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# OCCASIONAL PAPERS

**of the  
MUSEUM OF NATURAL HISTORY  
The University of Kansas  
Lawrence, Kansas**

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NUMBER 160, PAGES 1-33

24 SEPTEMBER 1993

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## **MICROHABITAT SEGREGATION AND SPATIAL RELATIONSHIPS AMONG FOUR SPECIES OF MOLE SALAMANDERS (GENUS *AMBYSTOMA*)**

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**ABSTRACT** Four environmental parameters were examined to determine if microhabitat segregation occurred within age groups of, or between, four sympatric species of *Ambystoma* (*A. texanum*, *A. maculatum*, *A. opacum*, *A. talpoideum*) in southern Illinois in 1989. Salamanders occurred under cover objects that were larger and more moist than other randomly chosen cover objects. Adults were under significantly larger cover objects than juveniles. Substrate moisture below cover objects was significantly different between species, but not between age groups. *Ambystoma texanum* and *A. talpoideum* were found in moister situations than *A. maculatum* and *A. opacum*. *Ambystoma maculatum* occurred under large cover objects and had the highest recapture rate. *Ambystoma opacum* also occurred under large cover objects. Few adult *A. talpoideum* were captured, but when found, they were under moist cover objects typically occupied by another species. Adults were most abundant in early spring; juveniles emerged at times beginning in midsummer. *Ambystoma texanum* cohabits cover objects more often than predicted, but males seem to avoid other males; *A. maculatum* and *A. opacum* were almost always the sole residents under cover objects.

**Key words:** Caudata, *Ambystoma*, Microhabitat partitioning, Sympatry, Spatial relationships.

Eleven species of mole salamanders (genus *Ambystoma*) inhabit eastern North America and several species often are sympatric in some parts of their ranges (Conant and Collins, 1991). Many *Ambystoma* are morphologically similar except for color pattern; artificial hybridization experiments (Nelson and Humphrey, 1972; Brandon, 1977) demonstrate remarkable genetic compatibility that attests to their similarity. Although almost all *Ambystoma* are reproductively compatible, phylogenetic similarity cannot be assumed, because gametic incompatibility is a poor predictor of relatedness (Frost and Hillis, 1990).

For most salamanders, there is little field evidence for any interaction, other than competition, among adults; the few exceptions are plethodontids. Among ambystomatids, most interactions have been observed between larval stages and little evidence has been found for either competition or predation among the adults. In contrast, the adults of some salamanders (e.g., Plethodontidae: *Desmognathus*), which also have a larval stage, are known to be both competitors and interspecific predators (Krzysik, 1979; Hairston, 1986). Although density-dependent population regulation has been documented in larval *Ambystoma* (Petranka, 1989; Van Buskirk and Smith, 1991), no clear regulating factor is apparent among the adults.

Many aspects of the terrestrial stage of ambystomatid salamanders are poorly understood. Features of their life history make them particularly difficult to study outside of their breeding migrations. These salamanders spend most of their lives in inaccessible retreats underground and only rarely move about on the forest floor, always at night just after, or during, periods of rainfall. The few direct observations available seem to indicate that these opportunistic, generalist predators employ a sit-and-wait strategy and occupy limited areas consisting of burrow systems (Gordon, 1968; Semlitsch, 1981). However, they also can be found above ground under logs and other objects.

The breeding migrations and reproductive behavior of *Ambystoma* are well documented. Several studies have concentrated on mechanisms regulating segregation of breeding pools (Williams, 1971; Keen, 1975; Wilson, 1976; Thompson and Gates, 1982). Differences in time of arrival, separation of breeding sites, and varying rates of larval development are the main mechanisms that have been proposed for maintaining or permitting sympatry among species.

Many ecological observations indicate that closely related sympatric species partition habitat and other resources to reduce competition (Lack, 1971; Sheppard, 1971; Werner, 1977). Schoener (1974a) summarized results of 81 observational studies that bear on resource partitioning in groups of three or more species. He found that habitat dimensions often were more important than food-type dimensions, which, in turn, often were more important than temporal dimensions in separating species. Means

(1975) provided an excellent example of competitive exclusion between two species of salamanders (*Desmognathus*). He found that the realized niche of one species was smaller than its fundamental niche where the two species were geographically sympatric.

Several studies have revealed habitat selection in *Ambystoma*. Observations are often quite general—e.g., for *A. opacum*: “This species is found in drier ground than is congenial to most salamanders” (Cope, 1889:55). *Ambystoma maculatum* occurred in areas significantly moister than areas without amphibians (Wyman, 1988). Tantalum<sup>182</sup> wire was implanted in the tails of individual *Ambystoma* leaving a breeding pool and different species preferred different shelters (Williams, 1973). *Ambystoma jeffersonianum* most often was found in small mammal burrows, *A. texanum* in crawfish burrows, *A. maculatum* in small mammal and blind burrows, and *A. opacum* in leaf litter and small mammal burrows.

Aggression and territorialism have been documented in several salamander species. Territorial interactions between the northern two-lined salamander (*Eurycea bislineata*) and the four-toed salamander (*Hemidactylium scutatum*) in an aquarium were observed by Grant (1955). Laboratory experiments also have documented aggressive behavior and territoriality in the green salamander *Aneides aeneus* (Cupp, 1980). Territoriality has been most clearly demonstrated in the redback salamander (*Plethodon cinereus*) by Jaeger et al. (1982). Individual *Plethodon* have discrete home ranges, mark their territories through chemical signals on the substrate, and show aggressive behavior toward intruders on their territories (Madison and Shoop, 1970; Jaeger and Gergits, 1979; Keen and Reed, 1985; Gergits and Jaeger, 1990).

Studies of aggressive behavior in ambystomatid salamanders have lagged behind those of other families. *Ambystoma tigrinum* was observed to show aggression in courtship and spermatophore deposition under natural conditions (Arnold, 1976). *Ambystoma gracile* demonstrated aggressive behavior when feeding in a captive situation (Licht, 1973). Martin et al. (1986) hypothesized that *A. texanum* establish feeding territories when they congregate near breeding sites; laboratory experiments (similar to those of Jaeger, 1984, and Jaeger and Gergits, 1979, that showed territoriality in *Plethodon cinereus*) did not provide evidence of pheromone-marking of territories by *A. texanum* or any aggression toward intruders. Martin et al. (1986) suggested that because *A. texanum* did not saturate their habitat, defense of territories would not be selectively advantageous. The authors suggested that *A. opacum* was more likely to be territorial because of its more extended above-ground season.

A few studies have demonstrated that *Ambystoma* probably occupy home ranges when not breeding (Williams, 1973; Semlitsch, 1981). *Ambystoma maculatum* were consistently found within a 300 cm<sup>2</sup> area in

rodent-burrow systems (Douglas, 1981). Jessup (1981) reported that when *A. laterale* were placed under a log occupied by another individual, no antagonistic behavior was observed, but the introduced salamander usually left the area within a few days.

Only recently has any evidence for territorial aggression been observed in mole salamanders. In the laboratory, *Ambystoma maculatum* demonstrated significantly lower movement frequency when kept with a conspecific (Ducey and Ritsema, 1988). This same study revealed that this species shared the refugium with the conspecific only 8.8% of the time, which was significantly less than if the animals were moving independently. Biting and other agonistic behavior has been observed in the laboratory during intraspecific encounters in several species of *Ambystoma* including *A. opacum* and *A. talpoideum* (Ducey, 1989).

Interference competition occurs between juvenile *Ambystoma maculatum* and *A. talpoideum* in the laboratory (Walls, 1990). Agonistic behavior was observed between pairs of recently metamorphosed individuals by staging encounters between "residents" and "intruders." The interactions were asymmetrical with *A. maculatum* being more aggressive than *A. talpoideum*. This demonstrated an ontogenetic shift in competitive abilities, because larval *A. talpoideum* are competitively superior (Walls and Jaeger, 1987). Experimental evidence that *Ambystoma* (including *A. maculatum*, *A. opacum* and *A. talpoideum*) increase aggression with decreasing food levels suggests the function of aggression in these species may be repulsion of conspecifics from individual feeding territories (Ducey and Heuer, 1991). Because these laboratory studies have documented aggression and territorial behavior, spacing of at least some species of *Ambystoma* in the field should be predicted.

Territorial behavior can be indirectly assessed by examination of spatial patterns of individuals. Dispersal patterns of two dusky salamanders (*Desmognathus fuscus*, *D. ochrophaeus*) were studied along a brook using boards as cover sites (Stewart and Bellis, 1970). Salamanders were distributed randomly even after many new individuals were introduced into the area. The distribution of slimy salamanders (*Plethodon glutinosus*) was influenced by interactions among individuals and did not simply reflect the distribution of suitable microhabitats (Wells, 1980). Spatial distribution patterns were utilized to ascertain that *P. cinereus* is territorial with greater clumping found in autumn, the courting season (Mathis, 1989). *Plethodon cinereus* exhibited a decrease in co-occurrence under cover objects from spring to summer, probably owing to intraspecific interference competition (Jaeger, 1979). The author hypothesized that resources became more limiting as the summer progressed and, consequently, competition increased.

