GEOGRAPHIC VARIATION AND DIMORPHISMS IN SONG, DEVELOPMENT, AND COLOR IN A KATYDID: FIELD AND LABORATORY STUDIES (TETTIGONIIDAE, ORTHOPTERA)

BY

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PREFACE

My first encounter with the katydid Neoconocephalus triops occurred on an unseasonably warm night in Feb. 1968. I left my Gainesville apartment after supper to get a book I had left in my car. While walking downstairs I saw katydids on the ceiling of the front porch and flying around the porch light. Once outside I saw others darting about the street lights like sphingid moths. Most impressive was that from every large tree and many shrubs katydids were making a continuous droning buzz much like a door buzzer.

I drove to some nearby pastures and counted 23 singing males in 100 yards of roadside. Returning home, I received a call from relatives 120 miles to the north in Georgia asking me about the "noisy grasshoppers" on their screens and shrubbery.

The next norning at school several people brought me specimens and several more commented about the "racket the previous night." One student complained that sleep was impossible because one of "those things" was singing outside his window on a bush. He threw hot water on the bush, but was kept awake by other singers in the distance.

I compared my observations with those of Dr. T. J. Walker, who had experienced this phenomenon before. Walker said that such an eruption of katydids occurs every winter in Gainesville. He noted that most of the singers found at this time were brown, and told of a contrasting summer eruption in which the katydids were mostly green and sang a different song. Walker also noted that katydids in the summer and winter groups were structurally identical.

We ended this conversation with a question that was to reoccur in our discussions for the next four years: "Do these two eruptions represent one or two species of katydids?"

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Neoconocephalus triops (L.) is a species of copiphorine katydid found throughout southern United States, the Caribbean, and northern South America. It is a single species, not two or more as previously thought. It is the first example of age and of prior adult diapause affecting singing wingstroke rate. It is the first tettigoniid known to break diapause in response to photoperiod and the first orthopteran known to have photoperiod-controlled brown/green color dimorphism. It is the first case of clinal variation in calling song. Furthermore the variation appears to be environmentally induced rather than genetically based. Also it is the first singing orthopteran (perhaps the first insect) whose life cycle is known as it varies from univoltine in the North to nonseasonal in the South. In some intermediate areas, a winter generation gives rise to all of the following summer generation and to some of the following winter generation. The summer generation gives rise to the remainder of the following winter generation.

Laboratory studies using live males showed that females came to calling males. Use of taped calling songs having different wingstroke rates (since they were recorded at different temperatures) suggested that wingstroke rate is important in female attraction.

INTRODUCTION

Neoconocephalus triops (L.) is a name applied to certain katydids of the subfamily Copiphorinae. Unlike other U.S. Neoconocephalus these katydids exhibit seasonal differences in color forms, acoustical signals, adult range, and diapause. Such differences give new impetus to a 215-year-old taxonomic question: Do these katydids represent one, or more than one, species? If one species, then how are differences in color, song, ranges, and diapause explained? If more than one species, why are they not morphologically distinguishable?

The taxonomic history of this katydid is one of nomenclatural chaos. Photographs of a specimen believed to be the 1758 Linnaean-type of "Gryllus triops" from the "Indiis" show clearly that it is not what is presently called Neoconocephalus triops.* Burmeister's 1838 description of Conocephalus obtusus appears to be the current N. triops.* Nomenclatural disorder was aggravated when specific epithets were given to the color morphs, and similar katydids from different localities were given different names. Rehn and Hebard (1915) concluded that the name Conocephalus fuscostriatus Redtenbacher, 1891, and N. mexicanus var. tibialus

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*T. J. Walker 1973: personal communication.

Karny, 1907, had been given to the brown phase and *G. triops* Linnaeus, 1758, *C. obtusus* Burmeister, 1838, *C. dissimilis* Serville, 1839, and *C. mexicanus* Saussure, 1859, had been given to the green phase. Rehn and Hebard (1915) concluded that all these names referred to a single species that should be called *N. triops*. They mentioned color dimorphism but failed to correlate it with season. They also speculated that the species was two-brooded. Hebard (Rehn and Hebard 1915) noted seasonal differences in song intensity, but failed to observe distinctive seasonal differences in song phrasing. Subsequent interest in song variation continued in spite of Mr. Rehn's warning concerning Hebard's observation: "Such mistakes [referring to differences in song noted by Hebard] are likely to occur in field observations unless extreme care is exercised" (Rehn and Hebard 1915). Like many taxonomists, Rehn collected and worked mostly on museum collections while abstaining from field observations (which often reveal biological phenomena important to recognizing species).

In the 1950s, Dr. T. J. Walker, a field biologist with an interest in insect sound communication, began to study "*Neoconocephalus triops*." In Gainesville, Florida, he found that year after year there were two distinct groups of singers--one winter and one summer. Each group sang a distinctly different song. The summer song was a discontinuous buzz, while the winter song started intermittently but usually became continuous. Sonographic analysis (Walker 1964) of the sound pulses showed that the summer group had a faster wingstroke rate than the winter group. This last discovery seemed particularly significant in relation to Walker's work on tree cricket calling songs (Walker 1957). In species with continuous and broken trills (similar to the songs of *N. triops*), sexually responsive females were attracted to songs with a pulse rate approximating that of the wingstroke of the conspecific males. Once calling song had made an initial division possible, morphological differences that would have been overlooked without the song difference were discovered. Song analysis helped Walker find many new species of sound-producing Orthoptera (Walker 1962, 1963, 1964, 1969, Alexander and Walker 1962, Walker and Gurney 1960).

In this manner, other workers also discovered additional species. R. D. Alexander (1957) found that the common field cricket of eastern United States was actually a complex of at least five species, each with a different calling song. More important, two other field crickets, *G. pennsylvanicus* and *G. veletis*, even after being recognized as two species, were difficult to separate by morphology. The ranges and calling songs are almost identical but *pennsylvanicus* overwinters as an egg whereas *veletis* overwinters as a juvenile so that the adults occur at different seasons (Alexander and Bigelow 1960). When adults of *veletis* and *pennsylvanicus* were kept together in the laboratory, hybrids were never produced; yet hybrids can be produced under laboratory conditions between other species of *Gryllus* with presumably a more distant common ancestry than that of *G. pennsylvanicus* and *G. veletis*.

From previous studies of the significance of calling songs and seasonally isolated populations, it seemed logical that "*N. triops*" was actually two species. Walker found additional evidence to support the two-species concept.

1) Seasonal life history--With the summer group becoming adults and singing in early summer, it appeared that they came from overwintering eggs like the other 12 species of *Neoconocephalus* in North America. The winter group, however, overwintered as an adult in diapause as does *Pyrgocorypha uncinata* (another katydid from the same subfamily and similar range to *N. triops*). Breaking of diapause was marked by singing during the first warm nights of winter.
2) Brown-green color dimorphism--Summer males and females were mostly green. Winter males were mostly brown yet winter females were mostly green (Table 5). The occurrence of sex-biased color dimorphism in only one group suggested separate gene pools.

3) Differences in range--Walker pointed out differences in the range of the two groups with the adult overwintering group extending farther north.*

Based on the available evidence, Walker decided that in Gainesville "_N_. _triops_" was two species. However, he was not sure what was happening in South Florida. His data were inadequate for him to decide whether one, two, or three species occurred in the Florida Keys. He speculated that the two Gainesville species might merge into one in the Florida Keys.

At the time of Walker's 1964 paper, the only evidence for the one-species hypothesis was the lack of morphological differences between the two groups in any one location and an apparent breakdown in seasonal isolation on the Florida Keys. Several students studied genitalia, stridulatory files, and wing venations but failed to find any consistent morphological differences between the two groups. The fastigium (pointed part of the head often referred to as cone) varied in size and shape geographically but not seasonally.

Dr. Walker and I felt that extensive field studies, outdoor rearing, and other experiments to vary environmental parameters were needed to demonstrate whether or not the two groups were genetically distinct and reproductively isolated from one another. If the two groups had separate gene pools,

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*Personal Communication, 1973.

then they should be considered separate species even though they were morphologically identical. If, on the other hand, they were found to share the same gene pool, they would be one species with seasonally distinct mate recognition signals and with sex-specific seasonal differences in the proportions of brown and green individuals. Neither situation was known to have a parallel in sound-producing Orthoptera. The answer to the question, "Does this represent one or two species of katydids?" was sure to add new concepts to katydid systematics and biology.

STUDY OF GAINESVILLE POPULATIONS

Rearing

Rearing experiments were conducted to determine the seasonal life history of the winter and summer groups. Indoor rearing was attempted to see if rearing from adult to adult was possible. Outdoor rearing was conducted in conditions as natural as possible to reveal the insects' natural life cycle. To check the significance of outdoor rearing results life history stages were monitored in the field and field-collected nymphs were reared.

Indoor rearing began in March 1968. Virgin adults collected as teneral adults in the fall and held until March in one-quart Mason jars were put in 12 aquaria (1 pair/ aquarium) containing sterilized soil and freshly planted bahia grass (*Paspalum notatum*). The Mason jars and aquaria were kept in a laboratory where photoperiod and temperature were variable. The females laid eggs by inserting their ovipositors into the soil and releasing one egg with each insertion. [In the field I saw oviposition only twice. Each time the ovipositor was placed between sheaths of *Paspalum urvillei* (Vasey grass). I suspect that this oviposition process may be more frequent than soil oviposition.]

Hatching occurred in four aquaria as shown in Table 1. Unfortunately most of the nymphs desiccated in a faulty bioclimatic chamber, but a few matured to adults. Some could have matured in time to mate in the summer group while others took so long that they only could have mated in the winter group. Though the katydids were reared in an unnatural environment, the temporal spread of offspring later proved to be significant.

Initial field-rearing experiments were conducted in six screen cages placed outdoors at the University of Florida's farm known as the Honey Plant (hereafter called "Honey Plant"). The cages were screen cylinders 24 in. in diameter and 24 in. high with a flat screen top. The soil under each cage was sterilized and planted with bahia seed. On 9 July 1968, six weeks after planting, two pairs of field-collected summer adults were put in each cage. During one year of biweekly inspections, the cages failed to yield any offspring. The experiment was repeated beginning in June 1969 with 12 additional aluminum screen cages 16 in. in diameter, 24 in. high, and crimped at the top. Again, no offspring were seen during one year of biweekly inspections. Negative results were perhaps due to egg desiccation by excessive heat since the cages were exposed to direct sunlight.

Successful outdoor rearing began during July 1971 at two partially shaded sites. New rectangular screen cages, 16 in. square at the top and bottom and 24 in. high were framed with 1 x 2 in. lumber treated with copper arsenate. A board frame was attached to the open bottom to extend the cage 6 in. into the fumigated soil. Twelve cages were placed in mesic hammock west of Gainesville and 15 under a large live oak at the Honey Plant. Bahia seed were planted in advance to allow a good stand of grass for oviposition and food. Only teneral (virgin) adults were placed in the cages. Hatching occurred in these cages and the nymphs were transferred to screen-topped, one-quart Mason jars for rearing to adulthood. These jars contained screen cylinders for perching and molting and were kept under a screened shelter at the Honey Plant to eliminate death from exposure to sun and rain, yet allowing near-natural temperature and photoperiod. A few nymphs taken from the cages were reared indoors to maximize chances of obtaining adults for song assay, but ants killed these before they matured.

Summer-collected female adults gave rise to adults that correspond to winter group adults (Table 2, rows 1 and 2). During Sept. 1971 I placed 19 field-collected winter group females and corresponding males in cages (Table 2, row 3). They never produced offspring even though most of them lived through April. On warm nights the same winter and spring I collected 6 winter adult females. When put in cages they produced offspring (Table 2, rows 4 and 5). It is noteworthy that the 1 adult reared from the females introduced 20 Feb. matured in time to be in the summer group. Yet the 4 adults reared from females introduced 21 April became winter adults even though they hatched only one to three weeks later than the individual that became a summer adult. If the fall-collected adults (Table 2, row 3) had mated under caged conditions at the time of first singing in the field (warm nights in Jan.), many of the resulting offspring might have become adults before the offspring from the female introduced 20 Feb. 1972 (Table 2, row 4). The importance of the variation in the adult dates of the summer generation will be explained in the next section. Slow (or late) growers of the winter group died unless they became adults before 1 Jan. Cold seems the most likely cause of death.

