

EFFECTS OF COVER OBJECT SPACING ON THE SOCIOECOLOGY OF THE RED-BACKED SALAMANDER, *PLETHODON CINEREUS*

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ABSTRACT: Territoriality has been well-documented in terrestrial plethodontid salamanders. However, most studies of territoriality have focused either on defense of single cover objects or on defense of areas of forest floor. In nature, cover objects tend to occur in groups, and little is known about how cover-object distributions affect territory defense and salamander spatial associations. We manipulated cover-object spacing within a home range and used mark–recapture data to examine the effects of these manipulations on intra- and intersexual spatial associations in the red-backed salamander, *Plethodon cinereus*. Similar total numbers of salamanders were found in the different treatments, and salamanders moved between cover objects with similar frequency regardless of cover-object spacing. However, male spatial associations were affected by cover-object spacing, with males never found simultaneously under adjacent cover objects. Furthermore, the spatial associations of males and females differed among the cover-object spacing treatments. Males and females shared the same cover object 76% of the time when cover objects were adjacent, but only 37% of the time when cover objects were separated by 1 m. Our results suggest that *P. cinereus* often use multiple cover objects within a home range, and that males may defend these while they are using them. Additionally, males and females appear to adjust their use of cover objects with respect to the home ranges of opposite sex salamanders.

Key words: Distribution; Home range; Plethodontid; Spatial association; Territoriality

PLETHODONTID salamanders have been model systems for the study of communication and sociobiology. Species in several genera have been found to have complex communication systems involving a range of visual and chemical cues (reviewed in Jaeger and Forester, 1993). Displays and movements convey aggression or submission, and chemical signals (pheromones and allomones) allow for species, sex, and individual recognition (Jaeger and Forester, 1993). These modes of communication may contribute to spatial distributions of salamanders on the forest floor (Mathis, 1991).

Both laboratory and field studies have found evidence for territoriality in terrestrial plethodontids (Mathis et al., 1998, 2000; Thurow, 1975). Laboratory evidence suggests that both male and female salamanders may defend territories (Horne, 1988; Jaeger, 1984; Marvin, 1998a). In *Plethodon cinereus*, this territoriality appears to be present during the spring and autumn courting seasons and the summer noncourting season (Jaeger, 1979; Mathis, 1989). Territorial behavior is directed

mainly toward same-sex individuals. Jaeger (1984) demonstrated that resident male *P. cinereus* exhibited more submissive behavior and less biting toward female intruders than male intruders, and Mathis (1991) and Marvin (1998b) found that home ranges of *P. cinereus* and *P. kentucki*, respectively, are segregated intrasexually but show significant overlap with individuals of the opposite sex. Additionally, male–female pairs have been shown to codefend a territory (Jaeger et al., 1995). Within these resident pairs, each individual shows significantly more territorial aggression toward same-sex intruders (Lang and Jaeger, 2000). These observations all suggest that territorial residents may be more tolerant of opposite sex invaders than same sex ones.

Most field studies of Plethodontid salamanders have examined social interactions under single cover objects such as rocks and logs (Jaeger et al., 1995; Mathis, 1990), or within areas of forest floor (Gergits and Jaeger, 1990; Marvin, 1998b; Mathis, 1991). However, the distribution of cover objects is highly variable in space, so equivalent areas of forest floor may contain substantially different densities of rocks and logs. This variability could have important influences on the socioecology of terrestrial salamanders. For example, sala-

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manders might defend multiple cover objects when cover objects are close together, or alternatively, closely spaced cover objects might lead to smaller territories (Grover, 1998; Kleeberger, 1985). Cover-object spacing could also influence the mating behavior of salamanders. In areas with many cover objects, males and females could maintain overlapping territories while defending separate cover objects. Alternatively, males and females could prefer to share cover objects even when multiple cover objects are available. Thus, the distribution of cover objects could have a variety of effects on intersexual spatial associations.