My study examines the distribution of *Ambystoma* in the field in an attempt to reveal interactions within or between four sympatric species (*A.*



*texasum*, *A. maculatum*, *A. opacum*, and *A. talpoideum*) inhabiting an island in an oxbow lake in southern Illinois. By examining the number of salamanders under a cover object, I could ascertain whether individuals were distributed in a clumped, uniform, or random manner. Individually marking the salamanders provided additional evidence about movements and site tenacity. I also measured several specific microhabitat parameters to determine if habitat partitioning occurs among the sympatric species, or between age classes within a species. Microhabitat differences along with spatial and temporal information may help explain distributions of *Ambystoma* on the forest floor and reveal mechanisms that allow the four species to coexist.

## MATERIALS AND METHODS

### DESCRIPTION OF STUDY AREA

The study area was a bottomland forest on an island in Horseshoe Lake, located on the alluvial flood plain of the Mississippi River (Sections 9, 10, 15, 16, T16S, R2W, Alexander Co., Illinois). Study plots were chosen from throughout the forested southern third of the island. The island is a nature preserve with little recent human disturbance in the forested portion (Fig. 1). The island is about 5 km E of the present Mississippi River channel and the forested portion covers approximately 63 ha. Swampy conditions predominate early in the year with a gradual drying of inundated areas in the summer. The gently rolling topography has a maximum relief of 3 m. The surface soil is composed of alluvial materials of varying textures on top of thick deposits of glacial outwash clays (Robertson et al., 1978). Half of the forest is recovering from disturbance in the late 1800s or early 1900s and the other half is relatively undisturbed (Robertson et al., 1978).

The woody flora is quite diverse, with dominant tree species being sweet gum (*Liquidambar styraciflua*), swamp red maple (*Acer rubrum*), American elm (*Ulmus americana*), bitternut hickory (*Carya cordiformis*), red ash (*Fraxinus pennsylvanica*), sugar maple (*Acer saccharum*), tupelo gum (*Nyssa aquatica*), northern red oak (*Quercus rubra*), and sassafras (*Sassafras albidum*). Red buckeye (*Aesculus discolor*) and pawpaw (*Asimina triloba*) are the dominant woody species in the shrub-sapling stratum.

The herpetofauna is remarkably diverse in this area: Horseshoe Lake Island was mentioned in Smith's (1961) accounts of all four species of *Ambystoma*. Other reptiles and amphibians encountered under cover objects on the island included the northern slimy salamander (*Plethodon glutinosus*), eastern spadefoot (*Scaphiopus holbrookii*), Fowler's toad (*Bufo woodhousii fowleri*), American toad (*Bufo americanus*), western chorus frog (*Pseudacris triseriata*), spring peeper (*Pseudacris crucifer*), northern

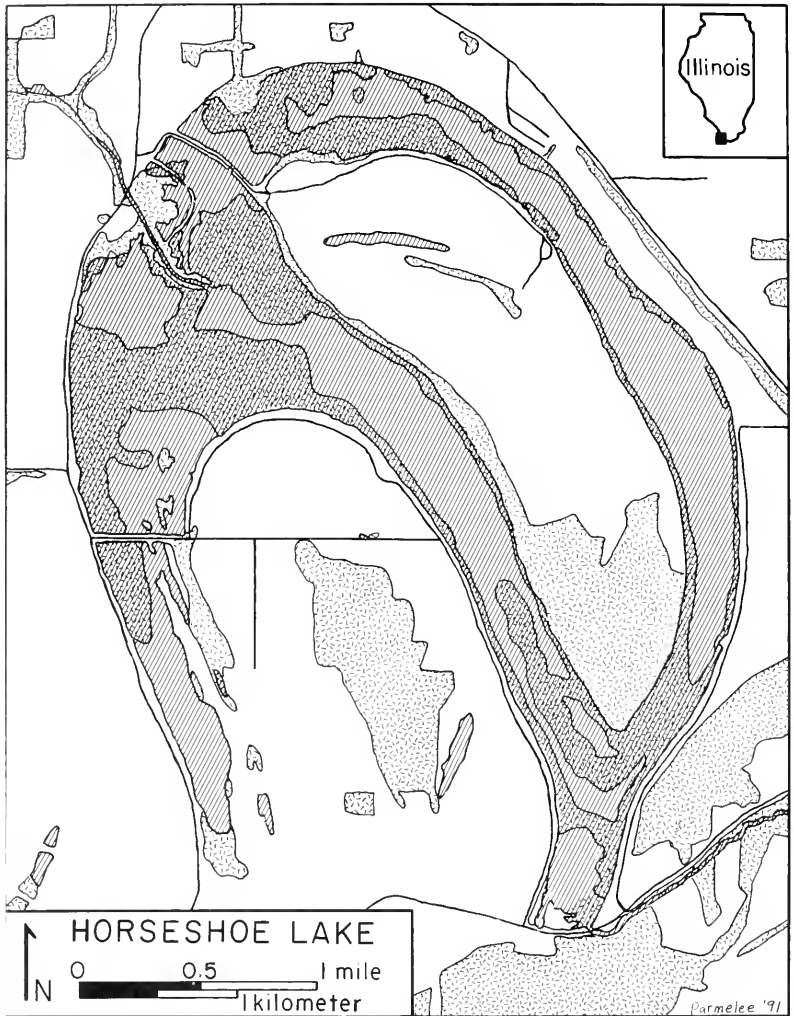


Fig. 1. Map of Horseshoe Lake Island. Water is indicated by hatching and forest by dashed lines.

cricket frog (*Acris crepitans*), southern leopard frog (*Rana sphenoccephala*), green frog (*Rana clamitans*), five-lined skink (*Eumeces fasciatus*), broadhead skink (*Eumeces laticeps*), smooth earth snake (*Virginia valerieae*), brown snake (*Storeria dekayi*), common garter snake (*Thamnophis sirtalis*), rat snake (*Elaphe obsoleta*), and worm snake (*Carphophis amoenus*).

Potential mammalian predators found under logs on the island were

shorttail shrews (*Blarina brevicauda*), eastern moles (*Scalopus aquaticus*), and white-footed mice (*Peromyscus* spp.).

### FIELD PROCEDURES

The site was visited 20 times between 25 March and 28 October 1989. Cover objects were turned over carefully in search of ambystomatids and then replaced. All cover objects were wood (either logs, branches, or pieces of bark); no stones larger than 2 cm<sup>2</sup> were found on the forest floor. When a salamander was found, a 10 × 10-m quadrat was established at the site with wooden stakes at the four corners; each quadrat was numbered. Of the 49 quadrats so established, each had 9–57 ( $\bar{x}$  = 19.3) cover objects. During each visit, every piece of available cover in the quadrat excluding leaves was turned. Each piece of cover was carefully replaced, and disturbance was kept to a minimum.

The species, sex, and distance from snout to posterior angle of vent (SVL) were recorded for each salamander found. Adults and juveniles were placed in separate categories; recently metamorphosed juveniles were readily distinguishable from adults by size and coloration. These individuals will be referred to as juveniles in this paper, although it is not known if all adults captured were sexually mature. The exact location of each salamander was plotted on a data sheet. The sex of adults was determined by examination of the cloacal region and other external characteristics (Bishop, 1941; Pfingsten and Downs, 1989). Each individual was marked by excising a unique combination of toes; injury was minimized by clipping the fewest number of toes possible (never more than 2 per foot). Some regeneration was observed, but the regenerated digit always was smaller and paler in color; regenerating digits were reclipped.

The length and width of the cover object that was in contact with the substrate was measured. The temperature of the substrate surface beneath the salamander was measured with a Curtin mercury thermometer. All salamanders were placed adjacent to their original cover objects as soon as possible. Substrate samples were collected from the area directly beneath each salamander and sealed in 8.0-ml glass vials. These vials were weighed in the laboratory to the nearest 0.001 g within 24 h on a Fisher XT digital balance. Vials with their caps removed were placed in a 105°C oven for 24 h. Preliminary tests with various soil textures revealed maximal loss of mass after 24 h. Immediately subsequent to removal from the oven, capped vials were weighed and the dry substrate samples transferred to individual envelopes. Substrate samples were qualitatively assigned to one of four categories based on particle size—(1) primarily fine soil (claylike); (2) coarse soil (more organic material than fine soil); (3) leaves; or (4) wood. Because many samples were a mixture of these substrate types, I scored them according to the most abundant component of the sample. The vials

then were cleaned, air dried, and weighed again. After the weight of the clean vial and cap was subtracted from both measurements, a total water content was computed.

Starting on 22 April, whenever a quadrat contained a salamander, two additional cover objects were examined. These cover objects served as controls to compare cover objects harboring salamanders with those that did not. Controls were chosen by walking 10–20 paces (randomly determined) in a random direction (chosen by throwing a stick in the air) and then picking the two nearest cover objects. A salamander was never found under these additional cover objects. Area measurements, as well as temperature and soil samples then were recorded. Temperature and soil samples were taken from the deepest part of the depression beneath the cover object, which usually was in the middle.