The important feature of Table 2 is that in Gainesville the summer group gives rise to only the winter group, indicating that the two groups are generations of the same gene pool. Another important feature of Table 2 is that Gainesville _triops_ is neither entirely univoltine nor entirely bivoltine but is both. Jackson and Peters (1963) refer to this condition as heterovoltine.

Outdoor rearing of field-collected nymphs also indicated that the offspring of at least some winter parents become summer-group adults (Table 3). The early-instar nymphs collected in late spring and early summer (as early as 22 April 1971) which gave rise to summer adults could only have come from the winter generation since outdoor rearing gives no evidence of overwintering eggs. The later in summer that early instars were collected, the greater the chance they would become winter _triops_. First instars were collected as late as 22 June 1972 (Table 3).

Rearing experiments as well as the results of field collections indicate that oviposition occurs over a long (three-month) period. This may be partly due to the long period of mating and oviposition extending from winter to late spring. In fact I collected eight winter female adults during June in lawns and fields in the Gainesville area (at least one month after the last singing was heard). One of these females when put in an indoor aquarium oviposited for five days before dying. Oviposition probably occurs throughout the five-and-one-half month period that the active winter adults are found in the field, thus contributing to the temporal spread of hatching. The physiological basis of the different growth rates of nymphs collected at the same time and stage is unclear (Table 3).

Mating of the winter generation starts in Jan. and oviposition extends through June, yet the summer group of reproductives appears to be limited to July and early Aug. The following two sections describe photoperiod experiments that show how the switch from summer to winter generation occurs within the common gene pool.

Photoperiodic Control of Color

Rearing evidence indicated one gene pool but left unexplained generation differences in song, diapause, and color. I suspected photoperiod as an environmental cue determining color because I found two green teneral males near a street light in Sept., when males under natural circumstances were brown.

By placing photoperiod chambers in a screened shed, I was able to control photoperiod while maintaining near-natural temperatures. The chambers measured 24 in. square by 40 in. high and were constructed of 1/4-in. plywood, lined with wall board, and illuminated internally by two 15-w fluorescent bulbs. Two-inch air conditioner hoses connected with a suction fan exhausted air from the chambers keeping them within ± 1.5°C of ambient temperatures. Timers controlled the day length at 15 hr. (long day) in one chamber and 11 hr. (short day) in the other chamber. The early July day length in Gainesville (30° N. latitude) is 14 hr. 57' (including civil twilight). The mid Dec. day length is 11 hr. 05' (including civil twilight). The two chambers approximated these natural day lengths.

During Sept. 1968, four field-collected brown males, two green females, and two brown females were placed in each chamber with dry dog food and water. These adults were observed from Sept. 1968 to May 1969, but no color changes occurred.

On 30 June and 1 July 1972 I placed field-collected last-stage, male nymphs in individual Mason jars. All nymphs found at this time in Gainesville were green. Five nymphs were placed in each of the two chambers and five more were placed next to the chambers in natural photoperiod (control). All nymphs became adults between 2 and 4 July (Table 4, A).

All adults were dissected on 24 July 1972 to determine the diapause state by reference to gonad size. Although there was no significant difference in gonad size for the three groups, fat tissue completely lined the abdominal cavity of the 5 individuals from the short-day chamber. Fat was not at all conspicuous in any of the other 10 individuals. Singing was heard from natural and long-day individuals but none from short-day individuals. In the field, singing was abundant during the three weeks that the long-day and control males were singing. The seasonal percentages of the two color forms of field-collected adults are different (Table 5).

The 15 nymphs were summer-generation triops as indicated by the control. However, individuals exposed to short days behaved like the adult overwintering generation that occurs in the field during late summer and fall. They molted to brown adults, failed to sing, and had large quantities of fat typical of winter triops as well as the only other local adult-overwintering katydid, Pyrgocorypha uncinata. Long-day and natural photoperiod individuals were like the summer generation: green, without conspicuous fat, and producing calling songs.

In order to test the effect of photoperiod on juveniles that normally become winter adults, 24 green, late-instar nymphs were collected between 15 Aug. and 1 Sept. 1973 and randomly placed under the same conditions as described for the previous experiment with the summer generation. Four nymphs died, and the rest molted to adults from 20 Aug. to 1 Oct. 1973 and were dissected three to eight weeks later (Table 4, B). At least three singers were again heard from the long-day chamber, but this time the control as well as the short-day groups were silent. The results of the two experiments (Table 4, A, B) were the same except for the natural photoperiod groups which paralleled in coloration the adults in the field. Also, two of the 15-hr. photoperiod group became brown. These two individuals were not necessarily different from presumptive summer-generation individuals in their response to photoperiod (Table 5).

Under field conditions most color changes evidently occurred during the later molts (Table 6). Of nymphs reared under natural photoperiods, only one individual of the summer group changed color before the last molt (N=96). Eight color changes (N=142) occurred before the last molt in the winter group (one before the penultimate molt). I have never collected a brown early-instar nymph (n>300) or observed a molt from brown to green in the laboratory (n>1500).

The day length for 15 Sept. in Gainesville (the week that most of the nymphs in Table 4 molted to adults) is 13 hr. 11 min. (including civil twilight) or 1 hr. 46 min. shorter than early July when most of the summer generation molt to adults.

Although the change in color is largely a photoperiod effect, it was not ascertained whether the color response was to a specific day length or to change (increase or decrease) in day length. However, the latter hypothesis in its simplest form is refuted since nymphs in the natural photoperiod (decreasing) became green adults (Table 4).

I failed to find an example in the literature of photoperiodic control of color in Orthoptera. However, one would expect such color dimorphism to be adaptive where bivoltinism is combined with seasonal habitat changes. Most orthopteran color changes occur with univoltine acridids in response to temperature, humidity, crowding, and light-wave length and intensity. Brown/green polymorphism is well documented in Acrididae, Tettigoniidae, Mantidae, Phasmidae, Cicadidae, and Lepidoptera. It occurs by means of pigment changes in epidermal cells during ontogeny or by polymorphism of the haemolymph color (Rowell 1971, Otte and Williams 1972). Rowell and Mukwaya (Rowell 1971) have shown that the rare purple phase of the copiphorine katydid Homocorophus nitidulus is controlled by a single dominant allele as is the pink color phase of Amblycorypha oblongifolia (Hancock 1916). A good example of environmental control of color occurs in Chortoicetes terminifera where the formation of green pigment instead of brown is a result of prolonged exposure to high humidity (Byrne 1962).

The physiology of tettigoniid pigments producing green/brown color dimorphism has not been investigated, although some work has been done on acridids. Pfeiffer (1945) showed that a high concentration of secretions from the corpora allata resulted in formation of green haemolymph in *Melanoplus sangunipes*. Extra corpora allata implantations into brown nymphs of *Acrida bicolor* resulted in an increased number of green morphs in the succeeding instar (Joly 1951, 1952). Joly et al. (1956) also showed that for the change from brown to green to occur the implantation of the corpora allata must be made late during the preceding instar, indicating that the pigment system is only sensitive to hormone concentration near molting time. Allatectomies of several nymphal acridids produced high proportions of the brown form (Rowell 1971). Girardie (1967) cauterized the A and B cells of the pars intercerebralis in *Locusta* nymphs, causing the nymphs to turn green. Apparently the presence of the A and B cells inhibits secretion of the corpora allata.

If the *N. triops* color-dimorphism system for males is similar to the above system for acridid grasshoppers, one would suspect that a long-day stimulus results in secretion by the corpora allata leading to production of the green pigment. Lack of the long day would cause the corpora allata to turn off, thus producing brown at molting time.

The *N. triops*' green/brown system probably evolved in association with seasonal foliage color changes. The brown color is adaptive during the tropical dry season or the temperate winter while the green is adaptive in the tropical wet season or temperate summer. Golding (1934) reported that green color forms in Acrididae are more abundant in the wet season and the brown more abundant in the dry season, resulting in cryptic coloration throughout the year.

I made no attempt to quantify the adaptive value of color dimorphism either sequentially or within a generation. Finding the winter singers in Gainesville (all brown) seemed easier than locating the brown summer singers (28% brown and 72% green) because I formed a one-color search image. During summer, selection favors the more cryptic green katydids unless they become so numerous that predators form a green search image. Then the brown form becomes more adaptive. The importance of search images involving brown and green colored morphs has been demonstrated in predator-prey relationships (Allen and Clarke 1968).

The percentage values in Table 6 are as one would expect when correlating color with field-background coloration in Gainesville, Florida, except for the high percentage of green females in the winter group. In 1969 I speculated that the winter females probably outlived the winter males. Since 1969 I have found eight green females in early June, one and one half months after the last males were heard. Tattered wings and dull green appearance indicated that these females belonged to the winter generation, not the newly forming summer generation which does not reach adulthood before late June. I suspect that most females continue ovipositing until late spring or early summer. By then the background foliage is green, and natural selection for concealment favors the green morph.

Another oddity is the 3% green males found in the winter group (Table 5). I found 10 unusual fall singers in the Gainesville area (5 brown and 5 green) singing from grassy areas near street lights. Since none were heard in the rural areas, even though most of my study was in such areas, it is likely that these 10 individuals were winter nymphs exposed to unusually long photoperiods created by street lights. These probably failed to go into diapause and therefore sang. I should emphasize that the 10 individuals is a biased high figure since every warm fall night I drove 10-30 miles listening and only located these 10 singers. Had these 10 been part of the normal summer or winter generation, I probably would have overlooked them. In fact every male adult collected in the fall away from street lights was brown and mute.

Diapause

Lees (1955) defines diapause as arrested development at any life stage where the return of favorable environmental conditions alone will not terminate the arrested development. If development is resumed as an immediate response to favorable conditions, the condition is known as quiescence. Beck (1968) uses "suppressed development" in lieu of "arrested development" since at least some form of development is usually continuous throughout the life of an insect. Adult (imaginal) diapause is mostly a suppression of the developing reproductive glands and is often referred to as "reproductive diapause" or "gonotropic diapause" (Beck 1968).

Male and female winter group triops become adults in late summer or early fall. They are in diapause as indicated by suppressed ovary development in females and lack of singing in males. Fat is conspicuous in diapausing males and females.

Whether diapause was a response to photoperiod was tested as previously described for the color experiments. Three weeks after the adult molt, the gonads and accessory glands were removed and preserved in 75% isopropyl alcohol for 1 week. Since the testes were oval shaped, the maximum and minimum diameters were recorded and averaged (Table 7). The measurements were made on a dissection microscope with an ocular marked in 0.01 mm. Only one testis from each specimen was measured since the other was often damaged or distorted during dissection. A T test ($p \leq 0.01$) showed no significant difference among the three groups of testes.

The male accessory glands were dried on a paper towel for 1 min. to remove surface alcohol before being weighed on a Mettler #15 balance. After the 1 min. drying period the glands only lost 1 mg. per minute due to alcohol evaporation. Since I completed the weighing within 30 sec., I disregarded the weight loss. Mean weights from the long-day and natural-early-summer photoperiods were similar (T test, $p \leq 0.01$) and were significantly heavier than the short-day or diapausing accessory glands (T test, $p \leq 0.05$) (Table 8).

The most noticeable difference between diapause and nondiapause individuals is in ovary weights (Table 7). The females were caught at the same time, stage, and place as the males, and the experimental conditions were the same. The ovaries were removed three weeks after the adult molt, preserved in alcohol and weighed on the Mettler balance. After the 1-min. drying time, the weight decreased about 4 mg. per minute. Weight was recorded at 30 sec. lapsed time, and 2 mg. were added to the observed weight. The difference between the diapausing and nondiapausing ovaries is significant at the 0.01 level (T test).

