopterygidae (Johnson and Morrison 1979).

The function of the abdominal motion in flight is unknown. In the Diptera, the halteres (modified second pair of wings) have been shown to act as specialized organs to maintain flight stability (Pringle 1948). They vibrate in a vertical or nearly vertical plane and, as gyroscopic indicators, reveal any change in the spatial orientation of the thorax via sensors at their bases. The halteres vibrate with the same frequency as the wings, but in antiphase. Since the same is true for the abdominal movements in lacewings, it is tempting to regard their abdominal vibration as an analogous gyroscopic mechanism to stabilize the orientation of the thorax during the slow hovering flight, thus keeping the insect in an upright position with regard to the horizontal plane. This possibility is supported by the similar orientation and abdominal movements of flying Plecoptera, Megaloptera (*Sialis* spp. and *Neohermes* sp.) and Mecoptera (*Panorpa* spp.) as observed in the field.

Indirect morphological evidence also supports this possibility. Whereas most other nocturnal insects have large ocelli, chrysopids and most other Neuroptera lack ocelli. An important function of the ocelli in locusts and other insects is to recognize relative changes in the height of the horizon (Taylor 1981) and thus to stabilize the flight position.

Based on the similarities between abdominal vibration during flight and courtship behavior, we suggest that tremulation behavior in lacewings and perhaps other slow-flying insects may have evolved from a particular "pre-adapted" feature in the take-off and flight behavior, where its main function might be flight stabilization.

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ARTHROPODS ATTRACTED TO LUMINOUS FUNGI

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Some fungi emit light. Luminescence may be present in mycelia [e.g. a number of *Mycena* species (Wassink 1978)] or in both mycelia and fruiting bodies [e.g. North American populations of *Panellus* (= *Panus*) *stypticus*, Buller 1924]. Lights have been described as blue, white, or green depending on the species (Buller 1924, Wassink 1978). Emission intensities vary considerably. In the forests of Borneo *Mycena* (= *Poromyцена*) *manipularis* are visible at ca. 40 meters (Zahl 1971). An Australian species¹ "pours forth its emerald green light" with sufficient intensity to read by (Lauterer 1900 in Buller 1924). North American forms, such as examined here, tend to be dimmer. The eye often requires several minutes of dark adaptation before their glows become visible.

The receiver(s) toward which fungi direct their luminous signals are unknown. Lights have been supposed to lure spore dispersing insects (Ewart 1906), but such an argument fails to account for mycelial lights (Ramsbottom 1953). There has apparently been no conjecture on the benefits mycelia accrue by glowing. The different environments of mycelia and fruiting bodies make it questionable whether their lights are directed at identical receivers or even serve similar functions.

Until this time any proposed reactions of animals to fungal lights have been speculative. I here present evidence that certain arthropods are more likely to be captured in traps baited with light-emitting mycelia and fruiting bodies than in controls containing fungus-free substrate or dead and dark specimens of luminous species. Several possible interactions between fungi and attracted arthropods are discussed.

¹Described as *Panus incandescens*, a name of doubtful taxonomic value (see Wassink 1978).

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METHODS

Test tubes (10×75 mm) were covered with Tack Trap®, a sticky trapping compound, and capped with a cork. Luminous twigs, conifer needles and leaf fragments, covered with mycelia of a *Mycena* sp., were put into 31 such tubes. An identical number of control tubes contained similar but nonluminous forest litter. Tubes with glowing fungi were placed as closely as possible to the original position of their contents (note that mycelia are most abundant deep in litter, but traps were placed on the litter surface). Controls were set ca. 80 mm to the side. Glass screw top vials (14×40 mm) were also coated with Tack Trap®. From 3–6 fruiting bodies of the luminous mushroom *Dictyopanus pusillus* were put into 72 such vials. An identical number of controls contained 3–6 *D. pusillus*, killed and rendered nonluminous by bathing in alcohol. Luminous and control vials were alternately placed, ca. 80 mm apart, on and by rotting logs on which *D. pusillus* had been found. Traps were put out at night, gathered the following morning, and arthropods stuck on their surfaces removed.

All specimens were captured during August in Alachua County, Florida.