To determine if apparently suitable, but unoccupied, cover objects existed, several unoccupied cover objects were examined. Between 13 May and 29 July, 97 unoccupied cover objects were chosen and similarly examined. On each of these sampling dates about 10 cover objects that looked suitable as salamander retreats were chosen from throughout the study area. Large size and an apparently moist substrate were the main factors in my choices. All cover objects chosen were different and never occupied by a salamander.

#### STATISTICAL ANALYSIS

As variances of the raw data were not homogeneous, a transformation was made before the analysis was performed. The logarithm of area and the arcsine of moisture were used on all further tests. The statistical programs *mystat* (Systat, 1989), and SAS (SAS Institute, Inc., 1985) were utilized in all further analyses.

Analyses tested for differences in moisture and area between cover objects with salamanders and those without (the randomly chosen cover objects). Because the dependent variable (presence or absence of a salamander) is a binary value, one would expect a curvilinear response function. The expected response function is a logistic function and can be easily linearized. A maximum-likelihood ANOVA was performed, and estimates were computed.

A two-way ANOVA tested differences between the species and age classes in moisture and area (recaptures were excluded). The GT2 multiple-range-test (Sokal and Rohlf, 1981) was performed because sample sizes were unequal. Regression analysis also was utilized to determine if there was a relationship between SVL and area of cover object for each species and age class.

The number of salamanders cohabiting a cover object was compared to a Poisson distribution to indicate if the different species were distributed in

a uniform, random, or clumped manner. The total number of cover objects examined within the study quadrats was used to calculate the expected frequencies; although all cover objects are not equally suitable, the Poisson distribution was considered most appropriate to model apparently "rare and random events" such as the distribution of *Ambystoma* under cover objects. Student's *t*-tests were utilized to compare the areas and substrate moistures of cover objects harboring one salamander to those harboring two or more.

## RESULTS

### POPULATION CHARACTERISTICS AND TEMPORAL DIFFERENCES

Of the 319 *Ambystoma* captured, *A. texanum* (227 or 71.2% of all salamanders) was the most abundant (Table 1). Adult *A. maculatum* were significantly larger than the other species (ANOVA,  $F = 27.32$ ; 3, 158 df;  $P < 0.0001$ ), which did not differ significantly from one another in SVL. However, *A. opacum* and especially *A. talpoideum* are much stockier and have proportionally larger heads and mouths than *A. texanum*. Juvenile *A. talpoideum* were significantly larger than juvenile *A. texanum* (ANOVA,  $F = 21.58$ ; 3, 152 df;  $P < 0.0001$ ), but there were no other significant differences in SVL among juveniles. None of the sex ratios differed from a 1:1 ratio (*A. texanum*,  $\chi^2 = 1.22$ ; *A. maculatum*,  $\chi^2 = 0.11$ ; *A. opacum*,  $\chi^2 = 3.56$ ; *A. talpoideum*,  $\chi^2 = 2.93$ ; 1 df,  $P > 0.05$  for all).

Salamanders were found on all sampling dates (Fig. 2), but the number of new adults and juveniles of each species varied throughout the season (Figs. 3-4). Throughout the summer the abundance of adult *A. texanum* diminished dramatically; similar trends were observed in adult *A.*

Table 1. Abundances, SVL (range in parentheses), and sex ratios (male:female) of four species and two age classes of *Ambystoma*.

Species	Number captured		Mean SVL (mm) (range)		Sex ratio
	Adult	Juvenile	Adult	Juvenile	
<i>A. texanum</i>	121	106	59 (43-81)	37 (30-43)	53:65
<i>A. maculatum</i>	18	30	80 (50-98)	40 (32-47)	8:10
<i>A. opacum</i>	18	2	55 (45-68)	39 (35-43)	7:11
<i>A. talpoideum</i>	5	19	54 (49-64)	43 (38-46)	4:1

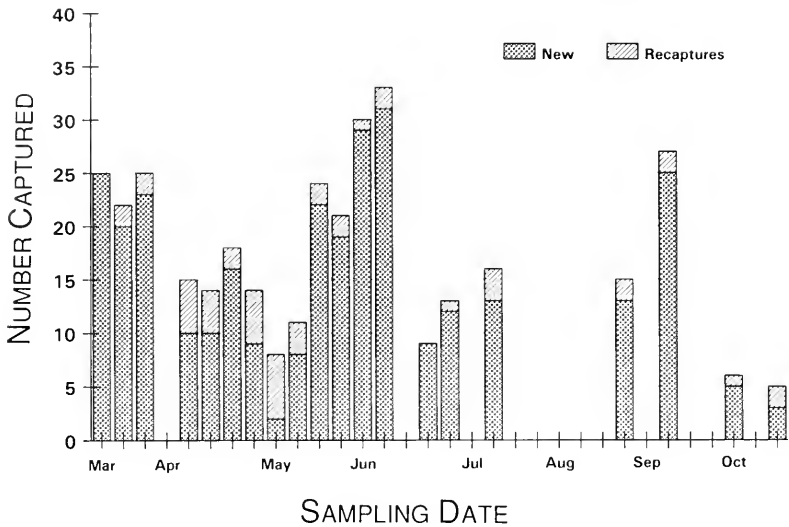


Fig. 2. Total number of *Ambystoma* captured for each sampling date.

*maculatum* and *A. opacum* (Fig. 3). Adult *A. talpoideum* were so rare that no trends are evident. The pattern of juvenile abundances suggests differences in emergence times. Juvenile *A. texanum* were encountered first at the end of May, whereas juvenile *A. talpoideum* were not encountered until the end of July; the first juvenile *A. maculatum* also appeared in May, but additional specimens were not captured until July (Fig. 4). Only two juvenile *A. opacum* were captured.

Salamanders were most abundant in June, which was the wettest month with 32.72 mm (12.88 in.) of rainfall (Fig. 5). Substrate temperature under the cover objects rose steadily before declining in September (Fig. 6).

#### MICROHABITAT DIFFERENCES

Area of cover object and soil moisture beneath it were not related ( $n = 567$ ,  $r = 0.028$ ,  $P > 0.50$ ). Soil moisture probably was related more to topography and amount of surrounding vegetation than to size of cover object. Salamanders were found under cover objects significantly larger and with moister substrates beneath them than control cover objects (Table 2). Both area and moisture had positive effects on the probability of finding a salamander under a cover object; the remaining variation is consistent with random effects.

Mean substrate moisture was higher beneath cover objects harboring salamanders than cover objects not harboring salamanders on all but two sampling dates—23 September and 14 October (Fig. 7). As expected,

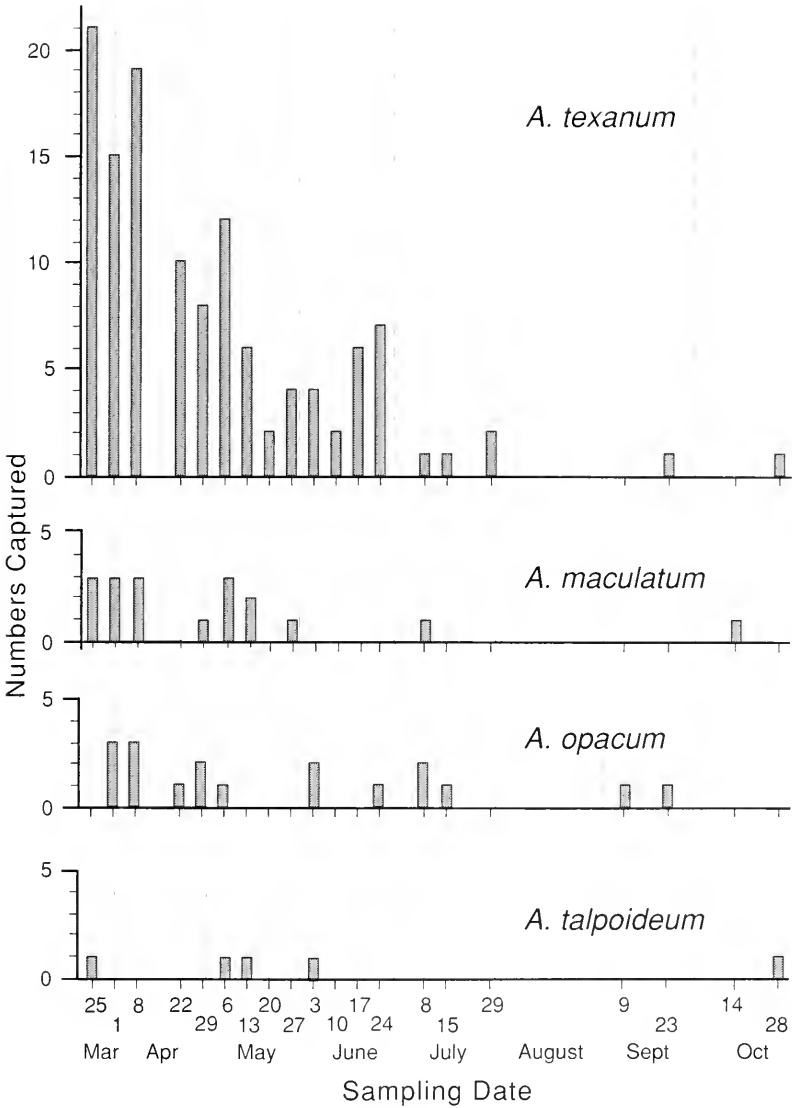


Fig. 3. Number of adult *Ambystoma* captured on each sampling date.

substrate moisture was closely associated with precipitation. There was an increase in moisture from May to June and a pronounced decrease from 8–15 July. A gradual drying of the substrate occurred from July to October. The mean area of cover objects harboring salamanders varied throughout the season and was always larger than the cover objects not harboring salamanders (Fig. 7).