The same experiment was continued with female nymphs collected during mid- and late summer with 10 individuals in each group. Under field conditions these nymphs matured into adult-diapausing winter individuals. The experimental photoperiods were the same as in the previous experiments and the results were in accordance with the previous experiments. Further weighings were unnecessary since by visual inspection I could classify ovaries larger than 100 mg. as "large" and ovaries smaller than 30 mg. as "small." I found no test ovaries of intermediate weight. Again, I found much fat in all individuals reared in short days.

Suppression of juvenile hormone output from the corpora allata is believed to initiate reproductive diapause in _Dytiscus marginalis_ (Joly 1945). This process is probably correlated with green/brown color changes as described earlier. Adult diapause is often characterized by decreased feeding, locomotion, oxygen consumption, and water consumption. Also, increased amounts of fat and glycogen are present which may be metabolized into eggs at diapause termination (de Wilde 1962). Hodek and Cerkasov (1958) found that diapausing coccinellid _Semiadalia undecimnotata_ adults do not produce sperm. However, sperm produced during late nymphal stages may be present in the diapausing adult. J. L. Nation found viable sperm in diapausing adult _N. triops_ testes and accessory glands though they may have been produced in the last-instar nymph.* In fact T. C. Emmel found viable sperm in testes of last-instar _N. triops_ nymphs that had not yet entered diapause.**

Diapause induction by photoperiod is well known. However the question remains whether the induction of diapause is a response to an absolute day length or to changing day length over a period of several days or weeks. According to

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*Personal Communication, 1972.

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Beck (1968) the latter has not stood up to criticism. In fact since most insects have a photoperiod-sensitivity period of only a few days (Danilevsky et al. 1970), it seems logical that the actual duration of light or dark period is the stimulus rather than change in day length. The change in day length between two consecutive days is very slight and might be obscured by differences in cloud cover. Detecting such differences would require an extremely sensitive measuring mechanism.

Little is known about the termination of diapause except that temperature is important in many temperate species (Danilevsky et al. 1970). This cue may consist of a period of prolonged chilling before the return of favorable conditions as in Bombyx. Danilevsky and Sheldeshova (1968) claim that the lack of a chilling period is one reason why temperate insects fail to penetrate into the tropical zones where temperature fluctuation is small. In a few cases diapause is terminated by photoperiod. Baker (1935) showed that certain tree hole mosquitoes enter diapause under short-day conditions and end it in response to long-day conditions. Trichopterans of the genus Limnephilus go into estival adult diapause in response to long days and end diapause in response to short days (Novak and Sehnal 1963).

In order to determine the effect of photoperiod on termination of diapause in triops, I collected 23 early-instar nymphs in June 1972 and reared them under short-day (9L:15D) conditions and outdoor temperatures as described in previous experiments. On 10 Aug. 1972 (two weeks after the last of the 10 females became adults), I randomly selected 5 females and put them under long-day conditions (15L:9D). On 21 Sept. I removed the ovaries from the 10 females and categorized them as large (<0.100 g.) or small (<0.030 g.). The short-day ovaries were small (n=5). The long-day ovaries were large (n=5). This is the first known example of an orthopteran breaking diapause in response to photoperiod.

When considering the adaptive significance of diapause, I am reminded of the yearly eruption of _N. triops_ singers during the first warm nights of winter (see preface). This eruption has always occurred within two weeks of 10 Jan. even when the winter has been unusually warm. Also, it is interesting that winter adults that mature under the ideal conditions of late summer and early fall fail to sing at the time, but store fat energy and sing in winter.

It is not known if _N. triops_ diapauses in the tropics. If dry-season adult diapause did occur, it might be adaptive since the relatively nonmobile nymphs would develop during the ensuing wet season. The adults could fly to wetter habitats during the dry season. Perhaps as adults migrated to temperate areas, the tropical dry season was replaced by the temperate winter and the overwintering adults were pre-adapted to the cold by the tropical dry season. Previous rearing experiments indicated that overwintering eggs do not occur and late nymphs exposed to winter conditions are killed. All other U.S. Neoconocephalus overwinter as eggs. The adult diapause could be a sign of recent entry into North America from the tropics. The only other adult diapausing North American katydid, Pyrgacorypha uncinata, is also the only other southeastern United States conehead known from the West Indies.

Causes of Seasonal Variation in Stridulatory Wingstroke Rate

Dr. T. J. Walker found significant differences between the calling songs of the two generations of N. triops. Along with easily heard differences in phrasing, he found a more subtle, yet reliable, dichotomy of wingstroke rate in Gainesville, Florida, specimens. These song differences which Walker described are attributable to the presence or absence of diapause.

I recorded and collected singers monthly from July 1960 to July 1962 in the following areas: Quitman (Brooks Co.), Georgia; Gainesville (Alachua Co.), Florida; Jupiter (Palm Beach Co.), Florida; Key Largo Key (Monroe Co.), Florida; and Big Pine Key (Monroe Co.), Florida (Fig. 1). The captured specimens were kept temporarily in ventilated snap-cap vials and then placed in screen-top, quart Mason jars containing dry dog food, watering vials, and screen perches. These jars were placed in a temperature-controlled low-noise room for recording.

Tape recordings were made with a D-33 dynamic microphone (American Microphone Co.) and a Kudelski Nagra III recorder at 15 in./sec. A 24-in. parabolic reflector was used during field recordings. The singers were recorded daily except for weekends and holidays until their death.

Audiospectrograms of the recordings were made on a Kay Sonagraph, and sound pulses were counted along a measured line in order to calculate the wingstroke rate. Recent high-speed cinematography indicates that the calling song is produced by alternate long- and short-wing closures (Walker 1974). The measurements of wingstroke rate in this dissertation were of the long closures only since they formed dark, easily countable lines on audiospectrogram paper.

Wingstroke rates plotted against temperature yielded graphs with high variation (Fig. 2) unlike the graphs obtained by Walker (1964). I found several sources that could account for the variation. First, Walker's recordings were from fresh specimens usually recorded less than a week after capture whereas my recordings were made from adults which I had kept alive as long as six months. Second, a few of my recordings were from the field where I was often unable to obtain the temperature of the singing insect. Only the ambient temperature near the microphone was recorded, which was in a different location and probably at a different temperature than the insect. A third reason for variation is that I recorded some fall singers. These had a wingstroke rate intermediate between the winter and summer population. (Possible reasons for this intermediate wingstroke rate will be discussed later.) If these three sources of error are removed, the variation decreases, giving a graph similar to that obtained by Walker and showing a significantly slower wingstroke rate for the winter generation (Fig. 4).

I did further work to determine if the slower wingstroke rate could be attributed to aging. Table 8 compares initial wingstroke rates (X_1) with terminal wingstroke rates (X_2) for eight individuals recorded at constant temperatures [25 ± 1°C] over a time span of at least six weeks. All were found as diapausing fall adults during Sept. 1962. Using a paired T test, the calculated T value of 6.5 shows that a significant wingstroke rate decrease occurs over the six or more weeks ($p \leq 0.001$).

It is not clear whether the slower initial wingstroke rate of winter generation males is simply the result of age and/or diapause or whether the generation itself has an influence. In order to find out I collected first-instar nymphs that were progeny of the summer-generation parents during the summer of 1972 and separated them into two groups, one reared under long-day and one under short-day conditions. All became adults during Sept. 1972. On 21 Sept. 1972 I placed the long-day reared group in the low-noise room set at long-day conditions. Recordings were made when singing began during the first week in Oct. The short-day reared individuals remained in diapause until put into the long-day, low-noise room on 1 Jan. 1973. Singing commenced in mid-Jan., and the initial songs were recorded. The first songs of the diapausing group showed a significantly slower wingstroke rate than those of the nondiapausing group ($p \leq 0.005$) (Table 9). Though both groups are first-time singers, either chronological age or the events of diapause could be responsible for the decreased wingstroke rate of the diapause group. It is also worth noting that the non-diapausing songs were phrased discontinuously whereas the postdiapause songs in this experiment and subsequent experiments were phrased continuously (discontinuous at first, then becoming continuous).*

A test specifically comparing the effects of aging and diapause involved testing 30 diapausing adult males collected from one locality in Alachua Co. from 19 Sept. to 28 Sept. 1972. Each specimen was placed in a quart Mason jar in a shed and exposed to outdoor temperatures and photoperiod. The specimens were divided into three groups (A, B, and C) and placed in the low-noise room (long-day photoperiod and constant temperature (25°C±1°C) at 45-day intervals.

Dates of first singing, and therefore age of first singing, varied systematically (Table 10).

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*Many postdiapause recordings were taken from the first part of the song which was discontinuous. The wingstroke rates are the same for the continuous and discontinuous phrasing during a single song.

Singers were recorded whenever heard from 1 Oct. 1972 until 29 April 1973. Comparisons of wingstroke rates of the first songs heard from Groups A and B, B and C, and A and C show no significant decrease in wingstroke rate from previous aging under natural conditions in the diapause state. Wingstroke-rate comparisons of Groups A and B as well as Groups B and C (45-day difference in exposure to diapause) are not significantly different ($p \leq 0.1$) (Table 10).

It seems evident that an effect on wingstroke rate occurs while an individual is aging whether while singing or while entering or breaking diapause. However, length of time in diapause seems to have no effect on wingstroke-rate slow-down (Table 10). Table 11 is a comparison of wingstroke rates of the first singing in Group C with the wingstroke rates of Group A singers tape-recorded at the same time. Both groups had been in diapause, but Group A singers had been singing for at least six weeks and had a wingstroke rate slightly slower than, but not significantly different from, Group C ($p \leq .1$).

The wingstroke rate slowdown associated with diapause explains the dichotomy of summer and winter songs. However, once diapause is broken and singing has commenced, additional slowdown may be brought about by laboratory conditions which unnaturally extend the insects' life. No one knows how long the singing adult lives in the field. During a one-month period in the spring of 1968, I marked 61 singing males.

Only 6 were relocated more than 24 hr. after capture. The longest recapture span was 11 days. These data only indicate that adults may sing for at least 11 days (Whitesell 1969). If the male singing span is only a few weeks in the field, little or no decrease in wingstroke rate could be expected. If singing should occur in the field for a longer period (one month or more), one would expect a decrease in wingstroke rate (Table 8).

The evidence indicates that the dichotomy in wingstroke rate between summer and winter generations is attributable to diapause.

Orientation to Calling Songs

Orientation to male calling songs is well documented in sound-producing insects. I have observed four *N. triops* matings in the field where females flew to singing conspecific males. Preliminary laboratory experiments using both live and taped calling songs were conducted in a low-noise room (8 x 5 x 8 ft.) lined with sound-absorbing tile and kept at 25° ± 1°C. In order to assure that the test adults had not mated, summer specimens were collected as nymphs and winter specimens were collected as diapausing adults. All were kept isolated in screen-top Mason jars. The summer adults were put in the low-noise room (15L:9D) and tested from 28 July to 14 Aug. 1972. The winter specimens were collected in Sept. and put in the low-noise room (15L:9D) in Oct. where they had sufficient time to break diapause before the testing dates of 16 to 22 Dec. 1972. Since summer singing did not start until about one week after the final molt, I allowed one-week maturation time before testing summer females. The room was illuminated by a 15-w incandescent red light which permitted singing and provided enough light for observations.

The first experiments were conducted by placing 11 caged males against one wall and 11 caged females against the other wall. When 1 or more males began singing, females often began running, jumping, or shaking. Such behavior usually occurs before mating (Whitesell 1969). If this female activity occurred, the jar top was removed allowing the female to escape. On 15 occasions after opening the jar, the female flew or walked at random, seemingly showing no orientation. On 4 occasions (one female is responsible for 2 of these) the female landed on the wall within 5 cm. of a singing male, walked down to the jar, and climbed onto the lid. The times elapsed from when the female left the jar until she reached the male jar were 99 sec. (including 5 bumps into the wall), 3 sec. (2 bumps), 6 (4), 3 (1), and 6 (3). This experiment showed that at least some females are attracted to singing males.