RESULTS

More arthropods were captured on traps baited with glowing fungal mycelia (*Mycena* sp.) and luminous fruiting bodies (*D. pusillus*) than their respective controls ($\chi^2 = 10.14$, $p < .001$; $\chi^2 = 6.41$, $p < .01$, see Table 1). Taxa significantly more abundant on luminous traps in the summed samples are Collembola ($\chi^2 = 12.81$, $p < .001$), and Diptera ($\chi^2 = 5.54$, $p < .025$). It is of interest that Collembola are not attracted to the bioluminescence of a sedentary luminous predator, larvae of the fungus gnat *Orfelia fultoni* (Sivinski 1982). Predators, i.e. spiders, ants, earwigs occur in a luminous: dark ratio that borders on significance ($\chi^2 = 3.76$, $p < .10$). Groups captured in statistically indistinguishable numbers on luminous and control traps are Isopods ($\chi^2 = 0.78$, $p > .25$) and Amphipods ($\chi^2 = 0.59$, $p > .25$). An unusual set of captures is the 5 crickets, *Eunemobius carolinus*, taken only with luminous mycelia.

Table 1. The numbers of Arthropods captured on traps containing luminous mycelia (*Mycena* sp.), luminous fruiting bodies (*Dictyopanus pusillus*), and their respective controls.

	<i>Mycena</i> sp.	Control	<i>D.</i> <i>pusillus</i>	Control	Summed Fungi	Summed Control
Collembola	22	8	31	14	53	22
Isotomidae/ Entomobryidae	21	8	12	7	32	11
Sminthuridae	1	0	19	7	20	7
Diptera	8	2	11	5	19	7
Phoridae	2	1	7	2	8	3
Sphaeroceridae	0	0	1	0	1	0
Cecidomyiidae	5	0	2	3	7	3
Ceratopogonidae	1	0	0	0	1	0
Psychodidae	0	1	0	0	0	1
Mycetophilidae	0	0	1	0	1	0
Predators	12	4	17	12	29	16
Araneida	3	1	7	4	10	5
Formicidae	9	1	9	8	18	9
Carabidae	0	1	0	0	0	1
Dermaptera	0	0	1	0	1	0
Hymenoptera	3	1	1	2	4	3
Isopods	32	29	37	30	69	59
Amphipods	0	1	9	7	9	8
Acari	0	1	1	0	1	1
Orthoptera	8	1	2	4	10	5
Gryllidae	5	0	0	0	5	0
Blattellidae	3	1	2	4	5	5
Cicadellidae	1	0	1	0	2	0
Thysanoptera	0	0	1	1	1	1
Unidentified	0	2	2	3	2	5
All Arthropods	86	49	113	78	199	127

DISCUSSION

Attraction of insects to fungal lights does not demonstrate that luring arthropods is the function of the bioluminescence. With this caveat in mind, note that an acceleration in the rate of certain fungus/insect interactions even as an effect of a bioluminescent signal is apt to influence the evolution of luminous fungi. In particular, the argument that fungal lights are functionless, and by implication harmless by-products of metabolism, loses force (see also Lloyd 1977). Bearing a light near arthropods is unlikely to be selectively neutral (for counterviews, see Buller 1924; Prosser and Brown 1961).

Some possible functions of fungal glows become more plausible with, or fail to find support in, the presented data. Both are discussed below.²

Attraction of spore dispersers: Stinkhorn fungi (Phallales) use odor, and perhaps color, to attract spore dispersing insects. Diptera, in particular, consume a sweet malodorous spore-containing mucous smeared on the fungal surface. Spores develop after being discharged in the insect feces (discussed in Ramsbottom 1953). An early conjecture on the function of fruiting body luminescence was that lights, like odor and color in stinkhorns, lure spore dispersers (Ewart 1906; see also Lloyd 1974, 1977).³

A large proportion of the animals attracted to luminous fungi are potential consumers of its spores. Many Collembola feed on fungal spores, mycelia, and fruiting bodies. Some members of captured Diptera families breed in fungi. The phorid *Megaselia halterata*, for instance, is a pest of cultivated mushrooms (Oldroyd 1964). Whether spores of *D. pusillus* pass unharmed through the insect gut is

²The following functions concern heterospecific receivers; however, bioluminescence is often intimately associated with mating (see Lloyd 1977). Sexual congress in relevant Basidiomycetes consists of exchange of nuclei between haploid mycelia. Is it possible that glows might direct the growth of photo-sensitive hyphae at this stage and so serve as mating signals? Such an explanation fails to account for luminosity in diploid mycelia or the fruiting body.

