Copeia, 1990(2), pp. 418–426

Intraspecific Spatial Relationships of Two Species of Terrestrial Salamanders

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Intraspecific spatial relationships of two species of terrestrial salamanders, *Plethodon teyahalee* and *P. jordani* were studied in the southern Appalachian Mountains. The movements of 24 *P. teyahalee* and 40 *P. jordani* individuals, uniquely marked with fluorescent dust, were monitored from May–Sept. 1983. Distances moved between recaptures were recorded, and the minimum convex polygon method was used to estimate home range areas. Both species occupied fixed home ranges, and all age classes of both species shared on average less than 10% of home range area with a conspecific of the same age or sex. Home ranges of *P. teyahalee*, the larger species, were smaller, more exclusive, and more likely to contain a retreat hole than home ranges of *P. jordani*. All 3 yr old or older *P. teyahalee* had at least one retreat hole in their home range, which they used nearly every night. It appears that retreat holes may be defended by *P. teyahalee*, but there was no evidence that retreat holes were in limited supply. Home ranges of *P. jordani* were not associated with cover objects or with retreat holes, which suggests that neither of these resources are defended. The only resource that appears to be used by both species is space (i.e., the forest floor itself, which contains the multi-purpose home range area that both species use for foraging and courtship). This study supports two predictions of the hypothesis that these salamanders are intraspecifically territorial: 1) individuals occupy fixed home ranges; and 2) these areas are exclusive with respect to rivals.

NUMEROUS field studies have shown that intra- and interspecific competition occur in natural populations of plethodontid salamanders (Hairston, 1980a, 1980b; Jaeger, 1971a, 1971b; Kleeberger, 1984). The existence of competition in salamander populations implies that there is some limited resource for which the species compete (Gause, 1934), although no resource needs to be limiting if competition is due to interference behavior, such as allelopathy or territoriality, rather than to exploitation (Gause, 1934; Gill, 1972). Previous studies have suggested a variety of possible resources for which salamanders may compete. *Plethodon cinereus* and *P. shenandoah* appear to compete for microhabitats that are moist and have abundant prey (Jaeger, 1971a, 1971b). Species of *Desmognathus* appear to compete for cover objects, and possibly for food (Kleeberger, 1984), although food is apparently not a limiting resource for *P. jordani* and *P. teyahalee*. (*P. teyahalee* Highton, 1983 is the new name assigned to the populations of *P. glutinosus* studied by Nishikawa, 1985a, 1985b, 1987; Hairston, 1980a, 1980b). The limited resource, if any, for which these species compete remains unknown, although underground retreat holes or nest sites have been suggested for these (Hairston, 1981) and other species of *Plethodon* (Fraser, 1976).

Interference behavior appears to play a role in salamander competition. Intra- and interspecific aggression have been observed in many species of plethodontid salamanders (Cupp, 1980; Gordon, 1952; Grant, 1955), including all species for which there is evidence of competition (*P. cinereus*, Jaeger, 1981, 1984; *Desmognathus* species, Keen and Sharp, 1984; Keen and Reed, 1985; *P. jordani* and *P. teyahalee*, Nishikawa, 1985a, 1985b; Organ, 1958, 1960; Hutchison, 1959; Thurow, 1976). *Plethodon cinereus* is the only species of salamander that has been shown to use aggression to exclude competitors from home ranges in the laboratory (Jaeger et al., 1982). Field studies also indicate that individuals of *P. cinereus* are less likely to share cover objects than expected by chance (Gergits, 1982). In addition to aggression, individuals of *P. cinereus* also defend home ranges by using pheromones to advertise ownership (Horne and Jaeger, 1988; Jaeger et al., 1986).

These field and laboratory studies suggest that interference either mediates competition through some form of territoriality, either defense of limited resources, or defense of an all-

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purpose home range in which no single resource is defended (Brown and Orians, 1970). In home range defense, space itself may become limiting if densities are high enough and overlap of adjacent home ranges is low enough to prevent some individuals from surviving or breeding (Brown and Orians, 1970). In either case, if interference contributes to competitive interactions, salamanders are predicted to use aggressive behavior for some type of territorial defense.

Data on spatial relationships of individuals in natural populations can be used to test two predictions of the territoriality hypothesis: 1) that individuals occupy fixed areas; and 2) that home areas are exclusive with respect to rivals. The purpose of this field study was to test these predictions in *P. jordani* and *P. teyahalee.* While previous studies of salamanders have shown that individuals space themselves farther apart from rivals than would be expected due to chance alone (Gergits, 1982; Wells and Wells, 1976; Wells, 1980), no study has quantified the overlap between home ranges of adjacent salamanders.