In another experiment I played tapes of male songs to individually caged virgin females. The use of taped songs eliminates the possible use of pheromones and sight during location. Also, variables such as pulse rate can be checked for their importance in attraction.

N. triops tapes previously recorded at different temperatures on the Nagra III recorder were made into tape loops and played back on the same recorder. The signal was amplified with an audio-ultrasonic amplifier (Alton Electronics Co.) and emitted through a high-frequency tweeter. Recordings played at different intensities in the low-noise room containing free-flying females failed to elicit phonotaxis. Finally, two females responded by running into the speaker cone when it was placed 6 in. from them. In both instances the sound intensity measured 6 in. from the tweeter was 80 dB on the A scale of the sound-level meter. More intense sounds failed to attract the females.

I decided to use this short-range attraction to discover the effects of different pulse rates on female attraction. Twenty-four virgin summer females were placed in cylindrical screen cages 9 in. long by 4 in. in diameter containing dry dog food and a water vial. The cages were put in a single row on the floor of the low-noise room. The speaker was placed next to a randomly selected end of a cage, and a dummy speaker was placed at the opposite end. A control tape of a cricket calling song was played for 2 min. to all specimens at 80 dB to make sure that the females would not be attracted to some aspect of the recording other than the katydid song. A test tape of 109 wingstrokes per second made by a discontinuously singing *triops* was played at 80 dB to each summer female for 2 min. before each test session to determine if they would respond to the song by either phonotaxis, shaking, or walking. Those that failed to respond were removed from the room. This screening procedure permitted more time with females that would respond to the natural pulse rate at 25°C. The process was not used in the winter experiments since I never had more than 10 specimens.

The test loops were played for 2 min. to an individual. The other individuals were covered with a cardboard box to isolate them from the extraneous movements and sounds of the observer. The individual test was considered positive if the female walked to the test-speaker end of the cage and stayed there for at least 20 sec. The results of the test sessions are shown fully in Table 12 and abbreviated in Table 13.

Interestingly both continuous and discontinuous recordings attracted summer and winter females equally, indicating that the breaks throughout the summer-group songs and at the beginning of the winter-group songs are not important for attraction.

Most interesting is that sessions 11-13 (Table 12) used recordings of *N. retusus* at 31 and 32°C, resulting in a high wingstroke rate that is comparable to *N. triops* at 25°C. There was better attraction to these recordings than to recordings of *triops* at higher and lower wingstroke rates, suggesting that wingstroke rate is an important attraction factor and that the wingstroke rate to which a female responds is a function of ambient temperature. During Aug. in North Florida _N. triops_ and _N. retusus_ may be heard singing near each other.

The highest percentage of success of phonotaxis for summer group _triops_ occurs in the wingstroke-rate range comparable to those found in the field (Fig. 3); however, the females were prescreened for response to this rate. Therefore the only sure conclusion is that summer females that do respond to the summer rates do not respond to rates that deviate by more than 10-20%. On the other hand, the attraction of the winter diapausing group is about the same throughout the wingstroke-rate range. In fact, two individuals (d and f) were attracted to the slowest and fastest wingstroke rate (Table 13). The large range of female-attracting wingstroke rates may be adaptive since the winter individuals in the field probably vary in adult age due to microclimatic differences (teneral winter adults are found from Aug. to Dec. in Gainesville). Also, the lack of pulse rate specifically in the North Florida winter group would not be as important as in the summer group when five other species of _Neoconocephalus_ can be heard within earshot of singing _N. triops_. No other _Neoconocephalus_ are singing in North America at the same time the winter group are singing.

Factors permitting species-specific attraction in _Neoconocephalus_ deserve more attention--particularly _N. triops_ with its generation differences in song. A good approach to this problem involves more sophisticated electronic equipment to reproduce the calling-song carrier frequencies. Also surroundings where the phonotaxis takes place should simulate field conditions since echoes in the small, low-noise room may have confused sound-orienting females. A larger room would eliminate much of the wall bumping which probably hinders in-flight orientation. Perch sites such as shrubs or grasses may be necessary for female-to-male orientation. Even considering the weaknesses of the experiment, female-to-male phonotaxis seems to occur and it appears that wingstroke rate is an important part of the process.

GEOGRAPHIC VARIATION

Introduction

Distributions of sound-producing insects are more easily studied than those of most other insects once the species-specific calling songs are identified. In fact, songs that are loud to the human ear, such as those of *N. triops*, may be heard 300 yards or more under optimum conditions. By covering large areas in a car, the known ranges of many species may be increased and new species may be discovered by their different calling songs. As shown in the previous section, diapausing and nondiapausing groups of *N. triops* may be identified by song phrasing and by collecting date.

Figure 1 shows the U.S. range of both generations. T. J. Walker reported *N. triops* on the Caribbean Islands of Hispaniola (Sept.), Puerto Rico (Jan., June), Jamaica (June, Nov., July), St. Croix (Jan.), Grand Cayman (June), and Trinidad (June, July). All specimens sang a discontinuous song identical to that of the summer generation found in the United States.* In fact, Walker believes that the discontinuous song may be heard in the West Indies year-round.

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*T. J. Walker 1973: personal communication.

Rehn and Hebard (1915) reported the southern range of triops extended to Colombia, S. A. Hebard (1932) collected many specimens from Mexico, and Ostmark* sent me specimens from La Lima, Honduras.

The known northern limit of summer populations is represented by one specimen I heard and collected in Georgetown Co., South Carolina. The continuous-singing winter generation, however, extends northward to Southeast Ohio** and southern New Jersey (Rehn and Hebard 1915) and as far south as Big Pine Key, where I heard and collected only a few continuous-singing specimens.

Calling Song

As mentioned in the introduction, one of the most outstanding differences between the winter and summer generations is the difference in singing wingstroke rate. With calling-song dimorphism unknown in insects, the difference in song originally led me to believe that I was working with two species.

I collected katydids in or near the survey areas and recorded them in the low-noise room under controlled temperatures. Songs of specimens that were recorded three weeks beyond the collection data were disregarded in hopes of minimizing age-dependent variation in wingstroke rate. Each

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*H. W. Ostmark 1960: personal communication.

**T. J. Walker 1973: personal communication.

point in Figs. 3-7 represents a different individual. Recordings were made in the laboratory under controlled temperatures. Field recordings were excluded since the ambient temperature of the singer often differed from the temperature at the recording site. All recordings were made on the same Nagra III tape recorder.

The North Florida (Fig. 3) and Central Florida (Fig. 4) graphs show a distinct difference in the pulse rates of the winter and summer populations. In fact, these points coincide closely with those found by Walker (1964) for Gainesville, Florida, specimens. The differences in the wingstroke rates are attributable to diapause as shown in the previous section. However, in the Keys (Figs. 5 and 6) the wingstroke rates of the winter and fall generations approach those of the summer generation, perhaps indicating less intense diapause; i.e., a proximate cause for this phenomenon is reduced selection for intense diapause in the Florida Keys, where the winters are mild and suitable for nymphal development. In colder areas (North and Central Florida), only diapausing adults survive the winter, as shown previously. In these areas there must be selection for more intense diapause and there are obvious differences in wingstroke rate between the diapausing and nondiapausing generation. In Jamaica (Fig. 7) no differences in population density or wingstroke rate were noted during field work in Nov., June, and July.*

Figure 8 summarizes the wingstroke rates of all areas. It is interesting to note that the rates of all the nondiapausing populations are very similar regardless of geography. Yet to the north (where the diapausing generation is more pronounced than the nondiapausing) winter wingstroke rates become progressively slower.

At first glance the adaptive significance of seasonal differences in phrasing could be due to the presence of other sympatric species of _Neoconocephalus_ with wingstroke rates similar to those of the summer group. However, in the laboratory females from both groups are attracted equally well to either the discontinuous or continuous song (Tables 12 and 13). Also the faster summer wingstroke rate, though differing from one sympatric species (_N_. _retusus_), is closer to two other sympatric species (_N_. _velox_ and _N_. _robustus_). The only reason I can find for the song differences is that they are produced by the physiological changes associated with diapause.

Life Cycles

Survey areas were laid out to determine seasonal changes in relative singing densities within a given area and to discover geographical variation in life cycles. The songs of

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*T. J. Walker 1973: personal communication.

sound-producing insects may be used not only in determining numbers and locations of singers but also in determining the life stage, since only reproductively mature males sing.

Each survey area consisted of a circular walk or slow speed drive (30 m.p.h.) beginning about 45 min. after sunset in a convenient rural area. Since every area was different in habitats and weather conditions, comparative data are more revealing than absolute numbers. Surveys were made monthly except in Gainesville, where weekly surveys were conducted (Fig. 1). For comparison, the weekly Gainesville graph (Fig. 9) is abbreviated in Fig. 10 to correspond with the monthly data from other locations. Also shown in Fig. 10 is an approximation of the singing season in Southeast Ohio, inferred from weather data, and South Carolina, inferred from North Carolina listening records by Fulton (1951).

Figure 9 shows a two-year, weekly analysis of a pasture locality near Gainesville, Florida. The peaks for each generation seem to coincide closely in the top two graphs. The lower graph is the singing density of the winter generation in a mixed hardwood hammock. The singing peak appears to be later, which may be explained by delayed reproductive maturation due to the shaded conditions in the forest understory.

Figure 10 indicates that northerly one-generation demes give way to two-generation demes in North Florida. In the Florida Keys three generations are likely, and continuous breeding may occur in the Caribbean. As one travels south, the winter (diapausing) generation is less prominent and sings earlier. In fact, on Big Pine Key the continuous winter song was heard on only three occasions and discontinuous singing was heard all year (Fig. 10). In the tropics neither Walker nor I have heard any continuous singers; yet Walker has heard discontinuous singers on five trips to the Caribbean (no trips were made during spring). Perhaps the Florida Keys represent a transition zone from temperate to tropical climates, with decreased selection for adult overwintering diapause and increased selection for continuous breeding. Perhaps overwintering adult diapause in temperate areas evolved from tropical dry season diapause. The tropical dry season and temperate winter seem to correspond (both seasons lacking green grass for nymphal food). Only adults survive the temperate winter (Table 2), and possibly only adults survive the tropical dry season. I found no evidence of adult diapause in the Florida Keys; a few singing adults (Fig. 10) and nymphs were found there year-round. However, a portion of the adults could have diapaused during the cool (Dec.-Jan.) or dry (April-May) seasons and I would not have detected it.

Both indoor- and outdoor-rearing experiments showed that eggs from single females hatched over eight-week periods (Table 2). Furthermore, field-collected early-instar nymphs reared under the same conditions became adults as much as seven weeks apart (Table 3). With large variance in dates of winter-adult mating, hatch, and rate of nymphal development, one would expect some external stimulus as photoperiod to synchronize singing and mating in their respective seasons. Nymphal development time coupled with the photoperiodic control of diapause and color explains the geographical ranges and relative sizes of summer and winter generations. Figure 11 is a hypothetical--yet I think realistic--modification of Fig. 10. The katydids require approximately four months of warm weather to develop from the singing of their parents to the photoperiod-sensitive last nymphal instars. The solid vertical line represents the critical photoperiod that triggers the color and diapause or nondiapause condition of the adult. The broken vertical line represents the first killing frost that terminates juvenile development. In Ohio (Fig. 11) there is not enough developmental time from the first singing date to the critical photoperiod line to allow for a nondiapausing (summer) generation. Thus in the North, the life cycle is strictly univoltine. In South Carolina, however, there is just enough time from the beginning of the winter singing to the critical photoperiod line to allow for a few summer singers. The fate of the offspring of these summer singers is unknown, but many are probably killed as in the Gainesville rearing experiments. Most of the offspring of winter singers go into diapause as adults and become winter-generation *triops*. In Gainesville, Florida, the offspring of first-half-of-the-winter singers have time to make the summer generation while the later half are caught by the short day and go into diapause. Most of the summer-generation offspring become winter adults, although some are probably killed by the cold. In other words, in Gainesville, Florida, the heterovoltine condition exists.