We performed a mark–recapture study on *P. cinereus* to determine the effects of cover-object spacing on the socioecology of this terrestrial salamander. We created three spacing treatments by setting out pairs of cover boards either adjacent to one another, 5 cm apart, or 1 m apart. These distances were chosen to reflect meaningful variation for salamanders, but to still fall within the same home range for an adult *P. cinereus* (~ 4 m²; Kleeberger and Werner, 1982) so that patterns would reflect salamander behavior rather than spatial variation in abundance. Within these treatments, we measured four aspects of salamander distributions: (1) the number of unique individuals of each sex per pair of boards, (2) the relative positions of same-sex salamanders underneath pairs of boards, (3) the frequency of movement between paired boards, and (4) the relative position of opposite-sex pairs under paired boards. For each of these variables, we determined how observed distributions of salamanders differed across the three cover-board spacing treatments.

MATERIALS AND METHODS

Study Site

Our study site was located in an area of mature deciduous forest on the campus of Washington and Lee University in Lexington, Virginia, United States (37° 47' 49 N, 79° 26' 38 W). This site is located along a northeast-facing slope that rises from the Maury River to an elevation of 320 m. Previous research at this site (Marsh and Goicochea, 2003) sug-

gests that salamander densities are high and similar to those found at Mountain Lake Virginia (e.g., Mathis, 1989, 1990). Cover objects composed of raw, white oak boards (20 cm × 15 cm × 2.5 cm) were placed in pairs on the forest floor in three different treatments: “adjacent,” “near,” and “far.” The adjacent treatment consisted of two boards laid directly adjacent to one another, touching along one edge, so that they formed a single continuous cover object. In the near treatment, two boards were laid approximately 5 cm apart so they were close together yet distinct. In the far treatment, two boards were laid approximately 1 m apart. Forty-five blocks consisting of one of each of the spacing treatments were placed throughout the study site and marked with a numbered flag. Blocks were placed at least 5 m apart, but less than 15 m apart. Although we did not remove natural cover objects from the study site, cover boards were always placed more than 1 m from natural cover objects so that board-pairs were closer to each other than to any natural cover objects. Each board in a pair was also marked as either A or B so that these could be distinguished.

Cover-Object Sampling and Mark–Recapture

We surveyed cover objects during three time periods: Fall 2007, Spring 2008, and Fall 2008. The Fall 2007 surveys consisted of five dates from 4 October to 15 November 2007, the Spring 2008 surveys consisted of 10 dates from 24 April to 29 May 2008, and the Fall 2008 surveys consisted of five dates from 30 September to 4 November 2008. Surveys were always conducted at least three days apart and most surveys were conducted one week apart. On each survey date, boards were lifted and checked for the presence of *P. cinereus*. When a salamander was found under a board, it was captured and then sexed using a portable fiber-optic light (Titan Tool Supply, Buffalo, NY). We also measured snout–vent length (SVL) and marked each adult salamander (≥ 32 mm SVL) with visible implant fluorescent elastomer tags (Northwest Marine Technology, Shaw Island, WA). Two marks, one upper and one lower, were injected ventrally under the skin in one of four colors. After marking, each salamander

was released back under the board where it was captured. Because we only used 16 different marks, salamanders were individually marked within spatial blocks, but the same marks were repeated in different areas of the study site. Ultimately, our data analysis focused on behavior within a board-pair, so movement among blocks was not a major concern. Furthermore, if we did have any questions about individual identity (e.g., putative recaptures with the same mark but of different sizes or sexes), we simply removed these individuals from our analyses. This happened with 6 of 630 salamanders.

Predictions and Data Analysis

We reasoned that if one salamander could exclude other same-sex salamanders from the board-pair for an extended period of time, this would lead to reduced counts of salamanders in any treatment where such exclusion occurred. Thus, we tallied the total number of unique male and female salamanders captured under each board-pair and tested for differences among treatments using likelihood ratio tests for linear mixed models (Pinheiro and Bates, 2000). Distance treatment was a fixed effect, spatial block was a random effect, and the number of unique males or females was the response variable. The numbers of salamanders per board-pair was treated as Poisson, though counts were moderately overdispersed (variance inflation factor = 1.24 for males and 1.54 for females). Separate analyses using quasi-Akaike Information Criterion (Burnham and Anderson, 2002) instead of maximum likelihood confirmed that our assumption of Poisson-distributed counts did not affect our results.