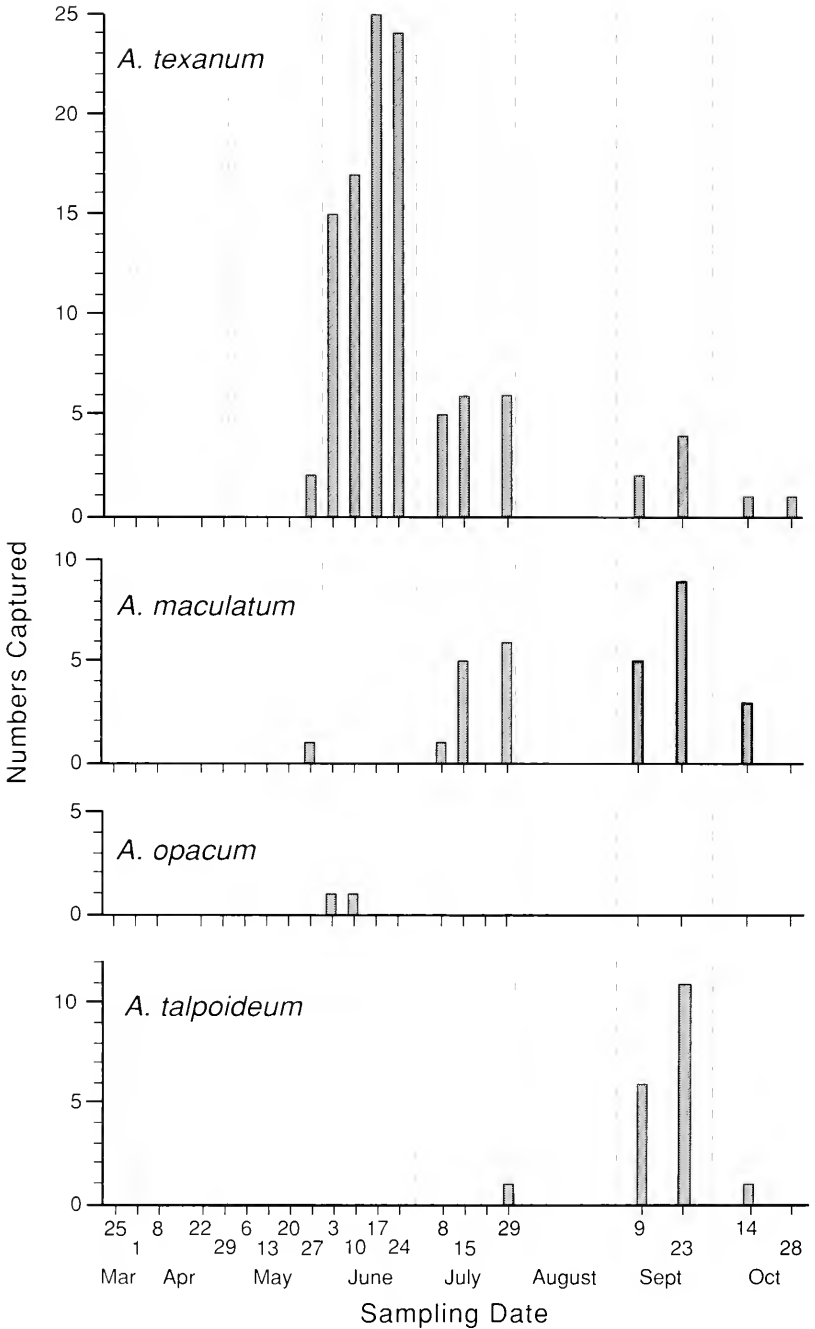


Fig. 4. Number of juvenile *Ambystoma* captured on each sampling date.



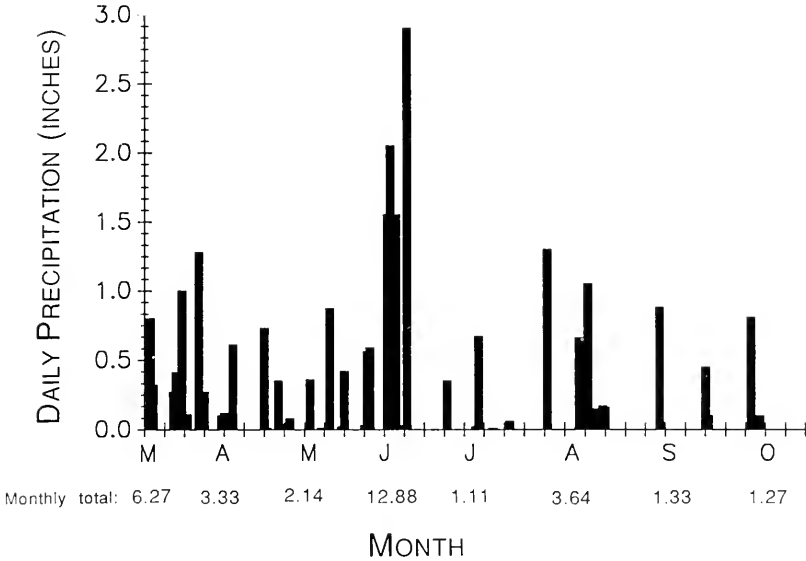


Fig. 5. Daily precipitation at Horseshoe Lake (1989). Data were collected from NOAA station in Olive Branch, Illinois.

The 97 cover objects chosen as seemingly suitable for, but unoccupied by salamanders had a mean area of  $0.43 \text{ m}^2$  ( $SD = 0.23$ ) and a mean substrate moisture of  $52.65\%$  ( $SD = 14.95$ ). They were significantly larger than control cover objects (ANOVA,  $F = 360.62$ ; 1, 358 df;  $P < 0.0001$ ), which had a mean area of  $0.09 \text{ m}^2$  ( $SD = 0.09$ ). They were also significantly larger than cover objects harboring salamanders (ANOVA,  $F = 45.24$ ; 1, 414 df;  $P < 0.0001$ ), which had a mean area of  $0.29 \text{ m}^2$  ( $SD = 0.31$ ). The chosen cover objects were significantly drier than those harboring salamanders (ANOVA,  $F = 29.21$ ; 1, 403 df;  $P < 0.0001$ ), which had a mean moisture of  $63.66\%$  ( $SD = 18.23$ ). They did not differ significantly from control cover objects (ANOVA,  $F = 0.02$ ; 1, 353 df;  $P > 0.50$ ), which had a mean moisture of  $52.48\%$  ( $SD = 13.72$ ).

Amount of substrate moisture was significantly different between species (Table 3) and mean area of cover object differed significantly between age classes (Table 4). Substrate moisture was significantly different between species, but intraspecific differences between adults and juveniles was slight (Fig. 8). Adult and juvenile *Ambystoma maculatum* had nearly identical average moisture values (adults =  $55.08\%$ , juveniles =  $55.28\%$ ). *Ambystoma texanum* was on a significantly moister substrate than *A. maculatum* and *A. opacum*. *Ambystoma talpoideum* also was in significantly moister situations than *A. opacum*. A two-way ANOVA did not reveal any overall significant difference between the four species in the area of cover objects. Adults of all species were found under significantly

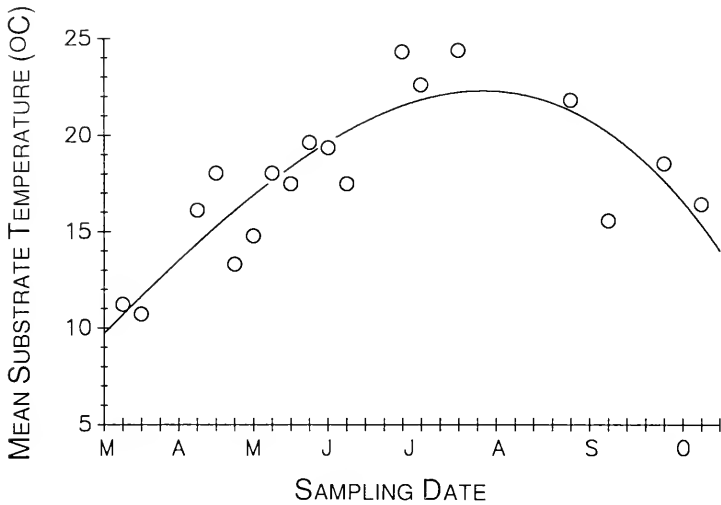


Fig. 6. Mean substrate temperature under cover objects for each sampling date. The regression line is plotted in curvilinear fashion.

larger cover objects than juveniles.