The data from Central Florida and the Keys indicate two or more generations in Central Florida and three generations or possibly continuous breeding in the Florida Keys.

The life cycle of *N. triops* in the Florida Keys and the tropics deserves further study. Particularly interesting is whether or not diapause occurs and, if so, whether it is an adaptation to cold or dry seasons. If tropical dry season diapause does exist, the token stimulus that initiates diapause is unknown.

Table 1. Hatch from winter adults placed in aquaria on 5 March 1968

Week of	Aquarium no.			
	2	6	7	7
14 April 1968	6	-	-	-
21	2	9	17	-
28	5	3	6	-
5 May 1968	-	-	6	-
12	-	-	16	-
19	-	-	2	-
26	-	-	0	-
2 June 1968	-	-	2	15
9	-	-	-	12
16	-	-	-	6
23	-	-	-	-
30	-	-	-	-
Total	13	12	49	33
Death date	20 June	12 June	11 May	*
F_1 adult dates**	27 June (1) 2 Aug. (1)		27 June (2) 27 July (1)	25 Sept. (1) 5 Oct. (1)

*Escaped 27 May 1968.

**Numbers in parentheses show number of adults maturing within one week of the indicated date.

Table 2. Summary of outdoor rearing attempts in 30 cages at two partially shaded sites near Gainesville, Florida

Parent group[a]	No. of adult females[b]	Date captured[c]	Dates of first and last hatch[d]	Total hatch[e]	Date of adult molt[f]	Total No. of adults[g]	Offspring group[h]
Summer	16	22-30 July 1971	1 Sept. 1971 6 Sept. 1971	121	1 Nov.-30 Dec.	20	Winter
Summer	8	3-21 July 1971	30 Aug. 1972 11 Sept. 1972	28	31 Dec.	1*	Winter
Winter	19	8-27 Sept. 1971	---	--	---	--	---
Winter	2	20 Feb. 1972	30 May 1972 28 June 1972	22	6 Aug. 1973	1	Summer
Winter	4	21 April 1972	7 June 1972 22 June 1972	115	1 Sept 1973	4	Winter

*Died during adult molt.

[a] Determined by collection data.

[b] One to three females per cage with equal number of males.

[c] Caged no later than one week after capture.

[d,f] Dates are accurate to ±3 days.

[h] Determined by comparing life stages of caged specimens with wild specimens on the same date.

Table 3. Maturation dates of field-collected, outdoor-reared nymphs, Gainesville, Florida, 1972

Nymphs collected			Adults reared		
Dates	Number	Approximate instar	Number	Dates	Generation (W or S)**
15 May	3	2	2	25 June	S
15 May*	6	1	1	2 July	S
20 May	5	1	2	16 July	S
22 May	5	2 + 3	1	16 July	S
			2	25 July	S
27 May	7	1	1	27 Aug.	W
				16 July	S
30 May	6	3	2	25 June	S
30 May	2	4	2	2 July	S
2 June	8	1 + 2	2	16 July	S
			1	13 Aug.	W
2 June	8	3 + 4	1	25 June	S
			1	9 July	S
			1	20 Aug.	W
2 June	4	5 + 6	3	25 June	S
7 June	4	1	1	30 July	S
			1	13 Aug.	W
7 June	3	3	2	2 July	S
			1	9 July	S
14 June	5	2	1	23 July	S
			2	30 July	S
14 June	5	4	1	2 July	S
			1	9 July	S
14 June	4	5 + 6	3	25 June	S
			1	2 July	S
22 June	6	3	2	16 July	S

Table 3--(continued)

Nymphs collected			Adults reared		
Dates	Number	Approximate instar	Number	Dates	Generation (W or S)**
22 June	7	1	1 1	23 July 10 Sept.	S W
22 June	5	5 + 6	4	2 July 1972	S
28 June	5	1 + 2	1	10 Sept. 1972	S
28 June	5	3	1	20 Aug. 1972	W
7 June	0	-	-	---	-
14 July	0	-	-	---	-
24 July	0	-	-	---	-
8 July	6	4; 4 + 6	1 1	27 Aug. 1972 3 Sept. 1972	W W
17 July	4	5	3	27 Aug. 1972	W

*A different collecting site is indicated by each line for a given date.

**Determined by comparing the adult date with life stages in the field. Adult molts after 10 Aug. were considered too late to tan and sing with the summer group.

Table 4. Color changes occurring during the ultimate and penultimate molts of green, male nymphs

Photoperiod	Adult color		Songs heard	Fat conspicuous*
	Green	Brown		
A-Early summer				
Natural	5	0	5	0
15 hr.	3	2	3**	0
11 hr.	0	5	0	5
B-Late summer				
Natural	0	7†	0	7
15 hr.		2	3	0
11 hr.		7††	0	7

*Fat completely lining the abdominal cavity obscuring the viscera.

**Two green, one brown.

†One individual turned brown during penultimate molt.

††Two individuals turned brown during penultimate molt.

Table 5. Number and percentages of brown/green colored morphs of *N. triops* collected in Alachua Co. during 1969-72

	Males				Females			
	Green		Brown		Green		Brown	
	No.	%	No.	%	No.	%	No.	%
Summer*	73	78	21	22	37	93	4	7
Winter**	5	3	142	97	47	69	21	31

*1 July-12 Aug.

**Dec.-May.

Table 6. Color of field-collected summer- and winter-generation nymphs collected in Gainesville from 1969-1971

Group*	Instars**	No. brown	No. green
Summer	1-3	0	41
	4	0	14
	5	0	13
	6	2	18
Winter	1-3	0	63
	4	0	22
	5	1	29
	6	13	28

*All nymphs were reared outdoors to at least last instar to determine if they belonged to the winter or summer group.

**I never differentiated the early instar which may be more or less than three.

Table 7. Sizes of early summer gonads and accessory glands of individuals reared under long-day, short-day, and natural conditions

	Photoperiod		
	Natural	Long day	Short day*
Testes			
Dimeter (range in .01 mm.)	55-155	107-136	83-167
n	5	5	5
$\bar{X}$	109	122	131
SD	38	13	36
Male assessory glands			
Weight (range in mg.)	10-26	17-25	5-11
n	5	5	5
$\bar{X}$	18	22	8
SD	7	3	3
Ovaries			
Weight (range in mg.)	198-350	143-416	12-18
n	6	5	5
$\bar{X}$	279	274	15
SD	56	102	3

*Fat conspicuous in all individuals in this column.

**Diameter = $\frac{\text{maximum diameter + minimum diameter}}{2}$.

Table 8. Initial wingstroke rate and final wingstroke rate of eight individuals recorded over a span of at least six weeks

First song	Last song	Difference
96.0	93.0	3.5
97.0	92.0	5.0
102.0	94.0	8.0
103.0	90.0	13.0
104.0	94.0	8.0
104.0	99.0	5.0
101.0	96.0	5.0
100.0	90.0	10.0
$\bar{X}$ = 100.88	$\bar{X}$ = 93.50	$\bar{X}$ = 7.19
SD = 3.04	SD = 3.02	SD = 3.18

*$t = 6.5$, $p \leq .001$.

Table 9. Wingstroke rates of short-day (diapausing) and long-day (nondiapausing) individuals reared from a single collection of nymphs*

Diapausing group	Nondiapausing group
104.0	105.0
98.0	116.0
95.0	110.0
96.5	110.0
	112.0
	106.0
$\bar{X} = 98.38$	$\bar{X} = 109.30$
SD = 3.95	SD = 4.02

*$t = 4.42$, $p \leq .005$.

Table 10. Initial wingstroke rates of three groups of katydids that underwent different durations of diapause*

Group	A	B	C
Date of collection	19-28 Sept. 1972	19-28 Sept. 1972	19-28 Sept. 1972
Date in low-noise room	1 Oct. 1972	15 Nov. 1972	1 Jan. 1973
First singing date	25 Oct. 1972	2 Dec. 1972	4 Jan. 1973
Wingstroke rate of initial song	96.5	104.0	101.0
	104.0	92.5	103.0
	97.0	98.0	101.5
	102.0	99.5	103.0
$\bar{X}$	99.88	98.50	102.13
SD	3.71	4.74	1.03

*T test	t value	Significant difference	p value
A-B	.445	No	$\leq .5$
B-C	1.50	No	$\leq .1$
A-C	1.18	No	$\leq .2$

Table 11. Initial songs of group C and the songs of group A at the same time*

Group A	Group C
98.0	101.0
93.5	103.0
98.5	101.5
103.0	103.0
$\bar{X}$ = 98.25	$\bar{X}$ = 102.13
SD = 3.88	SD = 1.03

*t = 1.95, p = 0.1.

Table 12. Attraction of female *N. triops* at 25 ± 1°C to recorded *N. triops* and *N. retusus* songs at 80 db

Test session	Wingstroke rate of tape	Continuous (C) or discontinuous (D) song	No. of ♀ tested**	No. of + responses†
Summer group females				
1	109	C	5	5
2	91	D	5	0
3	80	C	5	0
4	118	D	5	4
5	100	C	5	4
6	118	D	5	4
7	85	C	5	0
8	91	C	5	0
9	87	C	5	0
10	109	D	5	5
11*	114	C	5	4
12*	109	C	4	4
13*	113	C	9	7
14	109	D	7	4
15	128	D	7	0
16	126	D	7	0
17	123	D	7	0
Winter group females				
18	109	D	10	3
19	91	C	10	0
20	80	C	10	3
21	118	D	10	2
22	100	D	10	1
23	85	C	10	1
24	91	C	9	2
25	87	C	9	2
26	90	C	8	2
27	120	D	8	1
28	123	D	8	2
29	128	D	8	2

**N. retusus* tapes used (all other tapes were of *N. triops*).

**Summer-generation females were tested only if they first responded to a continuous song of *N. triops* of 109 wingstrokes/sec. by phonotaxes, shaking, or walking.

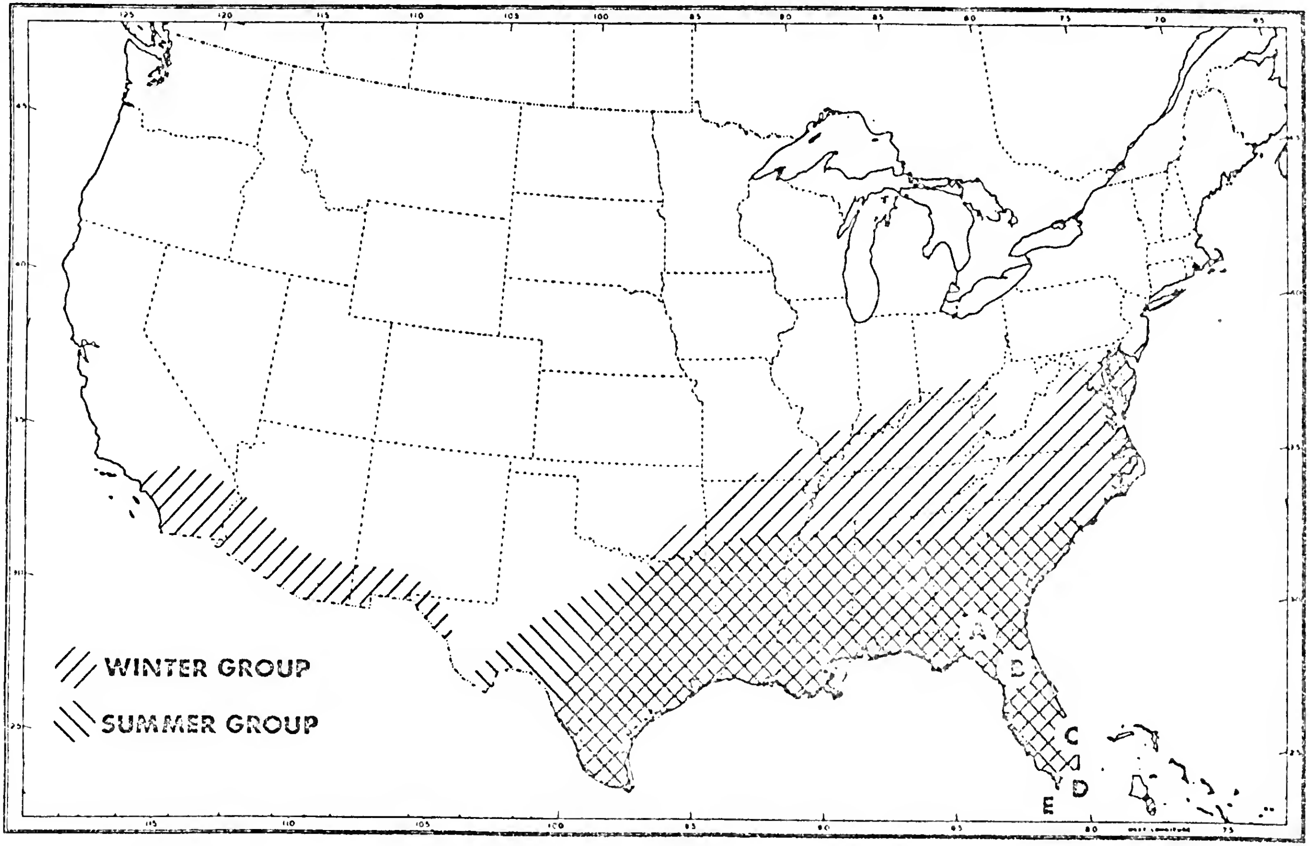
†+ = went to speaker end of cage and remained for at least 20 sec. during the 120-sec. test.