METHODS

I studied the spatial relationships of *P. teyahalee* and *P. jordani* at two sites in the southern Appalachian Mountains. One site was located in Great Smoky Mountains National Park, Swain County, North Carolina, near the Heintooga-Roundbottom Road, approx. 9.5 miles from the Balsam Mountain Campground (35°37′30″N, 83°30′22″W) at an elevation of 1370 m, and the other was located in the Balsam Mountains, Pisgah National Forest, Transylvania County, North Carolina, along Courthouse Creek (35°16′22″N, 82°53′20″W) at an elevation of 1065 m, in the same ravine studied by Hairston (1980a, 1980b). Although the species are sympatric at both of these sites (Hairston, 1980a, 1980b; pers. obs.), only one species was abundant enough to be studied at each site.

At both sites, the vegetation is intermediate between cove hardwood and northern hardwood forest. The predominant tree species are yellow birch (*Betula alleghaniensis*), beech (*Fagus grandifolia*) and hemlock (*Tsuga canadensis* and *T. carolinensis*), with an understory of witch hazel (*Hamamelis virginiana*), mountain laurel (*Kalmia latifolia*) and two species of *Rhododendron.* Large stumps and trunks of dead chestnut trees (*Castanea dentata*) were common at both sites.

At each site, I established a 10 × 10 m plot (36 stakes/plot at 2 m intervals). Because the stakes were marked with reflective tape, the location of salamanders could be accurately determined at night. Accuracy of location was improved to approx. ±0.1 m by using landmarks of known location as additional distance markers. Nineteen visits to the Smoky Mountains and 15 visits to the Balsam Mountains were made between 24 May–25 Sept. 1983. On each visit, the plots were searched thoroughly and systematically, 1–3 times/night. Searching began no earlier than 0.5 h after dusk (2000–2200 h Eastern Daylight Time (EDT), and continued for 0.5–3.5 h, depending on the number of salamanders found.

The age from hatching (1 yr, 2 yr, 3 yr or older) of each salamander found on the plots was estimated from approximate body size at the time of first capture (for sizes of *P. jordani* age-classes, see Hairston, 1983a, 1983b; for sizes of *P. teyahalee* age classes, see Highton, 1956). SVL was not measured in order to minimize handling. In May when marking was started, 1, 2, and 3 yr olds could be distinguished from each other and from adults with approx. 10% error (pers. obs.; Hairston, 1983a). Later in the year, 3 yr olds become indistinguishable from adults on the basis of size alone (Hairston, 1983a). The sex of adult salamanders was determined by presence (males) or absence (females) of a mental gland (Hairston, 1983b), and the sex of juveniles (1, 2, and 3 yr olds) was not determined.

Each salamander was marked uniquely with dry fluorescent dust, using a combination of three colors and 10 mark locations: right and left sides; neck, axial, midbody, inguinal and tail (Nishikawa and Service, 1988). Dust particles were sprayed into the skin with a low pressure spray gun. Marks were small (about 0.5 cm diameter) and could be seen under UV or visible light. Some marks remained visible for more than 2 yr after marking. No attempt was made to mark 1 yr olds (SVL ≤25 mm) because of their fragility. Salamanders older than 1 yr were marked and returned to the site of capture less than 5 min after marking.

Salamanders were marked on the plots from 25 May–18 July 1983. I marked 24 *P. teyahalee* on the Smoky Mountains plot, and 21 were recaptured at least once. Three juvenile and two adult salamanders without marks were found on the plot after marking was stopped. I marked 40 *P. jordani* on the Balsam Mountains plot, and

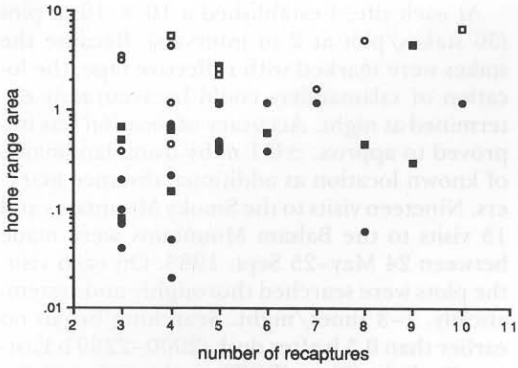

Fig. 1. The relationship between number of observations and estimates of home range area for all salamanders observed at least three times whose points of recapture were not on a straight line (n = 43). A semi-log plot is used because home range area varies over more than three orders of magnitude. Product-moment correlation coefficients for untransformed variables are not significant (see text). *Plethodon teyahalee,* closed symbols; *P. jordani,* open symbols; juveniles, diamonds; adults, squares.