Substrate temperatures differed significantly throughout the season (Fig. 6). Temperature also rose throughout the day. This close association between substrate temperature and time of capture (within and between sampling dates) complicated analyses of temperature differences. The mean substrate temperatures ( $^{\circ}\text{C}$ ) for adults and juveniles, respectively, were as follows: *A. texanum*, 14.13, 19.44; *A. maculatum*, 13.87, 19.43; *A. opacum*, 16.86, 19.90; *A. talpoideum*, 14.82, 18.47. Most juveniles were captured later in the season when temperatures were higher than earlier in the season when adults were more common. The only notable difference in temperatures within an age group is with adult *A. opacum*. This species was found throughout the season in a pattern similar to *A. maculatum* (Fig. 3), yet it was associated with higher substrate temperatures.

Salamander size and area of cover object were not correlated within species and age classes. Individual regression analyses showed no significant relationship between SVL and area of cover object for any category—adult *Ambystoma texanum*,  $r = 0.115$ ,  $P > 0.20$ ; juvenile *A. texanum*,  $r = 0.123$ ,  $P > 0.21$ ; adult *A. maculatum*,  $r = 0.106$ ,  $P > 0.50$ ; juvenile *A. maculatum*,  $r = 0.153$ ,  $P > 0.40$ ; adult *A. opacum*,  $r = 0.233$ ,  $P > 0.30$ ; adult *A. talpoideum*,  $r = 0.263$ ,  $P > 0.60$ ; juvenile *A. talpoideum*,  $r = 0.43$ ,  $P > 0.80$ . See Table 1 for sample sizes. The paucity of *A. opacum* juveniles ( $n = 2$ ) prohibited statistical analysis.

The number of salamanders found on each substrate type was converted to a percentage and reported by species and age class (Table 5). *Ambystoma*

*texanum* and *A. maculatum* were rather cosmopolitan in their occurrence on different substrates. In contrast, more than 70% of *A. opacum* were on primarily coarse soils and *A. talpoideum* was most common on leaves (> 50%) and less common on fine or coarse soils (< 20%).

The greatest dissimilarity between adults and juveniles was the more common occurrence of juveniles on leaves. Leaves were the most common substrate for juveniles of all species except *Ambystoma opacum*, whereas only 6% of adult *A. texanum* and none of the adults of the other species were found on leaves. A primarily coarse soil substrate was found under 59% of the randomly chosen cover objects: leaves (18%), fine soil (15%), and wood (9%) followed in abundance. Although area of cover object and substrate moisture were not correlated statistically, substrate type was related to area of cover object and substrate moisture. The higher the organic content of the substrate, the higher the percentage of water by weight (all means significantly different; ANOVA,  $F = 104.42$ ; 3, 305 df;  $P < 0.0001$ ). Mean area of cover object was significantly different among the four substrate types (ANOVA,  $F = 15.90$ ; 3, 305 df;  $P < 0.0001$ ). There was no significant difference between fine and coarse soil or fine soil and wood according to the GT2 multiple-range-test, but the other combinations were significantly different. Cover objects with leaves as the primary substrate constituent were smallest in area.

#### DISTRIBUTION AND RECAPTURE RESULTS

Thirty one individuals were recaptured with a total of 47 recaptures (Table 6). Only 14.7% of captures were recaptures and only 9.7% of the salamanders were captured more than once. *Ambystoma maculatum* was most likely to be recaptured, especially adults (27.8% of individuals recaptured). Mean recapture rate per sampling date (based on the pool of marked animals available) of adult *A. maculatum* was significantly higher than adult *A. texanum* ( $t = 2.02$ ,  $P = 0.05$ ). Five *A. texanum* were recaptured

Table 2. Maximum likelihood ANOVA and estimates for logistic response function of area of cover object and substrate moisture with presence or absence of a salamander being the two response levels.

Source/effect	df	Chi-square	$P$	Estimate	Standard error
Intercept	1	89.66	< 0.0001	-4.4961	0.4748
Moisture	1	62.52	< 0.0001	0.0563	0.0071
Area	1	74.86	< 0.0001	9.9531	1.1504
Likelihood ratio	517	551.49	> 0.1000		

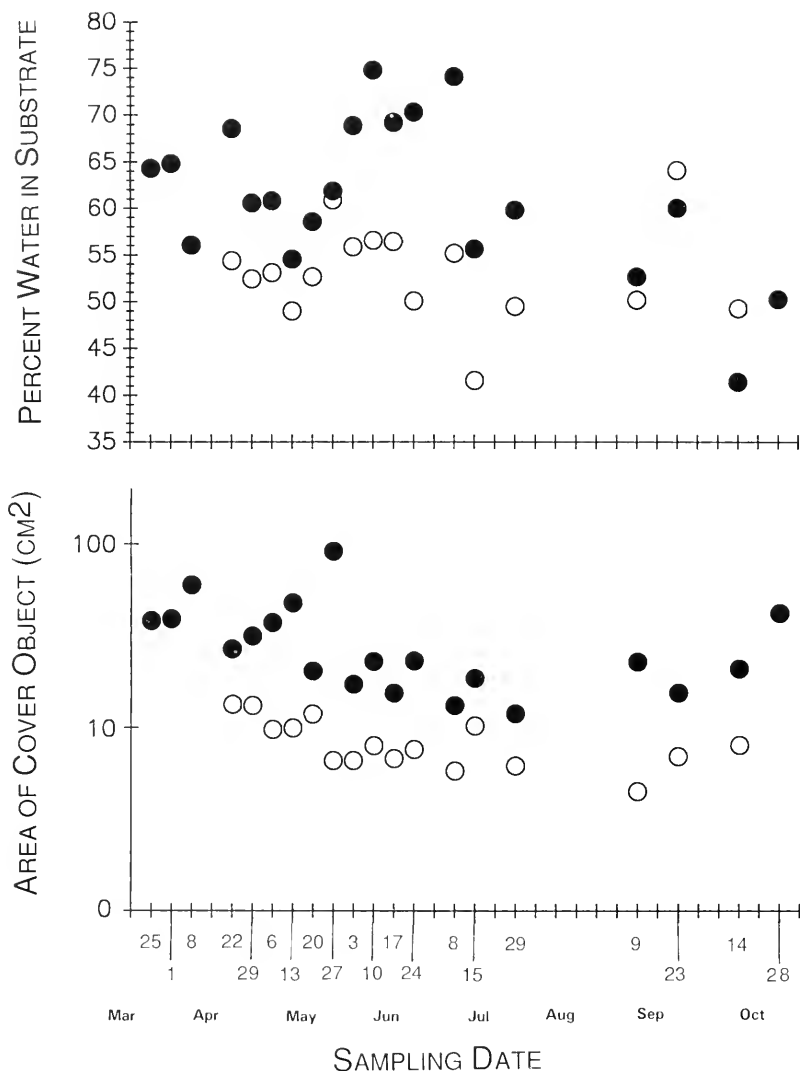


Fig. 7. Mean substrate moisture under cover object and area of cover object for cover objects with salamanders (solid circles) and control cover objects (open circles) for each sampling date. Area of cover object is on a logarithmic scale.

twice, and one was recaptured three times. One *A. maculatum* was recaptured twice, one was recaptured three times, and one was recaptured seven times. The latter (a female) was captured on 8, 22, and 29 April, 20 May, 24 June, 23 September, and 14 and 28 October under one of two adjacent logs. Her SVL was 84 mm when first captured and 86 mm on 28 October; no

Table 3. Results of two-way ANOVA for the dependent variable substrate moisture for *Ambystoma*. Means with the same letters are not significantly different according to the GT2 multiple-range test.

Source	df	SS	MS	F-value	P
Age	1	0.009	0.009	0.24	0.6232
Species	3	0.889	0.296	7.89	0.0001
Interaction	3	0.063	0.021	0.56	0.6409
Error	301	0.038			

Species and age group	Grouping	Mean moisture	SD
Adult	A	65.41	17.11
Juvenile	A	62.06	19.11
<i>A. texanum</i>	A	66.89	18.13
<i>A. talpoideum</i>	AB	61.54	14.25
<i>A. maculatum</i>	BC	55.20	15.83
<i>A. opacum</i>	C	48.21	14.87

Table 4. Results of two-way ANOVA for the dependent variable area of cover object for *Ambystoma*. Means with the same letters are not significantly different according to the GT2 multiple-range test.