Data on total counts provide only a broad assessment of territorial behavior because territories could shift over the course of the study. Thus, we also analyzed spatial associations of salamanders of the same sex at each capture event by determining: (1) whether the opposite board in a pair was simultaneously occupied by a salamander of the same sex, or (2) whether the opposite board was unoccupied by a salamander of the same sex. A pair of salamanders of the same sex was counted as a single data point to avoid problems of nonindependence. We reasoned that if sala-

manders exclude same-sex individuals from the opposite board in some treatments, this would produce different frequencies of occupancy across the three distance treatments. These differences were evaluated with a 2×3 Fisher's exact test (Freeman-Halton extension; Freeman and Halton, 1951); other approaches based on test statistics (e.g., Chi-square or G tests) are not generally recommended for sparse frequencies (Sokal and Rohlf, 1995).

Movement data may also reflect territoriality in that if salamanders defend an area of forest floor (as opposed to a single cover object) they might be expected to move frequently between boards. Thus, we tested differences in movement rates between boards across the three board treatments. To summarize movement data, we examined the relative positions of salamanders that were captured at least two times within the same board-pair. For salamanders that were captured more than two times, we used only the latter two captures to avoid including multiple nonindependent data points. Relative rates of movement were then compared among the three board treatments using a Fisher's exact test.

Finally, we used the relative spacing of males and females in the three distance treatments to evaluate the effects of cover-object distribution on intersexual spatial associations. For simultaneous captures of one male and one female within a board-pair, we recorded whether the male and female were found under the same board or under opposite boards. We predicted that males and females would likely inhabit opposite boards in closely spaced treatments (adjacent and possibly near boards) but that they would be more likely to share boards in the far treatment. This prediction was tested with a Fisher's exact test. All data analyses were carried out in R version 2.8.1 (R Development Core Team, 2008).

RESULTS

We captured 630 salamanders: 175 in the fall of 2007, 160 in the spring of 2008, and 295 in the fall of 2009. Across the board-spacing treatments, there were no significant differences in the total number of males ($\chi^2 = 0.5$,

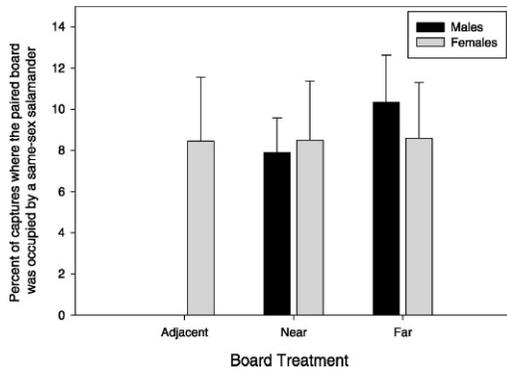


FIG. 1.—Percentage of total captures per treatment where the other board in a pair was simultaneously occupied by another salamander of the same sex. Error bars show SD based on a binomial. Percentages did not differ significantly between treatments for females, but did differ for males.

$P = 0.74$) or females ($\chi^2 = 1.6$, $P = 0.33$) encountered. A mean of 1.14 ± 0.14 SE males were observed in the adjacent boards, 1.21 ± 0.21 males in the near boards, and 1.25 ± 0.21 males in the far boards. For females, mean counts were 2.93 ± 0.30 in the adjacent boards, 2.61 ± 0.29 in the near boards, and 2.59 ± 0.34 in the far boards.

When we examined the occupancy patterns for each capture, we found no effect of board-spacing treatment on the distribution of female salamanders (Fisher's exact test, $P = 0.99$). When one board was occupied by a female, the other board was occupied 8.5% of the time in the adjacent treatment (11 out of 130), 8.5% of the time in the near treatment (9 out of 106), and 8.6% (8 out of 93) of the time in the far treatment (Fig. 1) by another female. For males, however, board spacing did have an effect on occupancy of the paired board (Fisher's exact test, $P = 0.04$). When one board was occupied by a male, the other board was never occupied in the adjacent treatment (0 of 55), but was occupied 7.9% (3 of 38) of the time in the near treatment and 10.3% (6 of 58) of the time in the far treatment (Fig. 1) by another male.

