AN ABSTRACT OF THE THESIS OF

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Abstract approved:

Plethodon albagula, the western slimy salamander, was examined during the non-breeding and breeding seasons for three aspects of territorial behavior: self-advertisement, aggression toward intruders, and ability to exclude intruders from artificial feeding territories in the laboratory. Individuals exhibited no ability to distinguish among substrates marked with tap water, conspecific fecal pellets, and self-produced fecal pellets. I concluded that this species does not recognize individual odors found in fecal pellets and may use vision or an unknown method of self-advertisement in territories.

When paired as residents and intruders, resident salamanders performed more aggressive behavior than intruders in the form of biting and moving toward the other animal. Intruders spent more time in submissive behavior, moving up the side of the testing chamber, than residents. Data collected during the non-breeding and breeding seasons indicated that male-male aggression escalated during the breeding season as competition for mates increased, whereas aggression between males and females decreased at this time. Female-female aggression remained low during both seasons. From these date I concluded that residents do show aggression toward conspecific intruders and have a high probability of excluding these intruders from their territories. In summary, this

research provides laboratory evidence for territorial behavior in *Plethodon albagula*.

TERRITORIAL BEHAVIOR IN THE SALAMANDER *PLETHODON ALBAGULA*

A Thesis

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by

Heather Dawn Forster

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Lynnette Sievert
Approved by Major Advisor

Greg Sievert
Approved by Committee Member

David Edds
Approved by Committee Member

Approved by Committee Member

Approved for Division of Biological Sciences

Timothy M. Downs
Approved for the Graduate Council

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PREFACE

Traditionally, animal behavior research has focused on mammalian and avian taxa. However in the past twenty years, previously understudied vertebrate groups have received increased attention. One such group is the salamanders (Class Amphibia, Order Caudata). Ethologists have discovered many complex social behaviors in these animals. My research focuses on one of the most important salamander behaviors, territoriality, and its changes between the breeding and non-breeding seasons.

My thesis has been prepared in a style appropriate for the journal Copeia published by the American Society of Ichthyologists and Herpetologists.

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The family Plethodontidae is the most speciose extant salamander family, comprised of over 250 species (Pough et al., 1998). Plethodontid salamanders can be numerous in nature, making up the largest proportion of vertebrate biomass in many woodland ecosystems (Burton and Likens, 1975). These animals are lungless and obtain all oxygen by gaseous exchange across the skin and buccal cavity (Pough et al., 1998). The plethodontid genus *Plethodon*, the woodland salamanders, in addition to being lungless, exhibits direct development with no aquatic larval stage and is completely terrestrial (Pough et al., 1998). This allows a female *Plethodon* to lay eggs on land and brood her clutch throughout development (Bachmann, 1984). The use of cutaneous respiration by plethodontids requires moist skin at all times, and during dry periods these animals are forced to retreat to patches of moisture beneath rocks and logs (Jaeger, 1980). Laboratory and field evidence indicate that many plethodontid species defend such cover objects as territories.

A territory is a defended area used by an animal for one or a combination of purposes (Brown and Orians, 1970). Gergits (1982), through his work with *Plethodon*, developed four essential characteristics for an animal to exhibit territoriality: (1) site tenacity, (2) self-advertisement, (3) defense of a home range, and (4) expulsion of intruders from the home range. Site tenacity has been measured in plethodontids by observing the occupancy of a fixed area. *Plethodon jordani*, *Plethodon oconaluftee* (Nishikawa, 1990), *Plethodon glutinosus* (Wells and Wells, 1976), *Plethodon cinereus* (Gergits and Jaeger, 1990a), *Plethodon kentucki* (Marvin, 1998a), and *Plethodon vehiculum* (Ovaska, 1988a) reside in stable home ranges in nature. Additionally, displaced *P. cinereus* (Gergits and Jaeger, 1990b) and *P. jordani* (Madison and Shoop, 1970) exhibit some ability to return to their original home ranges.

The second characteristic of territoriality, self-advertisement, appears to be accomplished in some *Plethodon* species through the use of pheromones deposited on the substrate. Pheromones of *P. cinereus* are produced in serous glands located posterior to the cloaca in adults and juveniles of both sexes (Simons and Felgenhauer, 1992; Simons et al., 1995). They are deposited by pressing the mid-ventral tail region against the substrate or passing the tail over a fecal pellet (Simons et al., 1994). Pheromonal cues can be sampled by touching the snout to the chemical-laden surface and allowing transmission of chemicals via capillary action along the nasolabial grooves to the internal nares. Here the chemicals come in contact with the vomeronasal organ and associated chemosensory structures (Dawley and Bass, 1989).