32 of these were recaptured at least once. Twelve juvenile and four adult salamanders without marks were found on the plot after marking had stopped. The plots were chosen specifically because they were known to previously contain individuals of both species. However, only two *P. teyahalee* were found on the Balsam Mountains plot, and only seven *P. jordani* were found on the Smoky Mountains plot during this study, and these have been omitted from the analysis. Thus, observation of each species on more than one plot was unfortunately not possible.

Whenever a salamander was observed, its location was recorded to the nearest 0.1 m, and the nearest cover object or retreat hole was noted. Age, sex, fluorescent mark, and any other distinguishing features (e.g., scars, or a regenerating limb or tail) were also recorded. On many occasions, a salamander was observed in a retreat hole on the plot and its fluorescent mark, if any, was not visible. When the salamander could not be extracted, an attempt was made to identify the individual on the basis of other information (i.e., species, age, sex, scars, regenerating limb or tail). It was often possible to observe these characteristics when a salamander was in a retreat hole and the mark itself was not visible. Location of the retreat hole was also used to identify the salamander (60 of 257 cases), but only if the age and species was determined and the observation fell within the exclusive home range of a marked salamander of the same species and age.

The distance moved between captures is an estimate of how far a salamander moves in the course of its normal activities, and can be used to estimate the probability of encounter between adjacent individuals. Distances moved by salamanders between captures were calculated and Mann-Whitney U-tests (two-tailed) were used for comparisons between age classes, sexes and species. Home range size was estimated as the area of the minimum convex polygon (MCP) that encloses all of the capture locations for each individual (Jennrich and Turner, 1969). Polygonal home range area can only be calculated for salamanders captured at least three times whose capture locations do not fall on a straight line. Estimates of home range area using the MCP method are often observed to increase asymptotically with the number of observations per individual, and thus will underestimate home range area if the asymptote has not been reached (Schoener, 1981). In this study, polygonal home range estimates were based on an average of 5.5 sightings/individual for *P. teyahalee* and an average of 4.3 sightings/individual for *P. jordani.* This is a higher recapture rate than has previously been reported for these species in any other mark-recapture study (Merchant, 1972; Madison, 1969; Nishikawa and Service, 1988). Home range areas were not significantly correlated with number of observations per salamander in either species (Fig. 1: untransformed product-moment correlation coefficients, *P. jordani*: juveniles, n = 12, r = 0.2522, $P > 0.05$; adults, n = 9, r = 0.1095, $P > 0.05$; *P. teyahalee*: juveniles, n = 4, r = 0.4283, $P > 0.05$; adults, n = 9, r = 0.4752, $P > 0.05$). Neither mean nor maximum estimates of home range area increase with number of recaptures, and minimum estimates do not decrease with number of recaptures. Mann-Whitney U-tests (two-tailed) were used to compare the home range sizes of different ages, sexes and species.

The areas of polygonal home ranges and the areas of overlap between adjacent home ranges were estimated by tracing the polygons (drawn at a scale of 1:40) on the magnetized tablet of a Zeiss IBAS digitizing computer. Area estimates were means (± 1% error) of at least five traces. Mann-Whitney U-tests (two-tailed) were used to compare overlap in home ranges among different ages, sexes and species.

Nearest neighbor distances (Clark and Evans,

TABLE 1. DISTANCE MOVED BETWEEN CAPTURES (M), HOME RANGE AREA (M^2), PERCENT OF NIGHTS SPENT IN A RETREAT HOLE, AND PERCENT OF INDIVIDUALS SEEN IN A RETREAT HOLE AT LEAST ONCE, FOR EACH AGE/SEX CLASS OF *Plethodon teyahalee* AND *P. jordani* (±1 SE).