³Insects may evolve an affinity for fungal lights due to "rewards," in food, shelter, etc., the fungus provides. An alternative is that attraction is due to fungal exploitation of arthropod "phototropisms." The function of "phototropisms" are often obscure. Some are apparently effects of orientation systems based on the relative position of celestial objects (see Lloyd 1977).

unknown. Nor is it known if attracted flies, such as phorids and cecidomyiids, would be useful agents of dispersal. Vagile adults may not feed on fungal materials. Protein consumption by cecidomyiids is particularly rare (see Sivinski and Stowe 1981). Spores may be moved, however, by attachment to the surface of a passing insect.

The topography and timing of luminous displays are often suggestive of guiding dispersers. In *Mycena pruinosa-viscida* and *M. rorida* from the Far Eastern tropics only the spores emit light (Haneda 1955). Most fruiting body lights are restricted to, or brighter in, the spore bearing hymenium (Wassink 1978) and *Panellus stypticus* glows most strongly at the time of spore maturation (Buller 1924). Conscription of dispersal agents is less likely to account for light-emitting mycelia, unless mycelial cells pass safely through the gut or can be carried to new locations on an arthropod's exoskeleton.

Attraction of carnivores: Predaceous arthropods were found on glowing traps in numbers that border on significance, and fungus/predator interactions can be imagined as important in the evolution of bioluminescence. Luminous fungi might concentrate carnivores about them by exploiting their "phototropisms." If predators arrive at rates effectively greater than lured fungivores, the resulting predator:prey ratio may favor the fungus (an argument similar to but more evolutionarily feasible than the "burglar alarm" theory of Dinoflagellate luminescence; Burkenroad 1943; see Buck 1978). Such an advantageous ratio is not obvious in my sample. Alternatively, carnivores could seek out luminous fungi as locales of high prey density. Glowing mushrooms might be mistaken for luminescent animal prey.

Attraction of fungivores: If luminous mycelia are unpalatable, or otherwise difficult to ingest, then fungivores attracted to lights might consume adjacent competitors.

Attraction of fertilizers: Lloyd (1974) suggests that arthropods lured by luminescent fungus might excrete beneficial materials and so aid growth. Any nutritional gain must be balanced by the metabolic expense of the signal.

Repulsion of negatively phototropic fungivores: Bioluminescence might repel an organism's negatively phototropic enemies or competitors (Nicol 1962; see also Sivinski 1981 and citations). Repulsion is particularly plausible in explaining luminous mycelia, some of

which occur buried in litter, inside rotting logs, or on roots deep underground where the opacity of the environment precludes attraction as a function of light.

Among surface dwelling arthropods, there is no indication of a light-avoiding taxon. This does not preclude repulsion. A rare, but dangerous, enemy could keep fungal lights burning but escape inclusion in the present sample, especially since mycelia baited traps were not placed in the area of greatest mycelial abundance, deep in the leaf litter. The intended receiver may not be an arthropod or even macroscopic. Protozoa sometimes respond to lights. A glow could repel certain pathogens and keep the fungus free of particular diseases.

Light as a warning signal: Lights emitted by unpalatable fungi might serve as warning signals directed towards nocturnal fungivores (a similar function has been hypothesized for ancestral flowers, Hinton 1973). Of North American fungi with luminous fruiting bodies, one, *P. stypticus*, is a bitter tasting purgative, while another, *Omphalotus olearius*, is a toxic hallucinogen (Miller 1979; the palatability of *D. pusillus* is unknown). *Pleurotus japonicus*, a luminescent Japanese species, is deadly poisonous (Buller 1924). However, the luminous fruiting bodies of Malaysian *Mycena manipularis* are quickly attacked by fungus gnats (Corner 1954; gnats could be specialists, immune to toxins). Again there is no evidence of arthropods avoiding fungal lights. My traps, of course, would fail to quantify the discouragement of deer or other large fungivores.

Like aposematic insects, luminous mushrooms often occur in clumps (kin groups?) (see illustrations in Buller 1924, Harvey 1957; also descriptions in Wassink 1978). Aggregations might intensify warning signals (Cott 1957) and be instrumental in the evolution of conspicuousness (Fisher 1930, for arguments concerning the kin selection of aposematism). Several tropical light emitters, however, apparently occur singly (see Wassink 1978).