Behavioral evidence for the use of pheromones as territorial markers indicates this practice is widespread in *Plethodon*. Laboratory tests with *P. cinereus*, *Plethodon shenandoah* (Jaeger and Gergits, 1979), *P. vehiculum* (Ovaska, 1988b), *Plethodon dunni* (Ovaska and Davis, 1992), and *Plethodon serratus* (Mathis et al., 1998) suggest the ability to distinguish between self-marked and conspecific-marked substrates, or between own and conspecific fecal pellets. *Plethodon glutinosus*, *P. oconaluftee*, and *P. jordani* are able to recognize individual, sex-specific, and species-specific airborne odors (Dawley, 1984). In species that have been shown to recognize chemical cues, pheromones may provide a weak warning against territory intruders (Simons et al., 1997). Conversely, *Plethodon ouachitae* (Anthony, 1995), *Plethodon vandykei* (Ovaska and Davis, 1992), and *Plethodon dorsalis* (Dahlgren, 1996) exhibited no evidence of ability to recognize conspecific territorial pheromones.

Site defense and aggressive behavior in salamanders, the third requirement of territoriality, was first documented in the plethodontids *Hemidactylium scutatum* and *Eurycea bislineata* (Grant, 1955). Laboratory studies provided evidence for site defense in *P. cinereus* (Jaeger, 1981; Jaeger et al., 1982), *P. dorsalis* (Dahlgren, 1996), *P. dunni* (Ovaska, 1993), *P. serratus* (Mathis et al., 1998), *P. ouachitae* and *Plethodon albagula* (Anthony et al., 1997), *P. kentucki* (Marvin, 1998b), and *P. jordani* (Selby et al., 1996). Aggressive interactions between conspecifics have been observed in nature for *P. cinereus* (Gergits and Jaeger, 1990a) and *P. jordani* (Hutchison, 1959). Aggression occurs through intimidation such as the all-trunk raised posture observed in many small *Plethodon*, moving or looking toward the other animal, or through physical attack such as biting and chasing (Jaeger, 1984).

Expulsion of intruders, the final criterion for territoriality, has been indirectly measured in *Plethodon* through field experiments in which residents of home ranges are removed from their areas. New, often smaller, individuals of *P. cinereus* (Mathis, 1990a), *P. kentucki* (Marvin, 1998a), and *P. ouachitae* (Anthony, 1995) move in to the vacated home ranges. The authors feel their results indicate previous expulsion of the new, smaller residents by the now-absent original residents.

For territoriality to be maintained in a population, individuals pursuing a territorial strategy must exhibit higher fitness than those who are non-territorial. Territorial defense can be costly, and may result in loss of fat stores through tail autotomy or scarring of the nasolabial grooves used for prey location in addition to pheromone detection (Jaeger, 1981). However, resources critical for an individual's survival are rarely distributed randomly in nature and territoriality allows an individual to monopolize all critical resources within a specified area (Gergits, 1982). Critical resources for plethodontids are moist patches beneath rocks and logs which prevent desiccation, high quality invertebrate prey beneath cover objects (Gabor and Jaeger, 1995; Mathis, 1990b), access to potential mates (Mathis, 1991), retreat holes (Marvin, 1998a; Nishikawa, 1990), oviposition sites (Hairston, 1981), or a combination of various resources (Heatwole, 1962).

Territoriality can be expected to regulate spacing of individuals in their habitat. Field studies of *P. cinereus* (Gergits and Jaeger, 1990*b*), *P. jordani*, *P. oconaluftee* (Nishikawa, 1990), and *P. kentucki* (Marvin, 1998*a*) indicate that spacing of individuals is associated with that of a critical resource. Conversely, *P. vandykei*, though exhibiting a high degree of site tenacity, often cohabitates with conspecifics (Ovaska, 1988*a*). Laboratory tests of pheromonal recognition and site defense also indicate that *P. vandykei* is non-territorial (Ovaska and Davis, 1992).