Source	df	SS	MS	F-value	P
Age	1	2.886	2.886	18.31	0.0001
Species	3	0.130	0.043	0.27	0.8434
Interaction	3	0.628	0.209	1.33	0.2648
Error	311		0.158		

Species and age group	Grouping	Mean area cm <sup>2</sup>	SD
Adult	A	38.81	35.52
Juvenile	B	19.13	21.69
<i>A. opacum</i>	A	54.96	57.79
<i>A. maculatum</i>	AB	31.23	36.56
<i>A. texanum</i>	AB	27.25	26.60
<i>A. talpoideum</i>	B	21.11	15.26

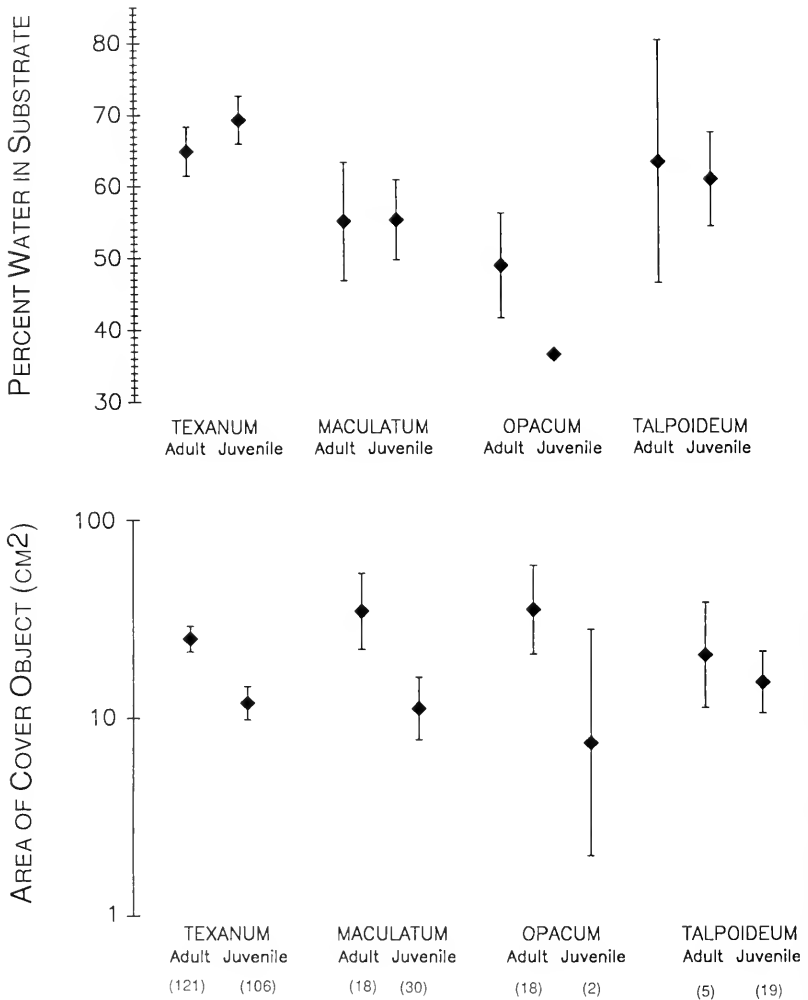


Fig 8. Mean substrate moisture and area of cover object for each species and age class of *Ambystoma*. Mean  $\pm$  2 SE and sample size are shown for each category. Area of cover object is on a logarithmic scale.

differences in SVL greater than 2 mm were observed in recaptured animals.

Recaptured salamanders usually had not moved far; 70.2% (33 of 47) were found under the same cover object. The farthest recorded movement was 19.7 m for a *Ambystoma texanum* (female, 69 mm SVL). Most often, a recaptured salamander was found under an adjacent cover object if movement was observed. *Ambystoma texanum* moved the farthest, but the mean distances moved must be interpreted with caution because of sample

Table 5. Percent of individuals of *Ambystoma* found on four substrate types.

Species and age class	<i>n</i>	Fine soil	Coarse soil	Leaves	Wood
All individuals					
<i>A. texanum</i>	227	21	26	20	33
<i>A. maculatum</i>	48	19	30	30	21
<i>A. opacum</i>	20	6	72	0	22
<i>A. talpoideum</i>	24	5	14	52	29
Adults only					
<i>A. texanum</i>	121	22	36	6	37
<i>A. maculatum</i>	18	28	44	0	28
<i>A. opacum</i>	18	6	71	0	24
<i>A. talpoideum</i>	5	20	60	0	20
Juveniles only					
<i>A. texanum</i>	106	21	15	36	28
<i>A. maculatum</i>	30	14	21	48	17
<i>A. opacum</i>	2	0	100	0	0
<i>A. talpoideum</i>	19	0	0	69	31

sizes. There were no sexual differences in recapture rates: *A. texanum*,  $\chi^2 = 1.7$ ; *A. maculatum*,  $\chi^2 = 0.2$ ; *A. opacum*,  $\chi^2 = 0$  (1 df,  $P > 0.05$  for all).

*Ambystoma texanum* shared cover objects with conspecifics more frequently than did the other species (Table 7). Eight cover objects sheltered both an adult *A. texanum* and either *A. maculatum* or *A. talpoideum*. There was no indication of aversion between salamanders; cohabitants often were in contact with each other under cover objects. There did not seem to be any consistent spacing under mutually occupied cover objects. Of the five *A. talpoideum* captured, two were sharing a cover object with *A. texanum*.

A Poisson distribution predicted the following pattern for adult *Ambystoma texanum*: one salamander/cover object, 130.3 cases; two salamanders/cover object, 0.9 case; three salamanders/cover object, 0.004 case (for 9976 cover objects examined). Compared to this distribution, adult *A. texanum* seemed to be highly clumped. Juvenile *A. texanum* followed a similar clumped distribution. The other species followed a random distribution because of their rareness compared to the total number of cover objects examined (e.g., expected for adult *A. maculatum*: 1 salamander/cover object, 28.9 cases; 2 salamanders/cover object, 0.04 case).

My field observations agree with the tabulated results that *Ambystoma opacum* and *A. maculatum* are almost always found alone, whereas *A. texanum* is more likely to share a cover object. Adult *A. texanum* were found sharing a cover object on 31.7% of the captures. Cover objects that harbored more than one salamander were significantly larger than those

Table 6. Recapture data for *Ambystoma*; no *A. talpoideum* or juvenile *A. opacum* were recaptured.

Category	<i>A. texanum</i>		<i>A. maculatum</i>		<i>A. opacum</i>
	Adult	Juvenile	Adult	Juvenile	Adult
Total number of recaptures	22	4	14	5	2
Individuals recaptured	15	4	5	5	2
Percent of captures that were recaptures	18.2	3.8	77.8	16.7	11.1
Percent of individuals recaptured	12.4	3.8	27.8	16.7	11.1
Percent recaptured under same cover object	59.1	100.0	71.4	80.0	100.0
Mean distance moved when under a new cover object (m)	6.3	—	4.2	2.5	—
Mean SVL of recaptured individuals (mm)	65	43	82	37	61
Sex ratio M:F	5:10	—	2:3	—	1:1

with only one salamander ( $t = 2.64$ , 55 df,  $P < 0.05$ ), but there was no difference in moisture between the two types ( $t = 0.40$ , 54 df,  $P > 0.50$ ).

Juvenile *Ambystoma texanum* were found sharing a cover object on 38.7% of the captures. However, only one juvenile was found with an adult ambystomatid other than *A. texanum*. A juvenile *A. texanum* was found 15 cm from an adult *A. maculatum* under a large log ( $5.93 \times 0.25$  m). The *A. maculatum* was in a hole and the juvenile *A. texanum* was on the surface at the edge of the log.

Frequency of associations among male and female *Ambystoma texanum* cohabiting a cover object was examined (Table 8). Two males were found cohabiting a cover object only once; these were in contact with one another under a large log ( $6.34 \times 0.16$  m). This lack of male-male co-occurrence was highly significant. Females were also found more often with males than other females. When the four cover objects (each harboring 1 male and 2 females) were removed from the analysis, there was still a significant male-male avoidance ( $\chi^2 = 8.33$ , 1 df,  $P < 0.005$ ), but no apparent female-female avoidance ( $\chi^2 = 1.47$ , 1 df,  $P > 0.10$ ).



Table 7. Number of *Ambystoma* under a cover object by species and age class. Recaptured individuals were included. Members of a mixed species and/or age group are in parentheses.

Species and age class	Number under one cover object			
	1	2	3	4
<i>A. texanum</i>				
Adult	90 (+7)	18	2 (+1)	—
Juvenile	64 (+4)	12 (+3)	2 (+1)	1
<i>A. maculatum</i>				
Adult	29(+3)	—	—	—
Juvenile	34	1	—	—
<i>A. opacum</i>				
Adult	20	—	—	—
Juvenile	2	—	—	—
<i>A. talpoideum</i>				
Adult	3 (+2)	—	—	—
Juvenile	12 (+1)	1 (+1)	—	—

Table 8. Frequency of associations among male and female *Ambystoma texanum* encountered under cover objects. When an individual was associated with more than one conspecific, all combinations were included. Expected frequencies were calculated from relative frequencies of males and females collected during the entire study. Chi-square tests the hypothesis that associations among males and females were proportional to their occurrence.