White fungi can reflect enough celestial light to be surprisingly obvious at night (noticed at twilight by Lloyd 1977). An assumption of similar receivers for the bright white and luminous signals of fruiting bodies allows the nocturnal aposematic signal hypothesis to be tested with a larger sample. Mushrooms that appear to me to be uniformly bright white include 6 toxic species, 13 edible and 5 whose

palatability is unknown (color and palatabilities from photos and text of Miller 1979). This distribution does not support the aposematism argument (in comparison with a random sample of 41 non-poisonous and 9 poisonous species $\chi^2 = 0.80$ $p > .25$).

SUMMARY

Arthropods, principally Collembola and Diptera, are attracted to the lights of luminous fungal mycelia (*Mycena sp.*) and fruiting bodies (*Dictyopanus pusillus*). Such attraction does not prove that bioluminescence has evolved to lure insects but does affect the plausibility of hypotheses concerning the function of fungal glows. The possibilities of lights being used to lure spore dispersers, attract consumers of fungivores and competing fungi, repel negatively phototropic fungivores, and serve as warning signals, are discussed.

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PSYCHE

INDEX TO VOLUME 88, 1981

INDEX TO AUTHORS

- Annette, Aiello. Life History of *Antaeotricha* sp. (Lepidoptera: Oecophoridae: Stenomatinae) in Panama. 163
- Carlin, Norman F. Polymorphism and Division of Labor in the Dacetine Ant *Orectognathus versicolor* (Hymenoptera: Formicidae). 231
- Carpenter, Frank M. Dedication: Robert E. Silberglied. 197
- Dahlstrom, Tina. See Topoff, Howard.
- Droual, Robert and Howard Topoff. The Emigration Behavior of Two Species of the Genus *Pheidole* (Hymenoptera: Formicidae). 135
- Duelli, Peter and James B. Johnson. Behavioral Origin of Tremulation, and Possible Stridulation, in Green Lacewings (Neuroptera: Chrysopidae). 375
- Edwards, G. B. Sound Production by Courting Males of *Phidippus mystaceus* (Araneae: Salticidae). 199
- Ginsberg, Howard S. Historical Development of Bee Foraging Patterns in Central New York State. 337
- Hathaway, Mary. *Polistes gallicus* in Massachusetts (Hymenoptera: Vespidae). 163
- Haverty, Michael I. See Howard, Ralph W.
- Hölldobler, Bert. Trail Communication of the Dacetine Ant *Orectognathus versicolor* (Hymenoptera: Formicidae). 245
- Hölldobler, B., M. Möglich, and U. Maschwitz. Myrmecophile Relationship of *Pella* (Coleoptera: Staphylinidae) to *Lasius fuliginosus* (Hymenoptera: Formicidae). 347
- Howard, Ralph W., Eldon J. Mallette, Michael I. Haverty, and Richard V. Smythe. Laboratory Evaluation of Within-Species, Between-Species, and Parthenogenetic Reproduction in *Reticulitermes flavipes* and *Reticulitermes virginicus*. 75
- Johnson, James B. See Duelli, Peter.
- Kearns, R. S. and R. T. Yamamoto. Maternal Behavior and Alarm Response in the Eggplant Lace Bug, *Gargaphia solani* (Heidemann) (Tingitidae: Heteroptera). 215
- Levings, Sally C. and James F. A. Traniello. Territoriality, Nest Dispersion, and Community Structure in Ants. 265
- MacKay, William P. A Comparison of the Nest Phenologies of Three Species of *Pogonomyrmex* Harvester Ants (Hymenoptera: Formicidae). 25
- Mallette, Eldon J. See Howard, Ralph W.
- Maschwitz, U. See Hölldobler, B.
- Möglich, M. See Hölldobler, B.