Contribution to the gene pool is the ultimate measure of an individual's fitness and thus the role of territoriality in mediating conspecific intersexual interactions is of particular interest. Field and laboratory studies provide evidence that male and female *P. cinereus* maintain exclusive territories during both the breeding and non-breeding seasons (Mathis, 1989). Defense of a territory during the breeding season can provide benefits above those enjoyed during the rest of the year. In the laboratory, fecal pellets of male *P. cinereus* fed high-quality diets (associated with a high-quality territory) are preferred by gravid female conspecifics. Males containing high-quality prey items in their stomachs possess territories that overlap with more female territories than males consuming poor quality prey items (Walls et al., 1989). Male *Desmognathus fuscus* preferentially court larger (more fecund) females, and these large body sizes may be in part attributed to high quality prey located within the females' territories and are thus an indication of the females' territory qualities (Verrell, 1994). To increase the potential for intersexual contact despite territoriality individual *P. jordani*, *P. oconaluftee* (Nishikawa, 1990), and *P. kentucki* (Marvin, 1998a) allow territory overlap with members of the opposite sex. Behavioral changes in aggression also commonly occur to facilitate courtship. Laboratory studies showed gravid female *P. cinereus* exhibited decreased aggression toward male intruders in their territory (Horne, 1988) and male *P. cinereus* in nature were observed entering females' territories in a submissive posture during the breeding season (Gergits and Jaeger, 1990a). Aggression between male *P. vehiculum* escalated as competition for mates increases during the breeding season (Ovaska, 1987).

The purpose of this research was to examine territoriality in the western slimy salamander, *Plethodon albagula.* Originally described as a subspecies of *P. glutinosus* from Bexar County, Texas (Grobman, 1944), *P. albagula* is today comprised of the type-locality population plus a wide-ranging allopatric population in the Ozark and Ouachita Mountains of Oklahoma, Missouri, and Arkansas based on the electrophoretic evidence of Highton (1989). *Plethodon albagula* is found in moderately moist deciduous woodland habitats with leaf litter-covered ground. During our collection of animals, individuals were encountered beneath large rocks or logs on slopes underlain by a complex network of talus material.

I tested *P. albagula* for three of Gergits' (1982) criteria for territoriality: self-advertisement, aggression toward intruding conspecifics, and ability to expel intruders from artificial feeding territories in the laboratory. Based on behavior observed in other eastern *Plethodon* and those species most closely related to *P. albagula*, I predicted that when given a choice between blank, own-marked, or conspecific-marked substrates, *P. albagula* would avoid substrates marked by conspecific fecal pellets. During resident-intruder interactions, I predicted (1) residents would exhibit aggressive behavior toward intruders, (2) residents would have a high probability of expelling intruders, (3) intrasexual aggression would increase during the breeding season, and (4) intersexual aggression would decrease during the breeding season.

MATERIALS AND METHODS

Plethodon albagula were collected in March and October 1997, in Delaware County, Oklahoma, and Carroll County, Arkansas. Animals were placed in plastic bags with damp paper towels for transport to the laboratory. Salamanders were housed individually in round plastic containers with one damp and one dry paper towel, at 20 C on a 14 L: 10 D (May to August) or a 12 L: 12 D (March to May and September to February) photoperiod. Paper towels were changed weekly or as needed. Animals were offered mealworms (*Tenebrio molitor*) or small crickets (*Acheta domestica*) two to three times per week.

SELF-ADVERTISEMENT.-- Detection and avoidance of feces were tested by allowing animals to choose between substrates marked by same-sex fecal pellets, self-produced fecal pellets, and water during the non-breeding season (January to February 1998). Testing chambers were identical to those used for habitation of salamanders during the non-testing period, 20 cm in diameter, 10 cm in depth . The bottom of each chamber was lined with two half-circles of Whatman brand filter paper. The half-circles were separated by about 3 mm of bare plastic to prevent diffusion of molecules between them. Each paper was marked either with 5 mL of tap water or a solution prepared by mixing one mashed fecal pellet with 5 mL of tap water and spreading this over the paper. The pellet was obtained from either the salamander's own habitation chamber or that of a same-sex individual, and all pellets were less than approximately two days old. The following combinations of substrates were used: blank-blank (control), conspecific-blank, or conspecific-own.