Sex	Number of associations			Chi-square	P
	Male	Female	Totals		
Male:					
Observed	1	19	20	12.80	< 0.001
Expected	9	11			
Female:					
Observed	19	10	29	4.97	< 0.05
Expected	13	16			

## DISCUSSION

The salamanders on Horseshoe Lake Island were not utilizing random cover objects on the forest floor. They were found beneath cover objects that were larger and covered more moist substrates than average. Also, there were many apparently suitable cover objects (by area if not by moisture) that were unoccupied by salamanders. It is possible that every cover object was within the home range of a salamander, because a plethora of evidence points to a large proportion of the population occurring underground at any one time. Many salamanders attempted to escape down burrows when I lifted their cover objects. The areas beneath many cover objects were riddled with burrows and holes of rodents, crawfish, and cicadas, among other animals. Many studies, including ones using individuals tagged with radioisotopes, found ambystomatids in burrows underground during their entire study (Douglas, 1981; Williams, 1973). Kleeberger and Werner (1983) followed *Ambystoma maculatum* using radioactive tags and found that 72% of their detections were underground, 21% were in or under decaying logs, and 7% were under wet leaf litter.

Most sources describe members of this genus as confirmed burrowers and there are many observations of ambystomatids uncovered more than 1 m below the surface (e.g., Gordon, 1968). However, studies have suggested that many species may have limited ability to dig their own burrows (Semlitsch, 1982; Parmelee, 1990). Semlitsch (1982) reported that *Ambystoma opacum* and *A. maculatum* only could enlarge existing holes or cracks and that *A. talpoideum* burrowed 50% of the time. However, *A. tigrinum* is an accomplished burrower; Gruberg and Stirling (1972) provided an excellent series of photographs of an individual excavating a burrow. Ducey (pers. comm.) examined the burrowing ability of most North American ambystomatids and apparently burrowing can be divided into two phases—breaking the surface and constructing the burrow.

Other possible evidence for most of the population being underground comes from the low recapture rates. Several individuals were recaptured in the same area after many weeks of absence. Although this could indicate extensive horizontal movements by the salamanders, it is more likely that the salamanders are entering burrows and resurfacing. This situation illustrates the difficulty in estimating population sizes of ambystomatids in a given area as terrestrial studies only account for individuals on the surface and censuses at breeding pools only sample breeding individuals. Some ambystomatids that breed in temporary ponds do not breed every year (Woodward, 1982). Husting (1965) found that only about one third of a population of *Ambystoma maculatum* bred in any one year.

Semlitsch (1981) reported that *Ambystoma talpoideum* in South Carolina were never associated with cover objects. He found them in elliptical

burrow systems under leaf litter. The mean depth of these burrows was 4.7 cm; the deepest was less than 9 cm underground. Adult *A. talpoideum* made up only 1.6% of the salamanders I captured, but the actual percentage of this species on the island may be much higher.

### HABITAT PARTITIONING

There must be a common limiting resource for resource partitioning to occur. No quantitative comparisons have been made between species of *Ambystoma* and prey sizes or prey taxa. However, earthworms (Lumbricidae) and beetles (Coleoptera) usually are the major constituents of their diets (Wacasey, 1961). Salamanders forage optimally at high food densities and are truly euryphagic, consuming any prey they are able to engulf (Maiorana, 1978a; Jaeger and Barnard, 1981; Jaeger et al., 1981). Because adults of several species of sympatric *Ambystoma* often are different in size (Conant and Collins, 1991), it is possible that size of preferred prey could be a factor that reduces competition. However, Schoener (1974b) noted that it is difficult for poikilotherms to specialize on food size because, unlike birds and mammals that mature quickly relative to their life span, populations of poikilotherms contain individuals of many different sizes at any one time. Maiorana (1978b) found that spatial resources and not food resources regulated the densities of two sympatric plethodontid salamanders.

Even if resource partitioning can be demonstrated, further studies are needed to reveal mechanisms responsible for patterns. Does interference or exploitative competition occur or is the observed pattern the result of the "ghost of competition past" as described by Connell (1980)? Also, although the species may be segregating along one or more habitat dimensions, Holt (1984) demonstrated that predation also leads to patterns of habitat partitioning among prey similar to those resulting from resource competition.

It should also be noted that alpha-selection (i.e., improved competitive ability by the acquisition of interspecific interference mechanisms) is a theoretically valid alternative to resource partitioning (Gill, 1972, 1974; Hairston, 1983). Nishikawa (1985) demonstrated that alpha-selection occurred in populations of *Plethodon glutinosus* in areas of intense interspecific competition.

Ecological segregation of juveniles may be selectively advantageous because competition may be most intense at the borders of common breeding ponds. Predation may be highest here also. Shoop (1974) found survival of newly metamorphosed *Ambystoma maculatum* to be closely related to climatic conditions at time of dispersal. Evaporation of the breeding pond can act as a stimulus for larvae to initiate metamorphosis and these juveniles can emigrate from the pond en masse (Semlitsch et al.,

1988). Also, many studies (e.g., Wilson, 1976; Stenhouse, 1985) have shown nonrandom directions of departure out of breeding ponds. Therefore, population densities of juvenile *Ambystoma* should be high along emigration routes in midsummer. Synchronous metamorphosis and non-random directions of emigration led Walls (1990) to hypothesize that aggressive contests for refugia occur. Post-metamorphic juveniles of *A. maculatum*, *A. talpoideum* and *A. opacum* aggressively interact and suggest the potential for territoriality in this genus (Walls, 1990; 1991).

Because many of these species are poor burrowers, naturally occurring burrows and cover objects should be both an essential and limited resource to salamanders. Refugia certainly vary in moisture and temperature characteristics as well as local food abundance. Apparent defense of refugia exists in several species of *Ambystoma*, but it is not clear whether individuals can expel intruders from defended areas (Ducey and Heuer, 1991; Walls, 1990). Juveniles must find moist terrestrial refugia, because the dry conditions of summer do not permit lengthy periods of travel across the forest floor. Pough and Wilson (1970) found that newly emerged *A. maculatum* were subject to severe temperature stress and dehydration upon emergence. Of juveniles they collected in the afternoon, 41% were in aggregations of at least two individuals, and the salamanders were found only under certain rocks with substrate temperatures less than 32°C. Because the breeding site was a rather open pond surrounded by rocks, potential competition may have been higher for terrestrial refugia than at Horseshoe Lake Island where large breeding ponds are surrounded by old-growth forest providing shade and many cover objects.

Interspecific competition among juveniles for cover objects may exist, because juveniles of all species used remarkably similar-sized cover objects. Moisture did vary among the juveniles. *Ambystoma texanum* was found under moister cover objects than *A. maculatum* or *A. talpoideum*, which preferred similar substrate moistures. Most likely these moisture differences relate to time of emergence. Most juvenile *A. texanum* were captured in June, the wettest month, whereas *A. maculatum* and *A. talpoideum* emerged later in the season, when conditions were drier.

Juveniles would be expected to be in suboptimal habitats because they have just emerged from breeding ponds and have had less time to survey terrestrial habitat. Possibly they are excluded from larger logs containing adults because of predation. Cannibalism is common in larval *Ambystoma* of different sizes (e.g., Stenhouse et al., 1983) and although there are no published records of adult *Ambystoma* cannibalism, adults of *A. maculatum* and the other larger species may include juvenile *Ambystoma* in their diets. The lack of co-occurrence of *A. maculatum* or *A. opacum* with smaller salamanders supports this hypothesis. Juvenile *A. texanum* are the most gregarious, but they were seldom found with adults of other species. The

small mouths of *A. texanum* probably limit their ability to prey on organisms as large as juvenile *Ambystoma*.

Predation may also come from the great abundance of juvenile southern leopard frogs (*Rana sphenocephala*) which used similar cover objects. I found these frogs from 15 July until the end of the study and counted 30 under cover objects within the quadrats on 10 September. Juvenile salamanders would be in the most danger from this potential predator and small cover objects would be the safest retreats as the frogs tended to occupy larger, more open cover objects. Studies of predation by snakes, shrews, and other predators are needed.

Because area of cover object and substrate moisture were unrelated, other physical conditions must have affected moisture below the cover objects. Such an environmental variable may be distance from the nearest pool of water (or previously filled depression). The high average substrate moisture of *Ambystoma texanum* may be a consequence of their shorter movements from the breeding pools. Pfingsten and Downs (1989) reported that this species tends to occupy low-lying retreats near breeding ponds and probably undergoes less extensive migration than some other species of *Ambystoma*. For 10 individuals in Indiana, the average distance from the pond to their summer retreat was only 54.2 m (Williams, 1973). There may be habitat segregation with *A. texanum* occupying the moister areas surrounding ponds and *A. maculatum* and *A. opacum* utilizing drier areas on higher ground.

If substrate moisture is highly correlated with distance from water, the occurrence of juveniles in drier situations is contrary to expectation. Juvenile *Ambystoma talpoideum* moved only half as far as adults from the breeding pond (Semlitsch, 1981). Williams (1973) also noted that juvenile *A. jeffersonianum* moved an average of only 92 m from the breeding pond which was considerably less than adults. The situation on Horseshoe Lake Island may be unusual, because in early spring about half of the forest was inundated. A movement of as far as 92 m in any direction would most likely place the juvenile near another pond. Dispersal distances may be short in such a low-lying area. Lower average substrate moisture among juveniles was most likely a consequence of being captured later in the season when conditions were drier. Juveniles are under more pressure to occupy moist refugia than adults because large salamanders dehydrate at a slower rate than small ones with a lower surface/volume ratio (Spotila, 1972).