- Newton, Alfred F. Jr. New Name for the Extinct Genus *Mesagyrtes* Ponomarenko (Coleoptera: Silphidae S.L.). 335
- Nimmo, Andrew P. Francis Walker Types of, and New Synonymies for, North American *Hydropsyche* species (Trichoptera: Hydropsychidae). 259
- Parker, F. D. See Tepedino, V. J.
- Pujdak, Susan. See Topoff, Howard.
- Richman, David B. and Willard H. Whitcomb. The Ontogeny of *Lyssomanes viridis* (Walckenaer) (Araneae: Salticidae). 127
- Rothstein, Aaron. See Topoff, Howard.
- Sivinski, John. Arthropods Attracted to Luminous Fungi. 383
- Smythe, Richard V. See Howard, Ralph W.
- Steiner, A. L. Anti-predator Strategies. II. Grasshoppers (Orthoptera, Acrididae) Attacked by *Prionyx parkeri* and Some *Tachyspex* Wasps (Hymenoptera, Sphecinae and Larrinae): A Descriptive Study. 1
- Stuart, Robin J. Abdominal Trophallaxis in the Slave-Making Ant, *Harpagoxenus americanus* (Hymenoptera: Formicidae). 331
- Tepedino, V. J. and F. D. Parker. The Effect of Flower Occupancy on the Foraging of Flower-Visiting Insects. 321
- Topoff, Howard. See Droual, Robert.
- Topoff, Howard, Aaron Rothstein, Susan Pujdak, and Tina Dahlstrom. Statory Behavior in Nomadic Colonies of Army Ants: The Effect of Overfeeding. 151
- Traniello, James F. A. See Levings, Sally C.
- Ward, Philip S. Ecology and Life History of the *Rhytidoponera impressa* Group (Hymenoptera: Formicidae). I. Habitats, Nest Sites, and Foraging Behavior. 89
- Ward, Philip S. Ecology and Life History of the *Rhytidoponera* Group (Hymenoptera: Formicidae). II. Colony Origin, Seasonal Cycles and Reproduction. 109
- Whitcomb, Willard H. See Richman, David B.
- Yamamoto, R. T. See Kearns, R. S.

INDEX TO SUBJECTS

All new genera, new species and new names are printed in CAPITAL TYPE.

- A comparison of the nest phenologies of three species of *Pogonomyrmex* harvester ants, 25
- Abdominal trophallaxis in *Harpagoxenus*, 331
- Alarm response in *Gargaphia*, 215
- Antaeotricha*, life history, 163
- Anti-predator strategies. II. Grasshoppers attacked by *Prionyx parkeri* and some *Tachysphex* wasps: a descriptive study, 1
- Ants, territoriality, nest dispersion, and community structure, 265
- Apis mellifera*, 337
- Army ants, 151
- Arthropods attracted to luminous fungi, 383
- Bee foraging patterns, 337
- Behavioral origin of tremulation in green lacewings, 375
- Chrysopidae, 375
- Cicadas, population ecology, 175
- Dedication: Robert E. Silberglied, 197
- Ecology and life history of the *Rhytidoponera impressa* group (Hymenoptera: Formicidae). I. Habitats, nest sites, and foraging behavior, 89
- Ecology and life history of the *Rhytidoponera impressa* group. II. Colony, seasonal cycles, and reproduction, 109
- Effect of flower occupancy on the foraging of flower-visiting insects, 321
- Eggplant lace bug, 215
- Emigration behavior of two species of *Pheidole*, 135
- Flower-visiting insects, 321
- Francis Walker types of *Hydropsychyche*, 259
- Gargaphia solani*, 215
- Grasshoppers, 1
- Green lacewings, 375
- Harpagoxenus americanus*, 331
- Harvester ants, 25
- Historical development of bee foraging patterns, 337
- Hydropsychyche*, new synonymies, 259
- Hydropsychyche alternans*, 261
- Hydropsychyche confusa*, 259
- Hydropsychyche reciproca*, 262
- Laboratory evaluation of within-species, between-species, and parthenogenetic reproduction in *Reticulitermes flavipes* and *Reticulitermes virginicus*, 75
- Lasius fuliginosus*, 347
- Life history of *Antaeotricha* sp. in Panama, 163
- Luminous fungi, 383
- Lyssomanes viridis*, 127
- Maternal behavior in *Gargaphia*, 215
- Mesagyrtes*, 335
- MESECANUS, 335
- Myrmecophilic relationships of *Pella* to *Lasius*, 347
- Neivamyrmex nigrescens*, 151
- New name for extinct genus *Mesagyrtes*, 335
- New Synonymies for *Hydropsychyche*, 259
- Notes on the population of ecology of cicadas in the Cuesta Angel forest ravine of Northeastern Costa Rica, 175
- Ontogeny of *Lyssomanes viridis*, 127
- Orectognathus versicolor*, 231, 245
- Parthenogenetic reproduction in *Reticulitermes*, 75
- Pella*, 347
- Pheidole*, 135
- Phidippus mystaceus*, 1
- Pogonomyrmex*, 25
- Polistes gallicus* in Massachusetts (Hymenoptera: Vespidae), 169
- Polymorphism and division of labor in *Orectognathus*, 231
- Prionyx*, 1
- Reticulitermes*, 75
- Rhytidoponera impressa*, 89, 109