Table 13. Abbreviation of Table 12, showing the percentage success of attraction to various wingstroke rates and the individual positive responses (same test as described in Table 13)

Wingstroke rate	Continuous (C) discontinuous (D)	Number trials	% success	Individual positive responses*
Summer group females				
80-89	C	15	0	
	D	0	-	
90-99	C	5	0	
	D	5	0	
100-109	C	14	71	b(2),f(2),g(3),i,k,n
	D	10	90	b(2),f,g,(2),i,k,n,p
110-119	C	14	71	b(2),f,g(2),i,j,k,n,p
	D	10	80	b,f(2),g(2),k,n(2)
120-129	C	0	-	
	D	21	0	
Winter group females				
80-89	C	24	21	a,d,e,f(2)
	D	0	-	
90-99	C	19	11	d,f
	D	8	25	a,f
100-109	C	0	-	
	D	20	20	a(2),h,i
110-119	C	0	-	
	D	10	20	f,g
120-129	C	0	-	
	D	24	21	d,f(3),i

*Individuals are designated by the letters a-p. Responses per individual are in parentheses.

Fig. 1. Range of N. Triops in the United States, based on personal observations and literature records (Walker 1973: personal communication). A-E are locations of weekly or monthly surveys. A - Quitman (Brooks Co.), Ga.; B - Gainesville (Alachua Co.), Fla.; C - Jupiter (Palm Beach Co.), Fla.; D - Key Largo Key (Monroe Co.), Fla.; E - Big Pine Key (Monroe Co.), Fla.


WINTER GROUP
SUMMER GROUP
A
B
C
D
E

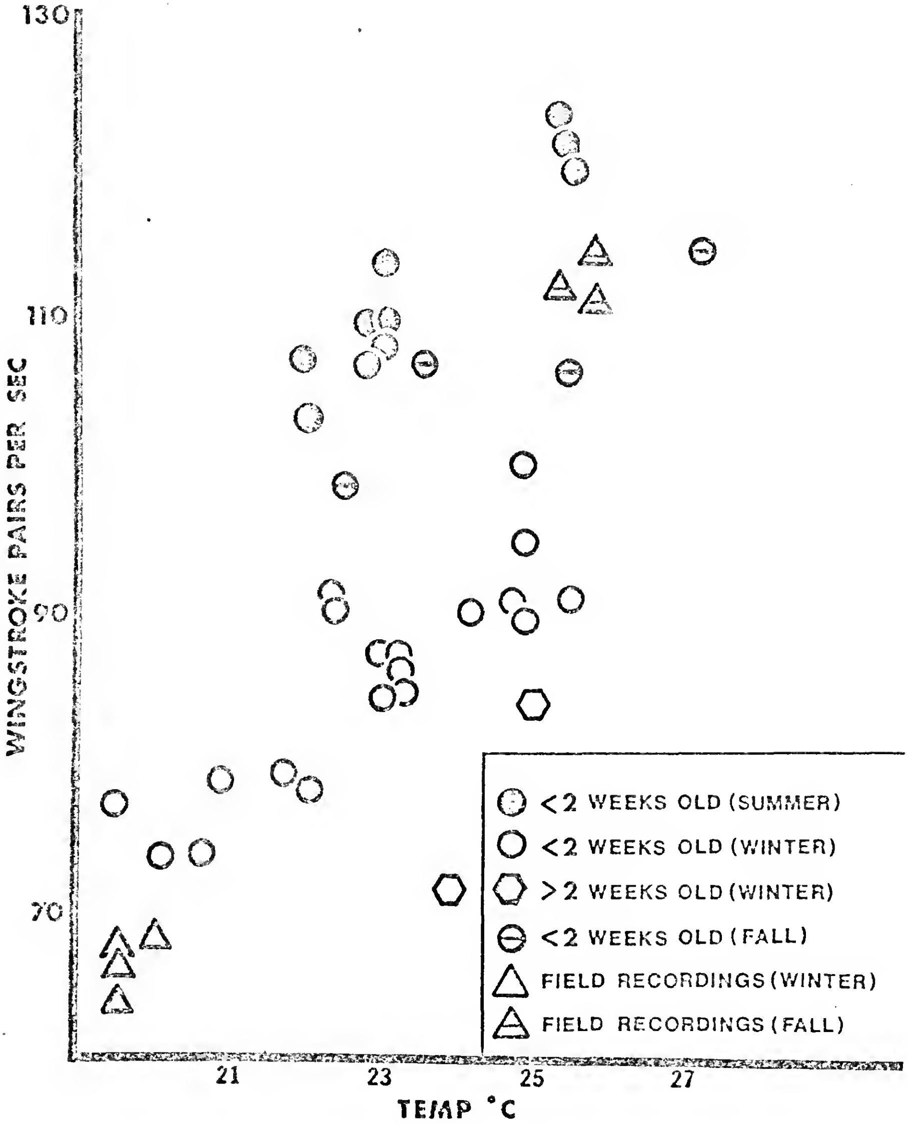


Fig. 2. Wingstroke rates of Central Florida (Palm Beach Co.) adults.

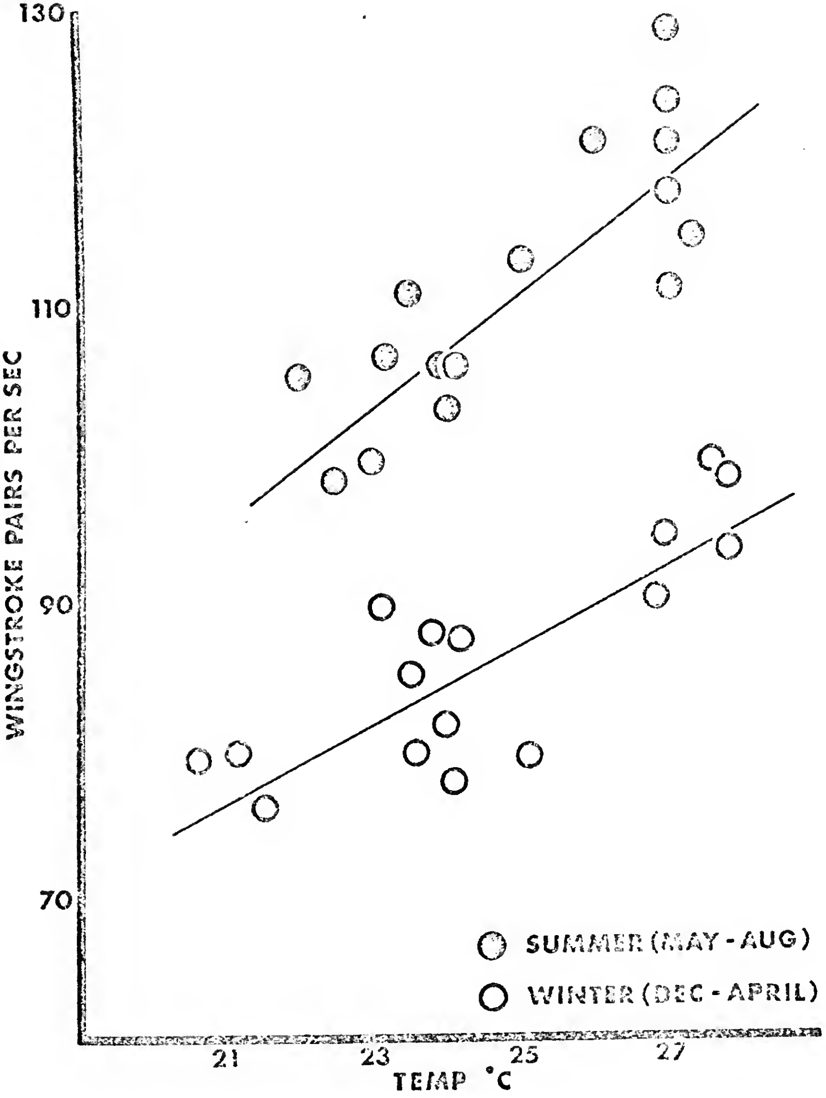


Fig. 3. Wingstroke rates of North Florida (Alachua Co.) field-collected adults. Regression line formulas: $\hat{y} = bx + a$; $\hat{y}$ (summer) = $3.98(x) + 12.13$; $\hat{y}$ (winter) = $2.61(x) + 22.19$.

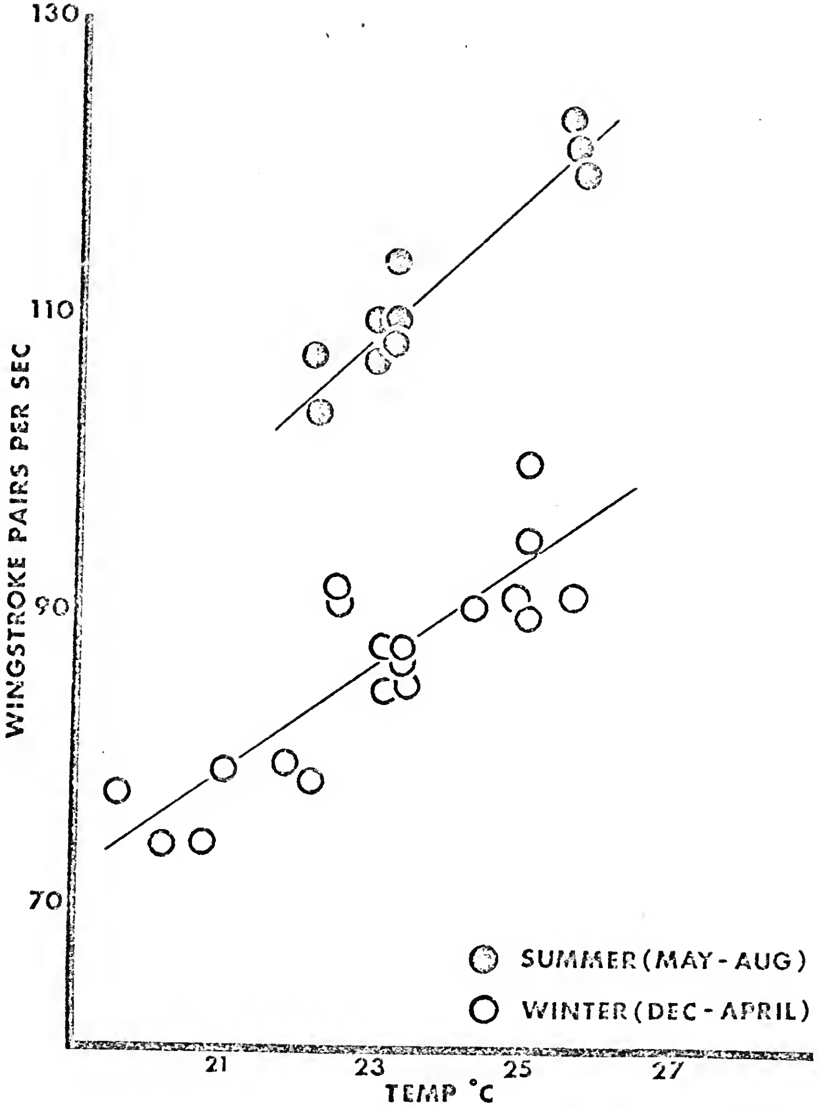


Fig. 4. Wingstroke rates of Central Florida (Palm Beach Co.) field-collected adults. $\hat{y} = bx + a$; $\hat{y}s = 4.67(x) + 1.98$; $\hat{y}w = 3.49(x) + 5.84$.