Differential interspecific occupation of cover objects with significantly different substrate moistures probably is not a result of interspecific differences in water requirements. Spight (1967) found that the availability of water in the substrate could not be used to make predictions about which salamander species occupies a given habitat. The rate of water uptake from saturated soils was correlated with body weight and dehydration deficit of

the salamanders, and no differences were found in rate of exchange or absorption threshold between species from different habitats. If all species can occupy the same range of substrate moistures, other factors must segregate the species in different moisture ranges.

It was not surprising that juveniles were most often captured in a primarily leaf substrate. Cover objects above leaf substrates were significantly smaller than those on other substrate types. A substrate of leaves probably reflected the amount of time that a cover object was on the forest floor. A cover object first falls on a layer of leaf litter and, over time, organisms degrade this layer. The distribution of fine and coarse soil were the result of regional differences in soil textures and only *Ambystoma opacum* seemed to have a strong preference for coarse soil.

#### TEMPORAL AND SPATIAL DISTRIBUTION

Seasonal segregation of the above-ground portion of the habitat is evident when data on all species are combined. Before 20 May, 72.8% of the adults were captured, whereas no juveniles were captured before this date. The adults of the four species do not seem to be temporally segregated. Numbers of *Ambystoma texanum* declined sharply from an initial high, whereas the other three species are more constant in their occurrence, but also are most abundant early in the year. Total number of salamanders captured and the amount of precipitation are closely associated. This relationship is caused mainly by the abundance of adult *A. texanum* the first three sampling dates and the abundance of juvenile *A. texanum* in June when precipitation was highest. The abundance of this species on the soil surface may be related to moisture availability.

Higher substrate moisture in the first half of the season seems to be a reasonable explanation for the greater abundance of salamanders at that time. However, possibly individuals are more likely to be above ground early in the year because they are emigrating from the breeding ponds to their summer home ranges. In Indiana, Williams (1973) found that the last *Ambystoma texanum* did not depart the breeding pool until 8 May in 1971. Usually, the last departures of *A. maculatum* were in March and the last adult had always departed the breeding pool by April. Also, early in the season the soil may be so saturated that underground feeding opportunities are reduced. This group of salamanders has well-developed cutaneous respiration (Whitford and Hutchinson, 1966); thus, flooded burrow systems would not be directly detrimental, but certainly many arthropods and annelids would be forced to the surface. I observed feeding by salamanders on two occasions—adult *A. texanum* feeding on small earthworms. Perhaps surface substrate moisture is only marginally tolerable most of the year, and during the spring the salamanders are taking advantage of this temporarily available habitat. Plethodontids on the surface were at an energetic

advantage to those underground because consumption of prey was limited underground (Fraser, 1976).

*Ambystoma opacum* is unique among ambystomatids in ovipositing on land in the fall. The only published observation of a breeding aggregation of *Ambystoma talpoideum* in Illinois was 8 November (Smith, 1961). Semlitsch (1981) found most individuals breed in December and January in South Carolina. Studies from many different areas have shown *A. texanum* breeds before *A. maculatum*. Keen (1975) observed breeding and egg deposition on 12–13 January for *A. texanum* and March 6–8 for *A. maculatum* in central Kentucky.

There is considerable variation among all species in larval period. Wilbur and Collins (1973) found that in a single pond some *Ambystoma maculatum* metamorphosed after only 57 days, and others not until 144 days. Because *A. opacum* juveniles were so rare, I will not discuss them in relation to the emergence of the other three species. The first juvenile *Ambystoma texanum* and *A. maculatum* were captured on the same day (27 May); during the next five sampling dates (3 June–24 July), 81 juvenile *A. texanum* and only one juvenile *A. maculatum* were found. Possibly this first *A. maculatum* had overwintered, as the amount of first-year growth is unknown. The general order of emergence I found was: *A. texanum*, *A. maculatum*, *A. talpoideum*.

Because this sequence differs from the presumed sequence of oviposition, the rates of larval development must be different among at least *Ambystoma talpoideum* and *A. texanum*. Some evidence for this is the significantly larger size of newly metamorphosed *A. talpoideum*. Possibly, *A. talpoideum* breeds later in the spring in this area, or there may be two breeding seasons (fall and spring); a definite breeding season has not been reported for this species in southern Illinois. Many studies have shown segregation of breeding times, but this is the only field study documenting a difference in abundance of sympatric *Ambystoma* juveniles on the forest floor over time.

The recapture data reveal that these salamanders rarely remain under the same cover object for an entire week. Possibly, marked individuals did not move far on the forest floor. They could have moved a few centimeters, but would be undetectable if they moved downward into burrows. My data suggest limited activity centers, where a few individuals were recaptured many times under the same cover object or an adjacent one. One *Ambystoma maculatum* was recaptured in the same area for almost the entire study.

The Poisson distribution was used as an approximation of a random distribution pattern; an assumption of this distribution is that all areas are equally suitable for habitation. It should be noted that the results clearly show that cover objects vary in their suitability for habitation. Therefore

some degree of clumping would be expected independent of how salamanders were behaving. Adult and juvenile *Ambystoma texanum* did not have exclusive use of particular cover objects. It was also unlikely that cover objects were supporting more than one territory because there was no evidence of uniform spacing (except for males). If *A. texanum* were defending cover objects from intruders, there would not have been as many salamanders co-inhabiting cover objects. Individual cover objects would often have a new salamander under them on different sampling dates. This would not be expected if the salamanders were utilizing cover objects as exclusive territories. *Ambystoma maculatum* and *A. opacum* appear to have exclusive use of their cover objects. This gives additional evidence toward territorial behavior in *A. maculatum* (as formerly suggested by Ducey and Ritsema, 1988).

This is the first report of a lack of male-male associations among *Ambystoma*. Many animals, including several species of plethodontids, have this pattern, but usually there is sexual defense of a breeding area. Because *Ambystoma* (except *A. opacum*) breed in common aggregations in water, what advantage does a male gain by selectively excluding other males from a terrestrial retreat?

I believe *Ambystoma* populations are controlled by factors other than density-dependent effects in the terrestrial stage. Predation and other forms of mortality are believed to be low among adults but virtually nothing is known about adult ambystomatid mortality. Whitford and Vinegar (1966) determined that 89.5% of the *A. maculatum* marked in 1962 were still alive 1 yr later. *Ambystoma maculatum* has survived in captivity for over 20 yr (Pope, 1944). Larval mortality is extremely variable and always high. Premetamorphic mortality was estimated to be 99.89% in *A. maculatum* and 91.18% for *A. opacum* annually (Stenhouse, 1987). Larval mortality was estimated to be 88–99% for *A. maculatum* (Shoop, 1974).

Fossorial animals are notoriously difficult to study, but this behavior imparts considerable protection to the animals from predation and environmental fluctuations. Because of high larval mortality, adults possibly do not saturate their habitat; thus, there is no selection for territoriality. Ovaska (1988) suggested that food was not limiting for *Plethodon vehiculum* during their active season and, therefore, defense of feeding territories would be uneconomical; the dispersal pattern of that species is similar to the pattern exhibited by *Ambystoma texanum* in this study.

Interspecific territoriality would be unnecessary if the four species of *Ambystoma* had completely different microhabitat preferences. Experimental evidence exists for microhabitat differences; on a soil moisture gradient, *A. maculatum* preferred higher moisture than *A. jeffersonianum* (Wacasey, 1961). Also, there are several anecdotal accounts of differences in habitat use by *Ambystoma*. Cagle (1942) reported the general habitats of



three species of *Ambystoma* in southern Illinois—*A. maculatum* most frequently deep in the interior of decaying logs; many *A. opacum* in dry situations (such individuals had smooth, dry skin and apparently were well adapted to the dry surroundings); and *A. texanum* under logs near water and at the bottom of crawfish burrows. These descriptions are similar to what I found at Horseshoe Lake Island, and the quantitative data I collected support the conclusion that these four species are utilizing different microhabitats. Whether they evolved independently in different habitats or evolved habitat partitioning in response to competition is unknown.

*Acknowledgments:* This study was submitted in partial fulfillment for the Master of Science degree at Illinois State University, Normal, Illinois. I would like to thank many people at this fine institution, mostly my major professor, L. E. Brown for his guidance and friendship throughout my work there. I also thank S. A. Juliano for statistical advice and numerous words of wisdom, S. K. Sakaluk, R. A. Anderson and D. E. Birkenholz for discussions and comments on the manuscript. W. E. Duellman and L. Trueb provided many helpful comments on the manuscript and figures. I thank the Illinois Department of Conservation and R. Garrison for permission to work on Horseshoe Lake Island; the Omar Rilett Scholarship Fund at I.S.U. for monetary assistance, and W. Tony Frankino for turning those logs and for feeling worse than myself the morning after Steve bought at Ouidas. Finally, I greatly appreciate the prodigious support from my parents.

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