Tests were performed from 2000 to 2400 hours CST. Immediately after preparing each testing chamber one individual was placed in the center of the arena beneath an opaque habituation dish (10 cm diameter ,2 cm deep) for 20 minutes. After this time, the dish was removed, the lid was placed on the chamber, and the animal's movements were observed. The total amount of time spent on each substrate was recorded during periods which the animal was not in motion for at least one minute. The animal's choice was the side on which it rested the longest. Illumination was provided by a 40-watt light directed away from the testing chamber. Data were analyzed using a chi-square test where $\alpha = 0.05$, to examine whether sides were chosen randomly (Zar, 1996).

SITE DEFENSE AND INTRUDER EXPLUSION.-- Aggressive behavior was examined using resident-intruder pairs in a testing chamber. Each animal was tested twice: once as a territory resident and once as an intruder to a territory. No two animals met twice, and a minimum of three weeks elapsed between testing an individual. Differences in body size have been shown to affect aggressive behavior in *P. cinereus* (Mathis, 1990a), therefore each *P. albagula* pair was matched for SVL and total body length, usually to within 5 mm. Forty-five pairs of animals were tested during the non-breeding season: 15 male-male, 15 female-female, and 15 male-female (8 male resident-female intruder and 7 female resident-male intruder) pairs. Forty-one different pairings were made during the breeding season: 15 male-male, 15 female-female, and 11 male-female (6 male resident-female intruder and 5 female resident-male intruder) pairs.

Testing occurred from June to August 1997 (non-breeding season) and during November and December 1997 (breeding season) between 2000 and 2400 hours CDT (non-breeding) or CST (breeding). Some animals were tested during both seasons. Test animals were housed in rectangular plastic testing chambers (35 x 25 x 12 cm) lined with damp Whitman brand filter paper and a crumpled dry paper towel for six to seven days to allow each animal to mark its territory with skin residues and feces. No paper towel refuge was available during testing to prevent the salamanders from hiding from one another, therefore the crumpled towel was removed from each chamber 24 hours prior to testing to allow for habituation to its absence. During testing dim illumination was provided by a 40-watt light bulb directed away from the testing arena. Each salamander was removed from its chamber and either replaced in its own chamber (resident) or placed into another animal's chamber (intruder), so that two animals, a resident and an intruder, were present in each testing chamber. Handling both salamanders served to eliminate stress differences between the two animals due to human contact. Both animals were placed individually under plastic opaque habituation dishes (10 cm diameter, 2 cm deep) in the testing chamber for 20 minutes. After this time, the dishes were removed, a sheet of transparent Plexiglas was placed over the chamber, and behaviors were observed for 20 minutes. Individual salamanders were identified by their unique dorsal and lateral spot patterns.

Aggressive and submissive actions of both salamanders were recorded for each trial. Biting was used to measure aggression. Moving towards (MT) the other animal was also recorded because this is regarded as a sign of aggression in some other *Plethodon*, but I did not use it as a measure of aggression. The frequency of performance of the behaviors by each salamander was recorded as well as which animal performed the behavior first during the trial. For biting, the region of the body towards which the bite was directed was also noted. Submissive behavior was indicated by escape, during which a salamander moved up the side of the chamber and often pressed its snout against the chamber lid. Total amount of time spent by each individual in escape behavior was used to measure submission. Number of times each individual performed escape and the individual which performed escape first during each trial were recorded, but these data were not used as a measure of submission.

Differences in behavior between residents and intruders within and between testing seasons were analyzed using a *t*-test assuming unequal variances (Zar, 1996). Data were analyzed for each trial type (male-male, female-female, and male-female) and for all classes combined. A Kruskal-Wallis analysis of variance was used to test for differences in behaviors among residents and among intruders in male-male, female-female, and male-female within a testing season. The Kruskal-Wallis test was followed by Dunn's multiple comparison test (Zar, 1996). To determine whether biting was randomly directed or aimed at certain body regions, a chi-square test (Zar, 1996) was used. Based on mean animal measurements (N = 40), the head accounted for 4% of total body length, the trunk 44%, and the tail 52%. All tests were considered significant at $\alpha = 0.05$.

RESULTS

SELF-ADVERTISEMENT. -- Salamanders did not differ significantly in the amount of time spent on unmarked (blank), self-marked, or conspecific-marked substrates. In trials during which both half-circles of filter paper were unmarked (control), 58.3% of animals spent more of the 20-minute testing period on the left side of the chamber than on the right side ($x^2 = 2.76$, df = 1, $P = 0.097$). When given a choice between unmarked filter paper and that marked by conspecific fecal pellets 53.6% of salamanders spent more time on the unmarked paper and 46.4% rested more frequently on the conspecific-marked substrate ($x^2 = 0.52$, df = 1, $P = 0.472$). In self-marked versus conspecific-marked substrate choice tests, 57.7% of salamanders preferred the self-marked paper and 42.3% spent more time on conspecific-marked paper ($x^2 = 2.37$, df = 1, $P = 0.124$).