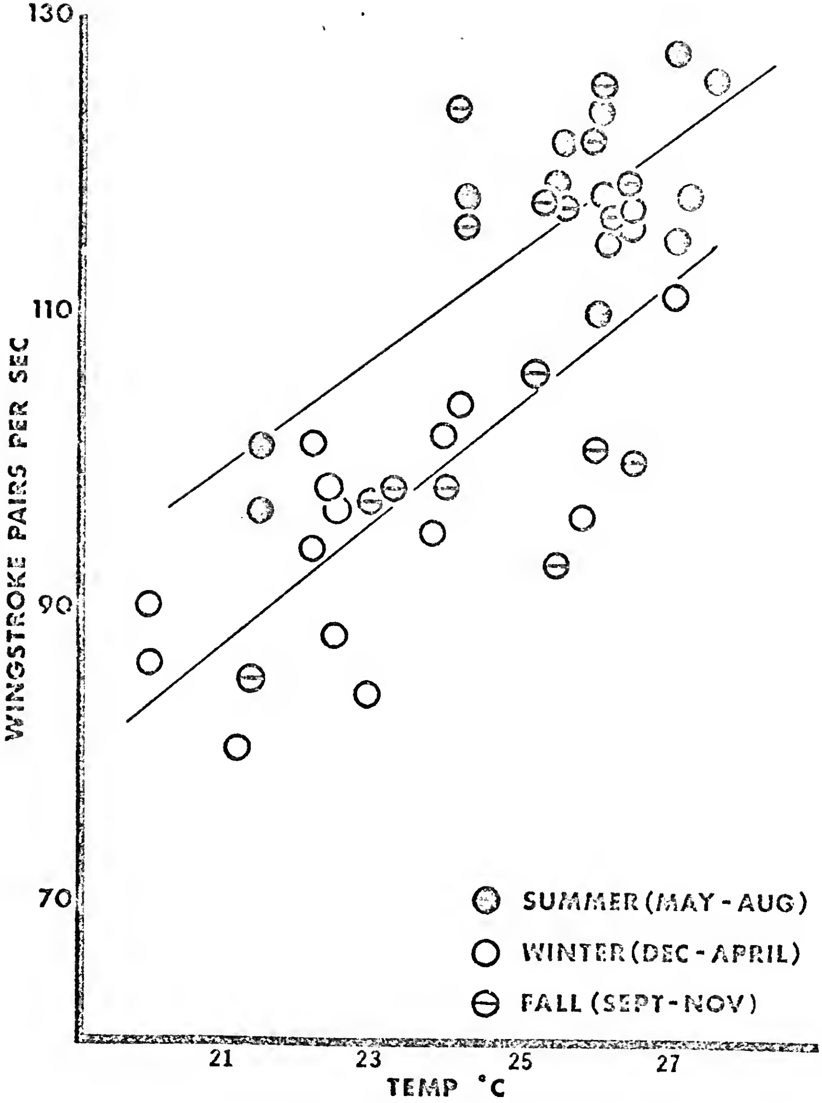


Fig. 5. Wingstroke rates of upper Florida Keys (Monroe Co.) field-collected adults. $\hat{y} = bx + a$; $\hat{y}s = 3.86(x) + 18.25$; $\hat{y}w = 4.40(x) - 4.26$.

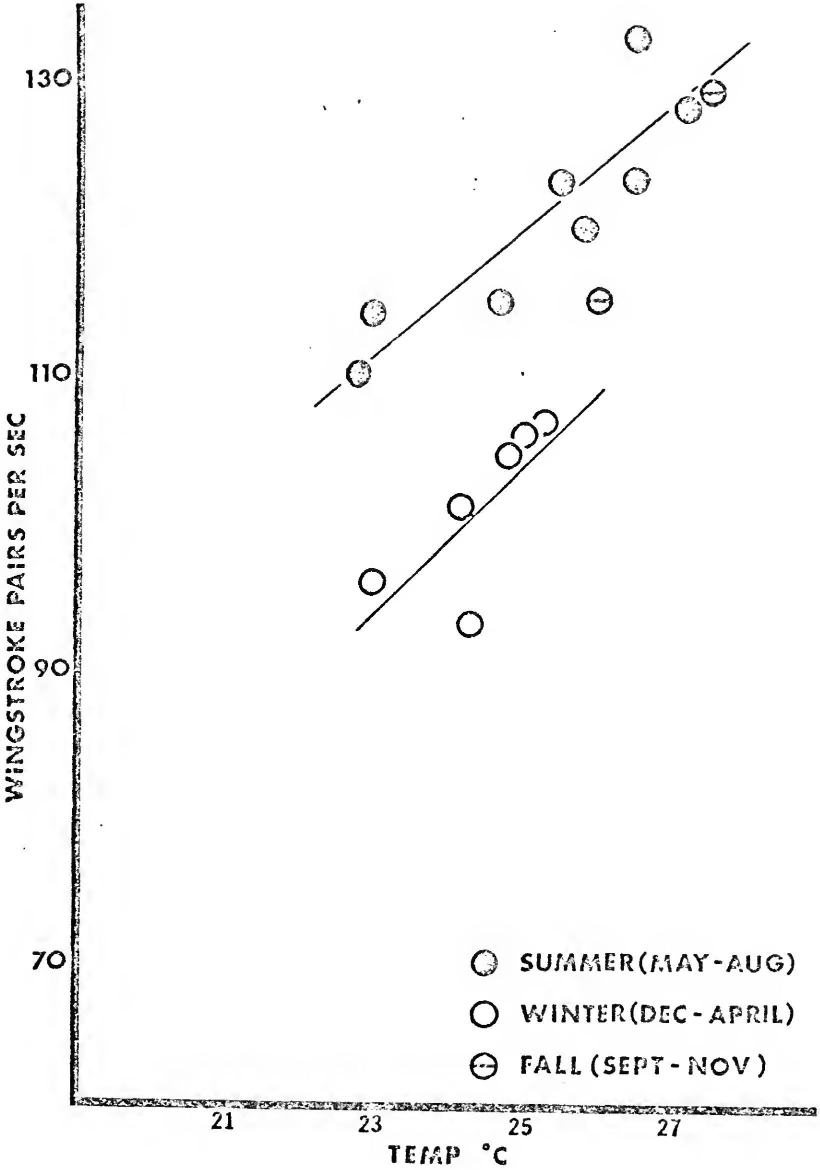


Fig. 6. Wingstroke rates of lower Florida Keys (Monroe Co.) field-collected adults. $\hat{y} = bx + a$; $\hat{y}x = 4.10(x) + 17.20$; $\hat{y}w = 5.19\ (x) - 25.40$.

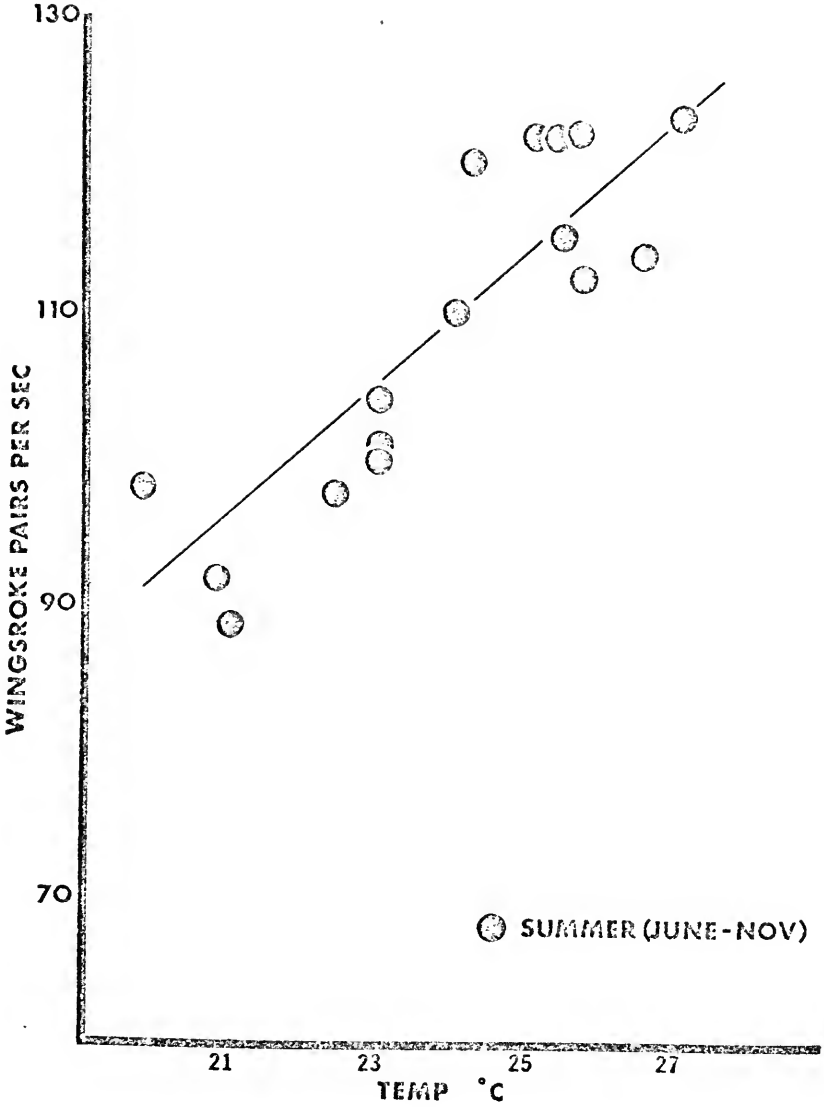


Fig. 7. Wingstroke rates of Jamaican field-collected adults (Walker 1973: personal communication). $\hat{y} = bx + a$; $\hat{y}s = 4.76(19) - 4.80$.