Age/sex class	Distance moved	Home range area	% Nights in retreat hole	% Individuals seen in retreat hole > once
Plethodon teyahalee				
2 yr olds	0.81 ± 0.13	0.37 ± 0.21	14.1 ± 5.9	50.0
3 yr olds	0.51 ± 0	0.06 ± 0	68.8 ± 18.8	100.0
Males	0.67 ± 0.12	0.49 ± 0.06	96.0 ± 4.0	100.0
Females	1.44 ± 0.30	1.03 ± 0.54	74.7 ± 7.8	100.0
Plethodon jordani				
2 yr olds	1.92 ± 0.32	1.52 ± 0.46	26.5 ± 6.9	57.1
3 yr olds	2.47 ± 0.80	2.98 ± 1.11	16.7 ± 7.7	44.4
Males	2.59 ± 0.85	5.04 ± 1.21	11.4 ± 8.6	28.6
Females	1.69 ± 0.40	1.87 ± 0.62	35.0 ± 14.0	66.7

1954) were used to analyze the dispersion of home ranges on the plots. Distances were measured from the geometric center of the home range of each salamander to the geometric center of the home range of the nearest neighbor. Expected distances E(r) between nearest neighbors for randomly dispersed home ranges are given by the formula $E(r) = \frac{1}{2}\sqrt{d}$, where d = density. The expected mean distances were adjusted for edge effects and non-independence of observations using Donnelly's (1978) correction.

RESULTS

The range of distances moved between captures was 0.0–3.0 m for *P. teyahalee*, and 0.0–8.0 m for *P. jordani*. Mean distances moved between captures (Table 1) were similar to the maximum distance that any salamander was observed to move between subsequent searches on a single night (1.12 m for *P. teyahalee*, 0.20 m for *P. jordani*). The mean interval between captures was 14.4 d (SE = 1.48) for *P. teyahalee* and 17.2 d (SE = 1.83) for *P. jordani*. Distance moved between captures was not significantly correlated with intercapture interval for either species (product-moment correlation, *P. teyahalee*, df = 76, r = 0.0264; *P. jordani*, df = 84, r = 0.1502). For both species, there were no significant differences between juveniles and adults or between males and females in the distance moved between captures. Juveniles ($P < 0.02$) and adult males ($P < 0.05$) of *P. jordani* moved significantly farther between captures than those of *P. teyahalee*, but the difference between females was not significant ($P > 0.10$).

Observed home range area varied considerably among individuals of both species (*P. jordani*, range 0.05–6.71 m^2; *P. teyahalee*, range 0.01–4.69 m^2). For both species, there were no significant differences in home range area between juveniles and adults or between males and females (Table 1). However, the home ranges of juvenile and adult *P. jordani* were significantly larger than those of *P. teyahalee* (Mann-Whitney U-tests, two-tailed, all $P < 0.05$). The differences in home range size between *P. jordani* and *P. teyahalee* cannot be explained as an artifact of differences in the number of observations per individual. *Plethodon jordani* were observed less often on average than *P. teyahalee*, and would be expected to have smaller home ranges than *P. teyahalee* if the differences were an artifact of capture frequency.

The home ranges of *P. teyahalee* on the Smoky Mountains plot and those of *P. jordani* on the Balsam Mountains plot are shown in Figure 2. Ten of the 17 home ranges of *P. teyahalee* are exclusive of all other conspecifics, while only two of 18 home ranges of *P. jordani* are exclusive of all other conspecifics. A majority of the home ranges of both species did not overlap with the home range of an individual of the same age or sex (Table 2). For *P. jordani*, fewer 2 yr olds shared their home ranges with another 2 yr old than with an older conspecific (Table 2). All 3 yr olds shared their home ranges with another 3 yr old and with at least one 2 yr old, and most 3 yr olds shared their home range

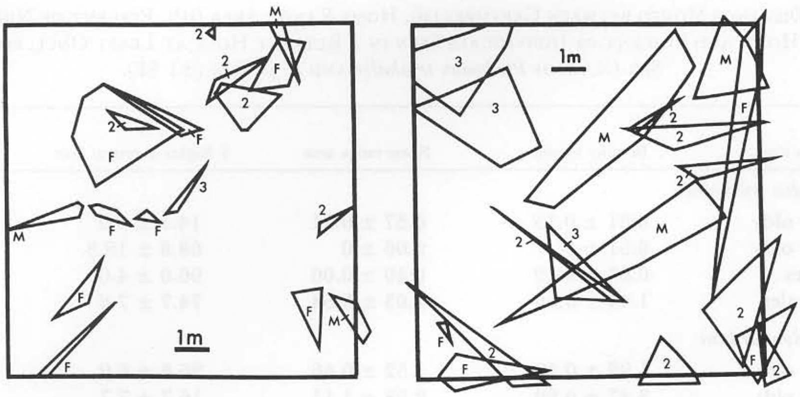

Fig. 2. Map of the home ranges of *Plethodon teyahalee* on the Smoky Mountains plot (left). Note the small size of home ranges, and the infrequent overlap between them. Map of the home ranges of *P. jordani* on the Balsam Mountains plot (right). Note the larger size of home ranges, and the more frequent overlap between them. M = adult male, F = adult female, 3 = 3 yr olds, 2 = 2 yr olds.

