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The Influence of Residency Status on Agonistic Behavior of Male and Female Ozark Zigzag Salamanders Plethodon angusticlavius

ABSTRACT.—Once territories become established residents often have a high probability of successfully defending their territories against intruders. This advantage often can be explained by intrinsic qualities (*e.g.,* size, body condition, experience) that make residents superior competitors. In addition, residency status can confer an advantage that is independent of fighting ability. We used a laboratory experiment to examine the effect of residency status on aggressive behavior by adults of the Ozark zigzag salamander (*Plethodon angusticlavius*), a small terrestrial salamander found under rocks and logs on the forest floor. We controlled for intrinsic effects by testing each individual as both a resident and an intruder in random order. Males and females were tested in same-sex contests in separate experiments. Based on an index that incorporated the frequency of aggressive and submissive postures, both males and females were significantly more aggressive as residents than as intruders. Bites were performed by both males and females, occurring in 11 of 38 pairings overall, and also tended to be more frequent in residents than in intruders ($P = 0.057$). These data are consistent with the hypothesis that both males and females defend feeding territories and that residency offers an advantage that is independent of fighting ability in this species.

INTRODUCTION

Territoriality involves the use of overt aggression and advertisement in area defense (Brown and Orians, 1970). Asymmetries between opponents can be used to settle territorial contests, thereby reducing the probability of escalation to dangerous levels of aggression (Maynard Smith and Parker, 1976). Prior residency is one asymmetry that may influence the outcome of territorial contests: residents generally have a high probability of expelling intruders (Krebs, 1982). Residents may win because of intrinsic characteristics that make them better fighters than intruders, such as asymmetries in size or strength (="resource holding potential" or RHP: Maynard Smith and Parker, 1976). However, prior residency sometimes results in an advantage that is independent of RHP. For some species residents win more often, even when residents and intruders are equally matched (*e.g.,* Krebs, 1982; Mathis *et al.,* 1998).

Terrestrial salamanders (Plethodontidae) have proven to be effective models for examining the influence of asymmetries on the outcome of aggressive contests (*e.g.,* Nunes, 1988; Gabor and Jaeger, 1995; Anthony *et al.,* 1997). Many species are territorial (*see* review: Mathis *et al.,* 1995) and individuals adapt readily to laboratory conditions where experimental manipulations are relatively easy to perform. For territorial salamanders a number of asymmetries have been identified which affect aggressive behavior, including fighting ability (*e.g.,* Townsend and Jaeger, 1998), resource quality (*e.g.,* Gabor and Jaeger, 1995) and residency status (*e.g.,* Mathis *et al.,* 1998).

For Ozark zigzag salamanders, *Plethodon angusticlavius* (formerly *P. dorsalis angusticlavius,* Highton, 1997), asymmetries in body size (Mathis and Britzke, 1999), experience (Mathis and Britzke, 1999) and parasite load (Maksimowich, 1998) have been shown to influence levels of aggression of males, but no studies have examined possible aggressive behavior of females. Our study examines whether prior residency offers an advantage in aggressive contests that is independent of other asymmetries both for males and females of *P. angusticlavius.* Comparisons of aggressive behavior in males and females may provide interesting insights into the function of territoriality.

METHODS

Adult male and female Ozark zigzag salamanders were collected in Newton County, Arkansas in the fall of 1997. Males (SVL: $\bar{x} \pm 1$ SD $= 40.6 \pm 4.05$ mm) were identified as having a mental gland and relatively little cloacal pigmentation whereas females (38.5 ± 3.86 mm) had dark cloacal pigmentation (Sever, 1978a, b). Individuals were transported in separate plastic bags to the laboratory where they were placed individually in petri dishes (15.0 cm diam, 1.5 cm height) lined with moist filter paper. Salamanders were fed 5–10 fruitflies, *Drosophila hydei,* approximately once a week and were kept in an

environmental chamber at 15 C on a 12L:12D light : dark cycle. Tests were conducted in March and April of 1998 between 1000 and 1700 h at approximately 18–20 C.