Board spacing did not significantly affect the tendency of salamanders to move between boards from one capture to the next (Fisher's exact test, $P = 0.62$). Salamanders moved between boards 27.3% of the time (6 of 22 recaptures) in the adjacent treatment, 40.0%

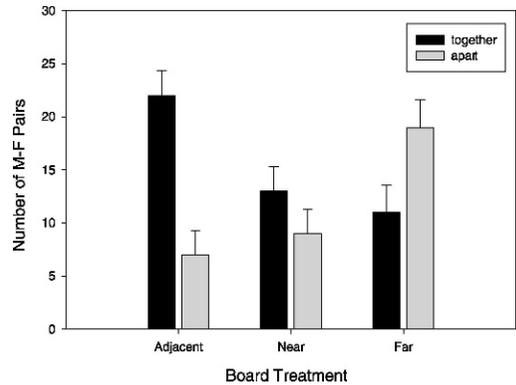


FIG. 2.—Number of times one male and one female were found together under the same board in a pair versus the number of times a M-F pair was found apart (i.e., one under each board in the pair) in each of the three board-spacing treatments. Error bars show SD based on a binomial. The three treatments differed significantly in relative positions of M-F pairs.

of the time in the near treatment (6 of 15 recaptures), and 25.0% of the time (5 of 20 recaptures) in the far treatment.

Finally, board spacing had strong effects on the tendency of male-female pairs to share the same board within a board-pair (Fisher's exact test, $P = 0.008$; Fig. 2.). Males and females were found under the same board 75.9% of the time in the adjacent treatment (22 of 29 pairs), 59.1% of the time in the near treatment (13 of 22 pairs), and 36.7% of the time in the far treatment (11 of 30 pairs, Fig. 2).

We have previously found that sampling cover boards more frequently than once per week, as we did during the spring survey period, can potentially influence salamander occupancy (Marsh and Goicochea, 2003). Thus, we reanalyzed our data excluding the spring survey period. Again, we found no effects of board spacing on the total numbers of males or females ($P = 0.58$ and $P = 0.75$ respectively), on patterns of occupancy by females ($P = 0.84$), or on movement rates between boards ($P = 0.19$). Our positive results also remained the same in this follow-up analysis: males once again were never found sharing adjacent boards ($P = 0.046$) and male-female pairs were more likely to share the same board when boards were closer together ($P = 0.006$).

DISCUSSION

Territoriality has been well-documented in terrestrial salamanders. Although many factors such as prey availability, salamander density, and geographic variation may affect levels of territoriality in natural populations (Gabor and Jaeger, 1995; Kleeberger, 1985; Mathis, 1989), our study explored the effects of cover-object spacing. For some of the response variables examined, we found similar patterns of cover-object use across spacing treatments. Similar numbers of salamanders were found in the adjacent, near, and far treatments, and individuals moved between cover boards with relatively equal frequency in all three treatments. Patterns of occupancy by female salamanders were not influenced by cover-object spacing, though these patterns did differ across treatments for male salamanders. In addition, males and females were much more likely to be sharing the same board in the adjacent treatment than in the more distant cover-board spacing treatments.

Our cover-board spacing treatments were designed to fall within the same home range ($\sim 4 \text{ m}^2$ for adult *P. cinereus*; Kleeberger and Werner, 1982), and the lack of an effect for salamander numbers or movement rates make sense in this context. In a previous mark-recapture study of red-backed salamanders, Bailey et al. (2004) found that adults alternate periods of surface activity with periods of temporary emigration, presumably to underground retreats. Although we did not formally test for temporary emigration, we observed broadly similar patterns in our study, with 80% of occupied boards sheltering more than one female over the course of the study and 48% sheltering more than one male. Additionally, only 3% of marked salamanders were recaptured under the same group of cover boards in subsequent seasons. Thus, salamanders appeared to emigrate from cover boards regularly rather than monopolizing a single cover board over the course of the study. As a result, cover-board spacing was not particularly important for predicting the total number of salamanders observed.

Even during periods of surface activity, salamanders moved regularly between cover boards; about 30% of our recaptures represented movements between paired boards.

Similarly high rates of movements between closely spaced boards were observed by Gillette (2003) under experimental cover boards and by Gergits and Jaeger (1990) under natural cover objects. Although red-backed salamanders appear to rarely disperse more than a few tens of meters (Cabe et al., 2007), movements between cover objects within a home range appear to be frequent regardless of the precise spacing of cover objects.