with at least one adult (Table 2). Less than 50% of adult *P. jordani* shared their home ranges with an adult of the same sex (Table 2). Most *P. teyahalee* did not share their home ranges with any conspecific, regardless of age (Table 2). Two female *P. teyahalee* with overlapping home ranges were the only salamanders observed in aggressive interactions during this study.

Individuals of *P. jordani* share a larger percentage of their home range area with conspecifics than is shared among individuals of *P. teyahalee* (Table 2). Both species exhibit a tendency for most of the age/sex classes to share a smaller percentage of the home range with individuals of the same age than with individuals of different ages (Table 2). All ages and sexes of both species share less than 10% of their home range area with a conspecific of the same age or sex (Table 2).

Because no salamander was active every night, it is possible that overlapping portions of home ranges were used by only one salamander at a time. However, no evidence for temporal partitioning of home range use was found. Of the five pairs of *P. teyahalee* with overlapping home ranges on the Smoky Mountains plot, all pairs were active together on at least one night (mean = 2.6 nights of simultaneous activity). There were 31 overlapping pairs of *P. jordani* on the Balsam Mountains plot, excluding male-female pairs which might have been courting. Of these, 61.3% were active together on at least one night. For both species, this is similar to the expected probability that two randomly selected, non-overlapping salamanders will be active on the same night.

Both species showed evidence of non-random home range dispersion. For *P. jordani,* the geometric centers of the home ranges of both males and females were significantly farther apart than expected if randomly dispersed (Table 3). For *P. teyahalee,* only the mean distance between males was significantly larger than random expectation (Table 3). The mean nearest neighbor distances of all age classes of both species were larger than the average distances moved between captures (Table 3) and greater than the maximum distance moved on a single night. Thus, both species have relatively low probabilities of encountering a same-aged conspecific in their nightly movements.

The use of nearest neighbor distances to analyze dispersion patterns is based on the assumption that habitat quality is uniform. It appears that this assumption is valid for *P. jordani,* at least over the relatively small area included in this study. A single *P. jordani* individual may move more than 10 m between captures and may occupy a home range area that is larger than 50 m². However, the home ranges of *P. teyahalee* are much smaller than those of *P. jordani.* Analysis of retreat hole use by the two species provides evidence that habitat quality may not be uniform for *P. teyahalee.*

Use of underground retreat holes differs among age classes and between species of salamanders (Table 2). One and 2 yr old *P. teyahalee* were found in retreat holes significantly

TABLE 2. PERCENT (IN PARENTHESES) OF EACH AGE/SEX CLASS OF *Plethodon teyahalee* AND *P. jordani* THAT SHARE THEIR HOME RANGE WITH CONSPECIFICS OF THE GIVEN AGE OR SEX AND MEAN PERCENT OF HOME RANGE AREA THAT IS SHARED (±1 SE).

	2 yr olds	3 yr olds	Males	Females
Plethodon teyahalee				
2 yr olds	(40) 1.4 ± 1.0	(0) 0 ± 0	(0) 0 ± 0	(40) 20.1 ± 20.0
3 yr olds	(0) 0 ± 0	(0) 0 ± 0	(0) 0 ± 0	(0) 0 ± 0
Males	(0) 0 ± 0	(0) 0 ± 0	(0) 0 ± 0	(33.3) 16.3 ± 16.3
Females	(25) 0.6 ± 0.5	(0) 0 ± 0	(12.5) 2.3 ± 2.3	(25) 4.15 ± 3.7
Plethodon jordani				
2 yr olds	(28.6) 0.3 ± 0.2	(14.3) 9.0 ± 9.0	(42.8) 16.6 ± 12.1	(57.1) 10.6 ± 5.8
3 yr olds	(33.3) 3.8 ± 3.8	(66.7) 6.0 ± 3.0	(33.3) 12.2 ± 12.2	(0) 0 ± 0
Males	(66.7) 1.6 ± 1.0	(33.3) 4.5 ± 4.5	(0) 0 ± 0	(66.7) 6.6 ± 6.5
Females	(100) 18.5 ± 7.5	(0) 0 ± 0	(25) 7.7 ± 7.7	(0) 0 ± 0