SITE DEFENSE AND INTRUDER EXPULSION . -- During the non-breeding season eight of 45 residents (17.8%) delivered a total of 43 bites (mean = 5.4 ± 1.80 per trial). During three of 45 trials (6.7%) intruders bit a total of 25 times (mean = 3.9 ± 2.27 per trial). No intruder bit during a trial in which the resident did not also bite. Number of bites inflicted did not differ significantly between residents and intruders ($t = 0.517$, df = 13, $P = 0.614$). Residents bit first seven times, and intruders bit first one time. This difference was highly significant ($t = 4.243$, df = 14, $P < 0.001$). The single incident during which an intruder initiated biting occurred when a female intruder bit a male resident lightly on the tail. The male did not respond immediately, as was frequently observed in other trials, but did perform aggressive biting later in the trial. Biting occurred twice in male-male pairs (13.3% of 15 male-male trials), once in female-female tests (6.7%), and five times between males and females (33.3%; Appendix, Table 1).

Biting increased in frequency during the breeding season, occurring in 15 of 41 trials (36.6%). Fifteen residents bit 120 times (mean = 9.9 ± 2.02 per trial) and fifteen intruders bit 116 times (mean = 8.9 ± 2.16 per trial). Number of bites inflicted did not differ between residents and intruders ($t = 0.260$, df = 26, $P = 0.797$), nor did number of bites differ significantly between the testing seasons ($t = 1.210$, df = 20, $P = 0.240$ for residents; $t = 1.316$, df = 18, $P = 0.204$ for intruders). As during the non-breeding season, residents during the breeding season bit first significantly more often than intruders ($t = 3.606$, df = 24, $P < 0.001$). Intruders bit first in one female-female pair and one male-female pair (female intruder). Residents did not bite more during the non-breeding season than during the breeding season ($t = 0.824$, df = 18, $P = 0.421$), nor did intruders bite more during the non-breeding season than during the breeding season ($t = 0.054$, df = 14, $P = 0.958$). Biting occurred in 13 male-male pairs (86.7%), one female-female pair (6.7%), and one time between a male and female (9.1%) during the breeding season (Appendix, Table 1).

Results of a chi-square analysis indicated that bites were distributed non-randomly along the length of the salamanders' bodies ($x^2 = 1277.59$, df = 2, $P < 0.001$). The head was the target of 74% of bites though it comprised only 4% of body length. Eighteen percent of bites were directed toward the trunk of the body, which made up 44% of body length. The tail, which comprised slightly more than half of the salamander body length, received only 8% of the bites.

Residents and intruders within each of the trial types (male-male, female-female, or male-female) did not differ significantly in the number of times they performed MT during the non-breeding season. However when all trials were analyzed together residents performed MT significantly more often than intruders ($t = 2.346$, df = 68, $P = 0.022$). No difference was detected between residents and intruders in who performed MT first during a trial within female-female ($t = 0.807$, df = 27, $P = 0.427$) or male-female ($t = 0$, df = 28, $P = 1.000$) pairs, or when all trials were analyzed together ($t = 1.835$, df = 86, $P = 0.070$). Residents performed MT first more frequently than intruders during male-male trials ($t = 2.683$, df = 24, $P = 0.014$; Appendix, Table 2).

During the breeding season residents performed more MT than intruders in male-male pairs only ($t = 2.409$, df = 15, $P = 0.029$). No differences were detected in which salamander performed MT first during a trial for any trial type or when all data were analyzed together. No significant differences were found when comparing MT frequency or initiation among residents of male-male, female-female, and male-female pairs, or when comparing intruders among the three testing groups during either the non-breeding or breeding seasons. Additionally, no differences were found between non-breeding and breeding season residents or between non-breeding and breeding season intruders for frequency of MT performance or initiation of MT during a trial (Appendix, Table 2).