- SilberglieB, Robert E., dedication to, 197
- Slave-making ant, 331
- Sound production by males of *Phidippus*, 199
- Statory Behavior in nomadic colonies of army ants: the effect of overfeeding, 151
- Stridulation in green lacewings, 375
- Tachysphex*, 1
- The emigration behavior of two species of the genus *Pheidole* (Formicidae: Myrmicinae), 135
- The ontogeny of *Lyssomanes viridis* (Walckenaer) (Araneae: Salticidae) on *Magnolia grandiflora*, 127
- Territoriality, nest dispersion, and community structure in ants, 265
- Trail communication in *Orectognathus*, 231
- Tremulation in green lacewings, 375
- Trophallaxis in *Harpagoxenus*, 331
- Walker types of *Hydropsyche*, 259
- Wasps, 1

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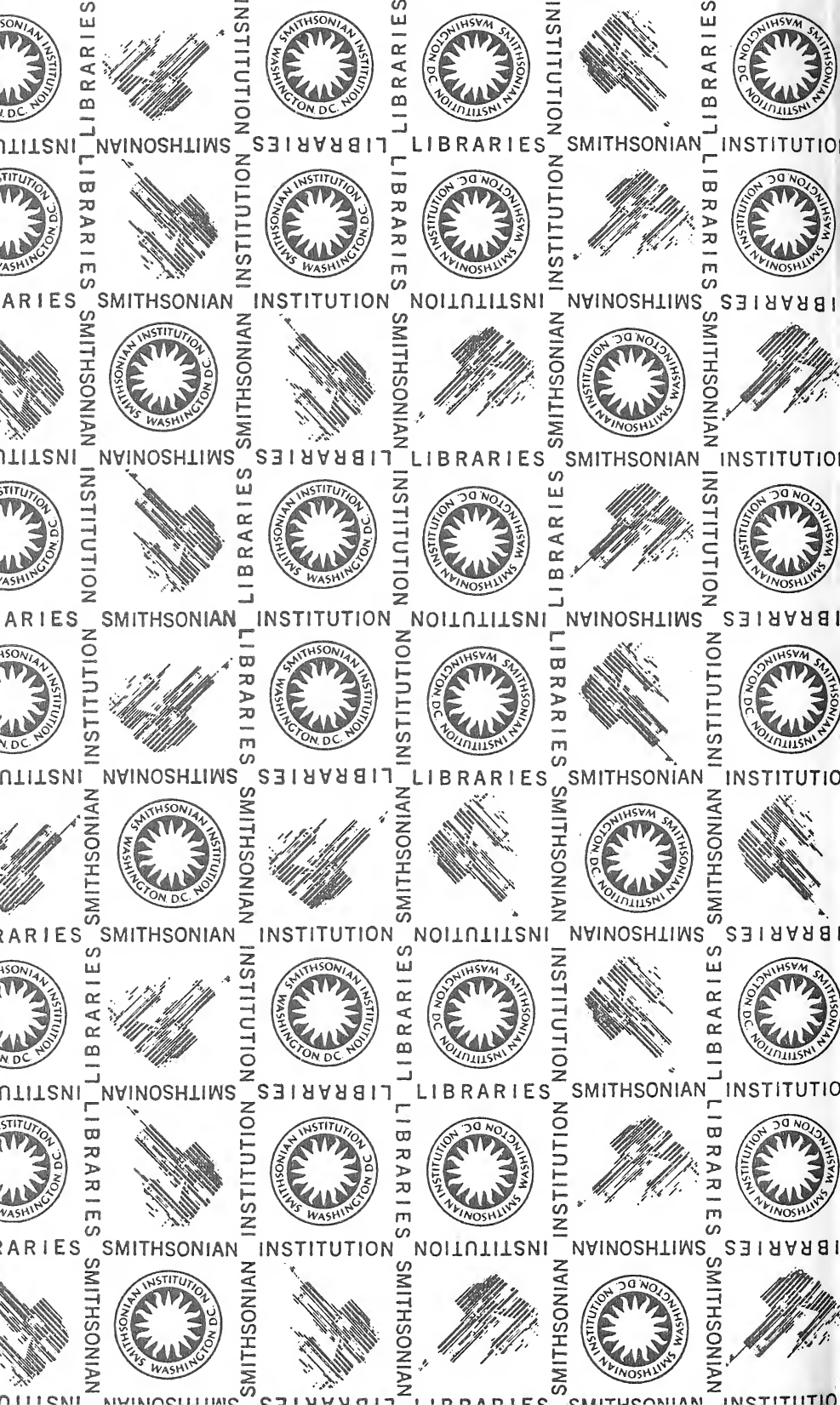
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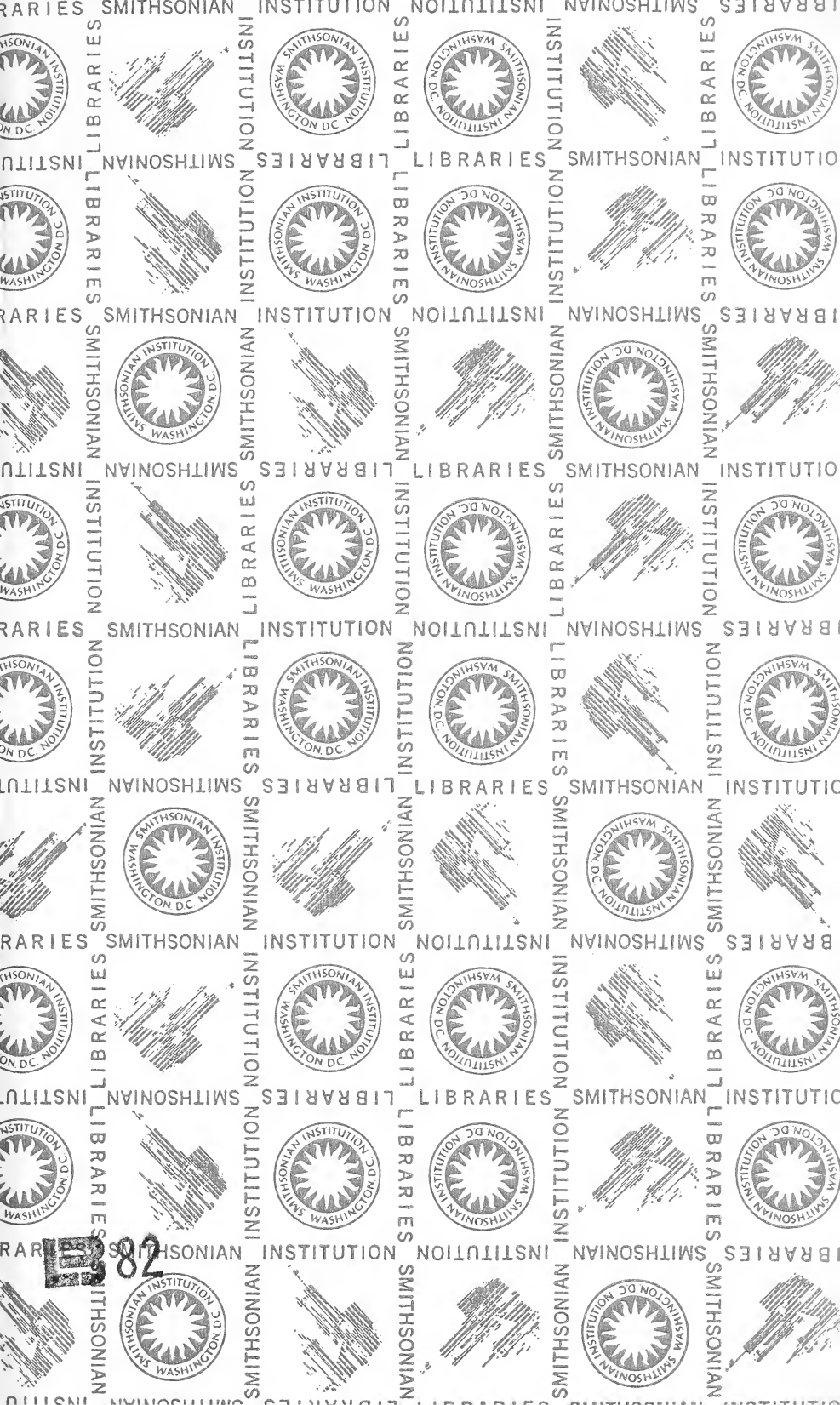
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82

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