less often than adults and 3 yr olds (Mann-Whitney U-test, $P < 0.002$). For *P. jordani*, the difference between 1 and 2 yr olds and older age classes was not significant (Mann-Whitney U-test, $P = 0.10$). One- and 2 yr old *P. jordani* and *P. teyahalee* (Table 2) did not differ significantly in the proportion of nights spent in retreat hole entrances (Mann-Whitney U-test, $P > 0.05$). However, all *P. teyahalee* older than 2 yr spent a significantly larger proportion of nights in retreat hole entrances than respective age classes of *P. jordani* (Mann-Whitney U-tests, all $P < 0.05$).

About half of the 2 yr olds of both species were observed in retreat holes at least once (Table 2). The difference between species was not significant (Fisher's exact $P = 0.29$). All 3 yr old and older *P. teyahalee* were observed in retreat holes at least once (Table 2). The percentages were lower for respective age classes of *P. jordani*, but only males differed significantly between species (Fisher's exact test, $P = 0.01$). Both plots had many more retreat holes than salamanders. Of the many retreat holes occupied by salamanders on the plots, none were known to have been used by more than one salamander. However, several salamanders were observed in more than one retreat hole.

DISCUSSION

The home ranges of *P. jordani* and *P. teyahalee* meet two of Brown and Orians' (1970) criteria for the spatial relationships of territorial species: home range areas are fixed, and they are mostly exclusive with respect to rivals. While low density may contribute to the exclusiveness of home ranges, and retreat hole association may contribute to overdispersion, the distance between neighboring individuals is still extremely small relative to the distance the salamanders are capable of traversing in one night. In fact, individuals of both species are physically capable of moving nearly 4 m in 1 min (Highton, 1956), which is farther than most individuals were observed to move during the entire field season. Thus, both *P. jordani* and *P. teyahalee* exhibit

TABLE 3. RESULTS OF NEAREST NEIGHBOR ANALYSIS FOR EACH AGE CLASS OF *Plethodon jordani* AND *P. teyahalee.* Distances are calculated from the geometric center of each home range. Densities are number of individuals per m². Expected mean distances between nearest neighbors are given by the formula $E(r) = 1/2\sqrt{d} + (0.051 + 0.041/\sqrt{n})L/n$, where d = density, n = sample size, and L = length of the boundary region (Donnelly, 1978). z-statistics are used to test the significance of deviations from random expectation. Probabilities (*P*) are two-tailed.

Age class	Density	Mean distance (m) Expected	Mean distance (m) Observed	*P*
Plethodon teyahalee				
2 yr olds	0.07	1.96	1.70	0.5028
3 yr olds	0.01	—	—	—
Males	0.05	2.30	3.65	0.0142
Females	0.08	1.80	2.32	0.1260
Plethodon jordani				
2 yr olds	0.13	1.41	1.67	0.2150
3 yr olds	0.08	1.80	2.25	0.1868
Males	0.06	2.09	3.22	0.0138
Females	0.05	2.30	3.82	0.0058

spatial relationships that support the hypothesis that they exhibit territorial defense of their home ranges. Behavioral observations also support the existence of territorial behavior in these species. In laboratory experiments, more than 70% of intraspecific encounters between adult *P. jordani* and *P. teyahalee* end in aggression (Nishikawa, 1985a, 1987). In natural populations, many adults have injuries caused by other salamanders, in which the imprint of the jaw is visible on the body (pers. obs.).

The estimates of home range size reported here are smaller than previously reported for these species (Highton, 1956; Madison, 1969; Madison and Shoop, 1970; Merchant, 1972), although the salamanders in the present study were monitored for an entire field season, and the home range estimates reported here are based on more recaptures per individual than any previous study in which toe-clipping was used to identify individuals (Nishikawa and Service, 1988).