Intruders moved up the side of the testing chamber more frequently than residents during the non-breeding season in male-female pairs only ($t = -2.244$, df = 28, $P = 0.033$). There were no significant differences in who performed escape behavior first during a trial between residents and intruders in any testing group or for all trials combined. Intruders spent more cumulative time in escape behavior than residents in all trial types. This difference was significant for male-female pairs, in which intruders spent a mean of 10.9 ± 1.72 min in escape behavior, and residents spent a mean of 5.0 ± 1.70 min of the 20-minute testing period in escape behavior ($t = -2.420$, df = 28, $P = 0.022$). Time spent in escape was also significantly greater for intruders when all data were combined (intruder mean = 10.4 ± 0.90 min, resident mean = 7.1 ± 1.10 min; $t = -2.269$, df = 86, $P = 0.026$; Appendix, Table 3).

During the breeding season intruders attempted escape more often per trial than residents in male-male pairs ($t = -2.252$, df = 25, $P = 0.033$). No significant differences were found between residents and intruders in which salamander performed escape first during a trial for any trial type or for all trials combined. However, intruders spent significantly more time in escape behavior than residents in male-male ($t = -4.751$, df = 23, $P < 0.001$) and female-female pairs ($t = -3.149$, df = 20, $P = 0.005$), and when all trials were analyzed together ($t = -3.105$, df = 76, $P = 0.003$). Number of times escape was attempted differed significantly when I compared intruders from male-male, female-female, and male-female pairs ($H = 7.012$, df = 38, $P = 0.030$; Dunn's multiple range test, $P > 0.05$). Residents from the male-male, female-female, and male-female trials differed significantly in the amount of time spent in escape during the breeding season ($H = 12.793$, df = 38, $P = 0.002$; Dunn's multiple range test, $P < 0.05$ for all comparisons).

No differences were found in the number of times escape was attempted between residents during the non-breeding season and residents during the breeding season, or between intruders during the two seasons. Residents attempted escape first more frequently during the breeding season than during the non-breeding season in male-female pairs ($t = 2.296$, df = 18, $P = 0.034$). Additionally, residents spent more time performing escape behavior during the breeding season than during the non-breeding season in male-female pairs ($t = 2.448$, df = 17, $P = 0.026$). Intruders performed escape behavior first during a trial more frequently during the non-breeding season than during the breeding season in male-female pairs ($t = -2.296$, df = 18, $P = 0.034$) and when all trial types were combined ($t = -6.415$, df = 63, $P < 0.001$). Intruders spent more time performing escape behavior during the breeding season than during the non-breeding season in female-female pairs ($t = 2.446$, df = 23, $P = 0.022$; Appendix, Table 3).

DISCUSSION

Results obtained from intraspecific resident - intruder pairs of *P. albagula* provide evidence for two of Gergits' (1982) criteria of territoriality: site defense and expulsion of intruders. Resident *P. albagula* initiated aggression, in the form of biting, significantly more often than did intruders, and intruders spent more time attempting to escape from the testing chamber, indicating successful expulsion of the intruders by the residents. These results are consistent with those previously obtained for *P. albagula* from the Ouachita Mountains (Anthony *et al.*, 1997).

Two-sided choice experiments of chemical avoidance yielded no evidence that *P. albagula* recognizes conspecific odors. These results are consistent with those of Anthony (1995), in which male *P. albagula* did not show any avoidance or preference for artificial burrows marked with the whole fecal pellets of conspecifics or with mud "pseudopellets." Pheromonal markers elicit only a weak avoidance response in *P. cinereus* (Simons et al., 1994), and may not be used in mediating territorial interactions in *P. albagula*. Alternatively, *P. albagula* may not deposit pheromones in fecal pellets.

Aggression was present, but low, during the non-breeding season in same-sex pairs, but moderately high between males and females. Partially overlapping male-female territories have been observed year-round in other *Plethodon* (Marvin, 1998a; Mathis, 1989; Nishikawa, 1990), and the intersexual aggression I observed during the non-breeding season may be a result of these overlaps if *P. albagula* is distributed in a similar manner in nature. *Plethodon* *albagula* may not often encounter adult same-sex conspecifics outside of courtship periods, but male-female contact may be frequent.