Effects of cover-board spacing on occupancy patterns appeared to differ between females and males. For females, the presence of a female under one board did not influence the probability of finding a female under the paired board across spacing treatments. For males, paired boards in the adjacent treatment never sheltered one male under each board, whereas occupancy of both boards by males was sometimes observed ($\sim 9\%$ of the time) in the near and far treatments. This latter result should be interpreted somewhat cautiously because it was based on a small number of male-male captures (9 in the near and far treatments versus 0 in the adjacent treatment). Nevertheless, this result is consistent with the territorial behavior of males observed in previous studies using single cover objects (e.g., Mathis 1990). Furthermore, although we made no a priori predictions about multiple captures under a single board, our data on board sharing appear to parallel the sex differences observed in terms of occupancy patterns within a board-pair. Over the course of our study, females were found together under the same cover object 22 times, whereas males were found together on only three occasions.

Spatial associations of male and female salamanders differed across treatments in that we found significantly more male-female pairs under a single board in the adjacent treatment compared to the other treatments. This finding was somewhat surprising because it is not clear why males and females in the adjacent treatment would prefer to share the same board given that the board-pair might be viewed as a single large cover object. Even in retrospect, it is not obvious why males and females would be more likely to be found together in this treatment. If one sex defended

the adjacent boards as a single large cover object and the other was attracted to these larger cover objects, one would still not necessarily expect to see both salamanders on the same side of the board. It is possible that because our data were taken during the courtship season, males and females want to be in close proximity to each other and this is facilitated with adjacent cover objects. With the far boards, it is conceivable that males and females have some difficulty finding one another, which would account for the tendency of males and females to be separated in this treatment. It is also possible that some additional feature of salamander socioecology explains the observed pattern.

One complicating factor in interpreting our results is that adjacent boards could make for better territories because they effectively consist of a single large cover board, and red-backed salamanders may prefer larger cover objects (Mathis, 1990; though not Gabor, 1995). It is therefore possible that our experimental manipulations altered territory quality and not just cover-board spacing. This scenario predicts that in adjacent treatments, the largest salamander captured should be larger than in the other treatments. In fact, we found no difference in the maximum SVL of salamanders captured in the adjacent treatment versus the near or far treatments ($F_{2,104} = 0.82$, $P = 0.45$ for males, $F_{2,196} = 2.42$, $P = 0.09$ for females with a trend toward larger salamanders in the far treatment). This suggests that differences in territory quality are unlikely to complicate the interpretation of our results.

Several other alternative explanations for our results need to be considered. One is that boards were new cover objects and, thus, salamanders did not really defend them. Cover objects were placed on the forest floor in August 2007 and we began sampling only several weeks after this. Although the number of captures did increase over the course of the study, the observed patterns of behavior did not. In comparing results for the four observed variables, in no case were the results from Fall 2008 significantly different from the results from Fall 2007. Moreover, as noted above, Gergits and Jaeger (1990) surveyed natural cover and observed similar results in

terms of rates of movement between closely spaced cover objects.

A second possibility is that cover boards are not considered high-quality cover objects by salamanders. Two lines of evidence appear to argue against this. First, at this same site, we found larger salamanders under these cover boards than under natural cover objects sampled at the same time (Marsh and Goicochea, 2003). Second, Gillette (2003) found strong evidence of territoriality under similar cover boards near Mountain Lake Biological Station in Virginia, where most research under natural cover objects has also been carried out (Mathis, 1989, 1990, 1991).

Although our experiment was not explicitly designed to determine the nature of red-backed salamander territoriality, our results appear to be inconsistent with a scenario in which territory defense is tightly linked to a single cover object. Movements between boards in a pair were relatively frequent from one capture to the next and salamanders did not appear to monopolize cover objects over the duration of the study. Based on the low frequency of board-sharing under a single board or under two adjacent boards, males did appear to defend cover boards while they were under them. Nevertheless, equivalent total numbers of males were found under the adjacent boards as compared to the other spacing treatments over the course of our study, suggesting that any defense of a single cover object is likely transient. Similar scenarios for salamander territoriality have previously been described by Nishikawa (1990) for *P. teyahalee* and *P. jordani* and by Ovaska (1993) for *P. vehiculum*. Though comparative data on more species are still needed, this type of territoriality may turn out to be somewhat general for terrestrial Plethodontid salamanders.

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