Juvenile and adult *P. jordani* move farther between captures and have larger home ranges than respective age classes of *P. teyahalee.* In fact, the home ranges of *P. jordani* were more than twice as large as those of respective size classes of *P. teyahalee.* This is surprising for two reasons. First, home range size increases with body size in most species of vertebrates (McNab, 1963; Turner et al., 1969; Christian and Waldschmidt, 1984). However, *P. teyahalee* is approx. 30% larger than *P. jordani,* in terms of either body weight or SVL. Second, territory size has been observed to decrease with density in birds, due to compression of home ranges as larger numbers of individuals pack themselves into a given area (Watson, 1964). In contrast, the density of *P. jordani* was nearly twice as high as the density of *P. teyahalee.* These results suggest that spacing behavior is based on different mechanisms in these salamanders.

Species differences are confounded with site differences in this study, because each species was studied intensively at only one site. Thus, interspecific differences in spatial relationships could be partly or completely due to differences between sites. However, the few observations of *P. jordani* from the Smoky Mountains and of *P. teyahalee* from the Balsam Mountains suggest that the species differences are independent of sites. The seven Smoky Mountain *P. jordani* had large (2.93 ± 1.9 m²), overlapping home ranges and used retreat holes infrequently, and the two Balsam Mountains *P. teyahalee* had small (<0.5m²), non-overlapping home ranges that contained at least one retreat hole.

All age classes of *P. teyahalee* and *P. jordani* share on average less than 10% of total home range area with a same-age or same-sex conspecific, although the home ranges of *P. jordani* overlap to a greater extent than those of *P. teyahalee.* Only in adults were the geometric centers of home ranges farther apart than expected by chance. This pattern of spatial overlap is quantitatively similar to that exhibited by territorial birds, as exemplified by the great tit (*Parus major*), one of the best studied bird species in terms of intra-individual spatial relationships (Krebs, 1971).

Juveniles overlap to a greater extent with older conspecifics than with other juveniles, perhaps because they are not as effective in expelling older individuals and/or because they are tolerated within the home ranges of adults. The home ranges of 3 yr old *P. jordani* overlapped extensively with all ages of conspecifics. Three years may be the dispersal age, as 3 yr olds also have the lowest recapture probabilities (Nishikawa, 1985a).

For all age classes of both salamander species, the mean distance between same-aged conspecifics was greater than the mean distance moved in one night. For *P. teyahalee,* the distance between nearest neighbors was greater than the mean distance between recaptures. This suggests that, for both species, encounters between same-aged conspecifics are infrequent, and furthermore that rivals may be avoiding each other, perhaps by some sort of pheromonal advertisement. Brown and Orians (1970) pointed out that defense of a territory may include advertisement (e.g., vocalizations or scent marking) as well as overt aggression. Several studies suggest that other species of *Plethodon* use odors to induce avoidance behavior in conspecifics (Jaeger and Gergits, 1979; Dawley, 1984; Jaeger et al., 1986).

The relatively large home ranges of *P. jordani* were not associated with cover objects, retreat holes or other habitat features, and the activity of individuals was not concentrated in any particular area. Individuals of *P. teyahalee,* in contrast, exhibited a strong association with underground retreat holes. Every individual of *P. teyahalee* older than 2 yr had at least one retreat hole in its home range, and was found in a retreat hole entrance on more than 65% of the nights on which it was active. This observation can perhaps account for differences in habitats between the two species. *Plethodon teyahalee* is found in habitats that are drier and warmer on average than those of *P. jordani,* such as south-facing slopes and lower elevations (Hairston, 1951). It has always seemed peculiar that the heat and desiccation tolerance limits of the two species are very similar (Spotila, 1972), given the differences in habitat. A greater tendency toward retreat hole use by *P. teyahalee* may help to reconcile these apparently contradictory observations. By selecting microhabitats (i.e., retreat holes) that are cooler and moister than the habitat as a whole, *P. teyahalee* may be able to occupy habitats that are warmer and drier on average than those of *P. jordani.* This may also account, at least in part, for the lack of microsympatry of these species on the two plots.

Acknowledgments

This research was conducted at the Highlands Biological Station. I thank N. Hairston, Sr. and P. Service for their help during all stages of this project. I thank P. Crowley, R. Jaeger, L. Katz, and P. Service for their constructive comments on this manuscript. The research society of Sigma Xi, the Smith Fund and the Wm. R. Kenan Professorship Fund of the University of North Carolina, the Highlands Biological Station, and the Highlands Biological Foundation provided financial support for this research. I thank the US National Park Service for permission to work in Great Smoky Mountains National Park.

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Accepted 5 June 1989.