Results of male-male testing pairs were similar to those obtained by Anthony et al. (1997) for male *P. albagula* from the Ouachita Mountains during the spring (non-breeding season). Anthony et al. (1997) found biting in a higher proportion of trials (48% versus 13.3% in this study). Differences may exist in aggression levels of male *P. albagula* between the spring and fall, though neither season involves breeding activity by males. Additionally, *P. albagula* used by Anthony et al. (1997) were obtained from a portion of the species' range in which *P. albagula* is sympatric with highly-aggressive *P. ouachitae* (Anthony et al., 1997), but the animals used in my study were from the Ozark Mountain portion of the species' range and are sympatric with only the smaller congener *Plethodon angusticlavius* (Highton, 1997). Thus the intensity of aggression exhibited by *P. albagula* may be influenced by interspecific interactions as well as intraspecific ones.

Breeding season had a strong influence on aggressive behavior. Though female-female aggression remained low, aggression between males increased dramatically. This follows the pattern observed by Ovaska (1987) for *P. vehiculum*. The operational sex ratio of *P. albagula* is unknown, but is male-biased in *P. kentucki* (Marvin, 1998a). If *P. albagula* also exhibits a male-biased operational sex ratio, increased male-male aggression during the breeding season can be interpreted as a result of competition for mates in addition to territories. Competition among females related to reproduction is likely for oviposition sites. *Plethodon albagula* probably oviposit in the spring (R. Highton, pers. comm.) and thus spring would be the time expected for increased female-female aggression, if it occurs.

Male-female aggression decreased during the breeding season, as seen in field and laboratory for *P. cinereus* (Horne, 1988; Thomas et al., 1989; Gergits and Jaeger, 1990a). Decreased aggressive behavior between the sexes is vital to allow mating opportunities. Breeding season tests of *P. albagula* yielded results that were qualitatively, as well as quantitatively, different from those in the non-breeding period. Females spent large amounts of time on the side of the testing chamber, seemingly in escape behavior, and were often approached by the males. The male soon rested next to her, their bodies touching. Several males were observed tapping their snouts along the females' bodies, but none attempted to rub his mental gland on the female's skin, an initial phase of courtship behavior (Arnold, 1977). Snout tapping may be a very early stage of courtship, but, in general, *Plethodon* species exhibit a low propensity to mate in the laboratory (A. Mathis, pers. comm.). Alternatively, snout tapping may be a show of non-aggression, as it was observed occasionally during both seasons in female-female pairs. Thus during the breeding season, the interactions between males and females were dependent not on residency status, as was the case during the non-breeding season and in same-sex pairs during both seasons, but instead were a result of the salamanders' sex.

These experiments provide laboratory evidence for site defense and expulsion of intruders, two characteristics of territoriality. Though the expected method of self-advertisement through pheromonal marking was not observed in this research, *P. albagula* possibly uses vision or an undiscovered method for advertising its presence in territories. Studies on site tenacity by *P. albagula* and distribution of individuals in nature would be useful for further elucidating the role of territoriality in the social interactions and spacing of *P. albagula*.

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APPENDIX

Table 1. Frequency of biting by *Plethodon albagula* in laboratory resident-intruder pairs during the non-breeding and breeding seasons.

Values in parentheses are number of pairs tested.

	Non-Breeding		Breeding	
	#	%	#	%
Male-male	2 (15)	13.3	13 (15)	86.7
Female-female	1 (15)	6.7	1 (15)	6.7
Male-female	5 (15)	33.3	1 (11)	9.1
All trials	3 (45)	17.8	15 (41)	36.6

Table 2. Mean number of times MT was performed by residents and intruders in laboratory pairs during the non-breeding and the breeding seasons.

* indicates values that differ significantly within a testing season at $\alpha = 0.05$.

	Non-Breeding			Breeding		
	#		%	#		%
Male-male	1.27		0.27	2.10	*	0.67
Female-female	0.67		0.60	0.73		0.73
Male-female	1.86		0.60	0.80		1.80
All trials	1.27	*	0.80	1.25		0.98

Table 3. Mean number of minutes spent by residents and intruders in laboratory pairs during the non-breeding and the breeding seasons.

* indicates values that differ significantly within a testing season at $\alpha = 0.05$.

	Non-Breeding			Breeding		
	#		%	#		%
Male-male	6.9		9.7	3.4	*	13.1
Female-female	9.3		10.5	10.2	*	15.2
Male-female	5.0	*	10.9	11.1		4.5
All trials	7.1	*	10.4	7.9	*	12.3

Signature of Graduate Student

Lynnette Sievert

Signature of Major Advisor

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