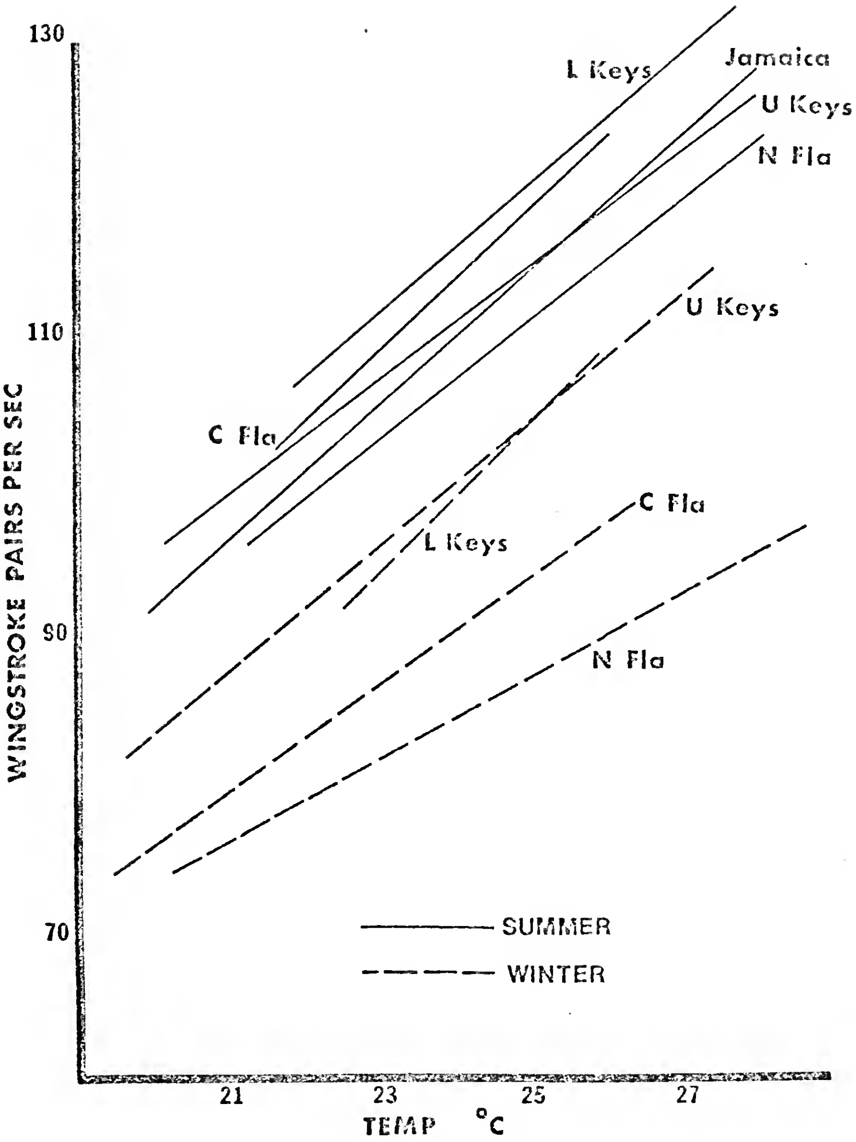


Fig. 8. Comparative linear regression lines of wingstroke rates of field-collected adults from North Florida to Jamaica.

Fig. 9. Singing densities of three Gainesville, Fla., Weekly survey areas. Asterisk represents surveys that were too cold for maximum singing (<20°C).

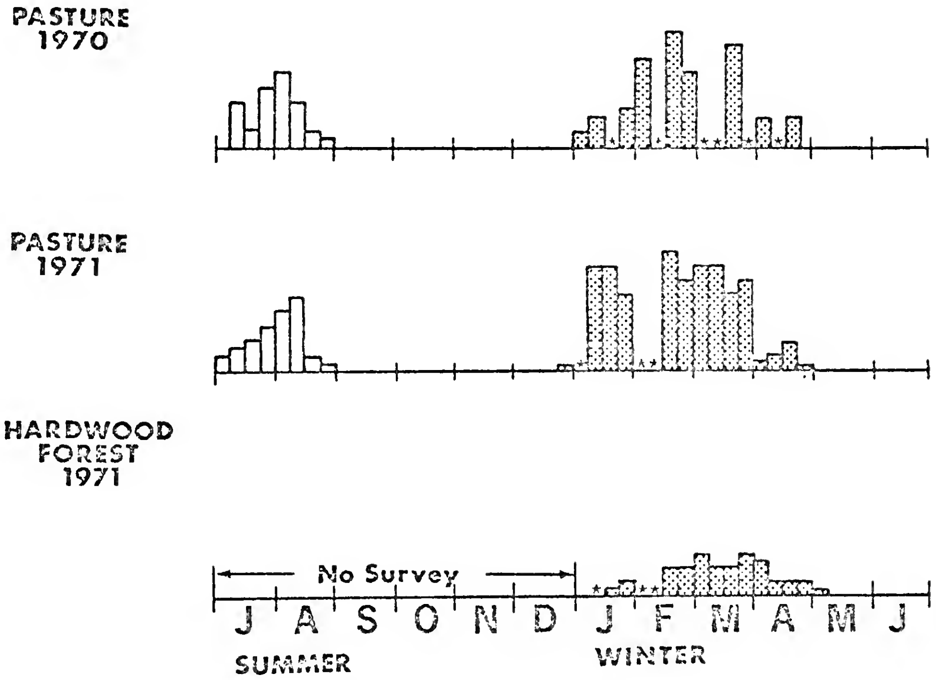
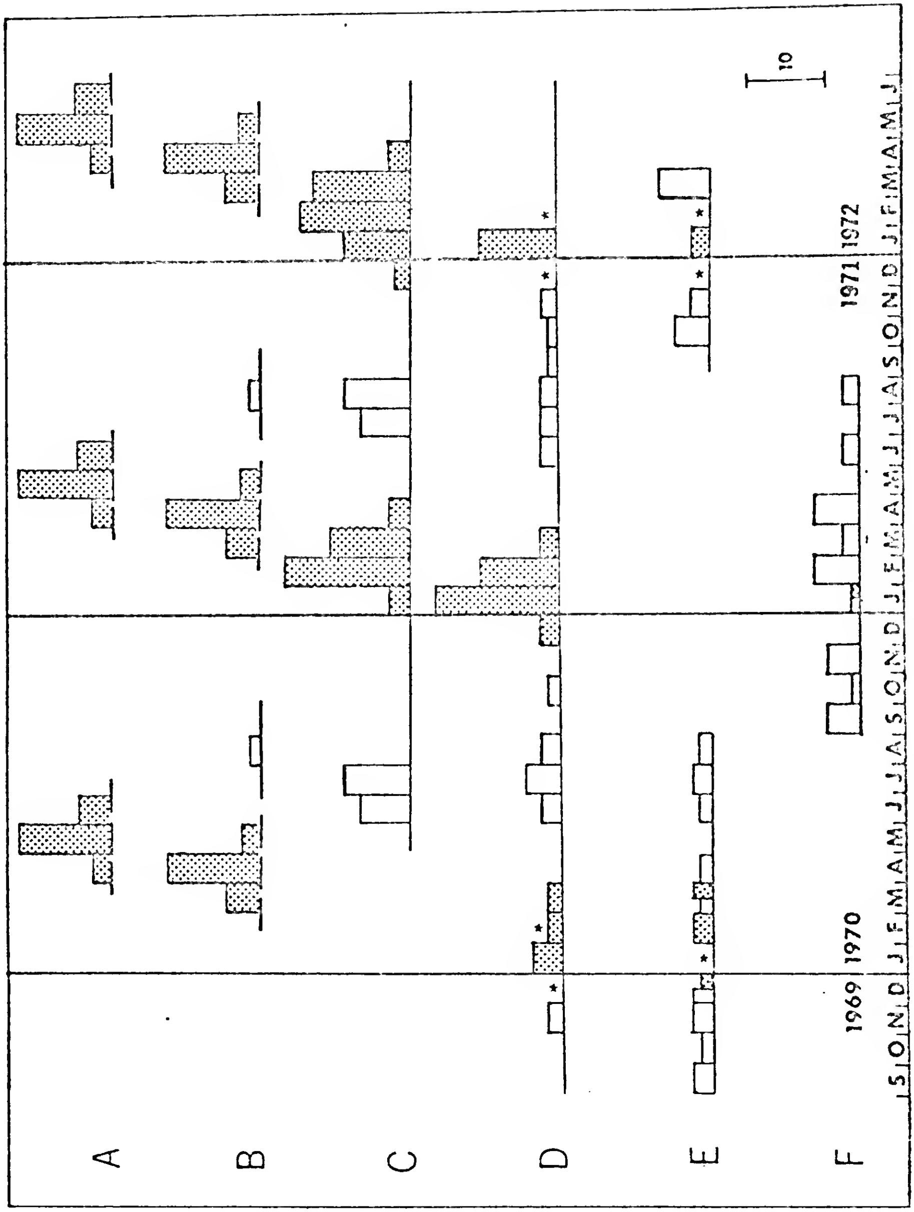

PASTURE 1970
PASTURE 1971
HARDWOOD FOREST 1971
No Survey
J A S O N D J F M A M J
SUMMER
WINTER

Fig. 10. Singing densities from monthly surveys. A - SE Ohio; B - South Carolina; C - Gainesville (Alachua Co.), Fla.; D - Jupiter (Palm Beach Co.), Fla.; E - Key Largo Key (Monroe Co.), Fla.; F - Big Pine Key (Monroe Co.), Fla; * - too cold for maximum singing; shaded area - winter group based on song phrasing; unshaded area - summer group based on song phrasing; base lines indicate actual surveys; graphs with broken base lines [illegible] based on literature records and weather data.


A
B
C
D
E
F
S O N D J F M A M J J A S O N D J F M A M J J A S O N D J F M A M J
1969
1970
1971
1972
10

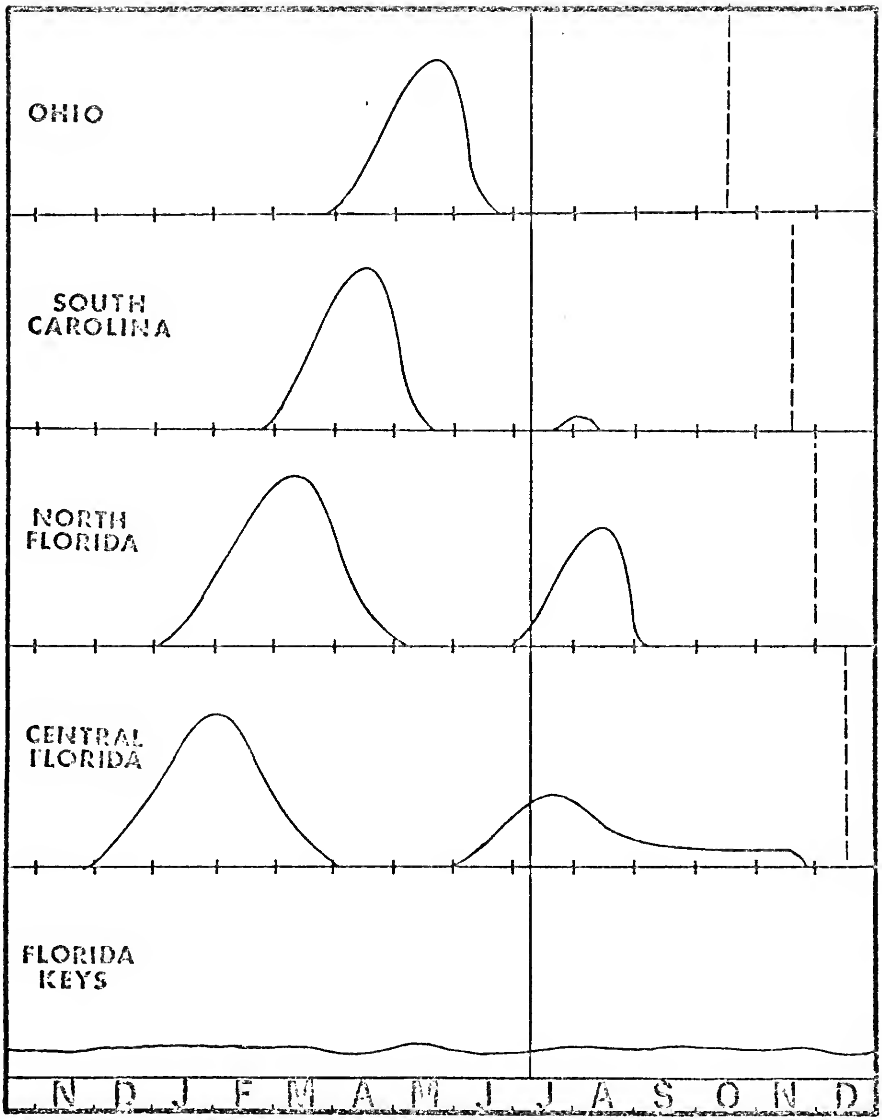


Fig. 11. Comparative monthly singing data from eastern United States. Solid vertical line represents last data that day length will permit molting to nondiapausing adults. Broken vertical lines represent first frost.

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Mr. Whitesell is presently employed as a research associate working on the Lovebug Project at the University of Florida.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Thomas J Walker

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

Thomas C. Emmel

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Associate Professor of
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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the College of Agriculture and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

June 1974

Dean, College of Agriculture

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