Testing chambers were clear plastic cell culture dishes (24 × 24 cm) lined with moist paper towels. We placed salamanders into individual testing chambers 4 d before testing so that they could mark the substrates with identifying pheromones.

We paired salamanders according to snout-vent length so that the size asymmetry between individuals was <2 mm. Male-male (n = 20) and female-female pairs (n = 18) were tested in separate experiments. Because it was difficult to identify individuals, we placed one dot of green fluorescent powder just anterior to the forelimbs of one salamander in the pair and just posterior to the forelimbs of the other individual. We randomly designated individuals in each pair as residents and intruders. Immediately before a trial we removed the intruder from its chamber and placed it under an opaque habituation dish (petri dish: 8.5 cm diam) at one end of the resident's chamber. Residents were handled similarly and placed under a habituation dish at the opposite end of the chamber. After 5 min we removed the habituation dishes and recorded the behavior of both individuals for 20 min. All individuals were tested twice, once as a resident and once as an intruder with the order of testing determined randomly. The same observer scored behavior of the same individuals in both tests to reduce possible effects of interobserver variability.

We recorded the frequency of the following behavioral patterns: (1) BITEs—a salamander grasps another with its open mouth, (2) MOVE TOWARD (MT)—an individual approaches its opponent (from any distance) in a direction that will result in eventual contact if movement is not ceased, (3) LOOK TOWARD (LT)—a salamander turns its head in the direction of the other, (4) MOVE AWAY (MA)—an individual moves so as to increase the distance between the opponents and (5) LOOK AWAY (LA)—a salamander turns its head so that it terminates visual contact with the other salamander. If MT and LT occurred simultaneously the behavior was scored only as MT, and if MA and LA occurred simultaneously the behavior was scored only as MA. BITE, MT and LT are considered to be aggressive behavioral patterns and MA and LA are considered to be submissive patterns (*e.g.,* Jaeger, 1984; Anthony and Wicknick, 1993; Mathis *et al.,* 1998).

For statistical analyses we combined the data from the four postures into an index of aggression. The index was calculated as: (MT + LT) − (MA + LA). BITEs were not included in the index but were analyzed separately. Other researchers have also combined data from multiple behavioral categories into a single score for analyses (*e.g.,* Selby *et al.,* 1996; Camp 1999), but there is no standard method of calculating aggression indices for salamanders. Because each individual was tested twice, we compared aggression indices for residents and intruders using the Wilcoxon matched-pairs signed-ranks test (Siegel, 1956). We used one-tailed tests due to the well-supported predicted directions of differences between residents and intruders. In previous studies, when residents and intruders exhibited different levels of aggression, residents were more aggressive and less submissive than intruders (Wiltenmuth, 1996; Anthony *et al.,* 1997; Mathis *et al.,* 1998). This pattern is true for both male and female salamanders, although fewer data are available for females (Horne, 1988; Marvin, 1998).

RESULTS

The number of aggressive moves (MT, LT) generally exceeded the number of submissive moves (MA, LA), leading to positive indices of aggression for both residents and intruders. For both females and males aggression indices were significantly greater for residents than for intruders (females: $T = 23.5$, $n = 18$, $P < 0.005$; males: $T = 39$, $n = 19$, $P < 0.025$; Fig. 1).

BITEs were performed by only 7 females and 4 males (29% of all pairings). Because the aggression indices were qualitatively similar for males and females, we combined the data for males and females for statistical analysis of BITEs. In the combined analysis individuals tended to bite more often as residents than as intruders, but the difference was not significant at the level of $\alpha = 0.05$ (residents: $\bar{x} \pm 1$ SE = 3.1 ± 1.62, range = 0–19 bites per trial; intruders: $\bar{x} \pm 1$ SE = 1.0 ± 0.45, range = 0–5 bites per trial; $T = 12$, $n = 10$, $P = 0.057$).

DISCUSSION

Adults of both males and females of *Plethodon angusticlavius* were more aggressive as residents than as intruders. Because our study controlled for asymmetries in RHP by testing each individual in both

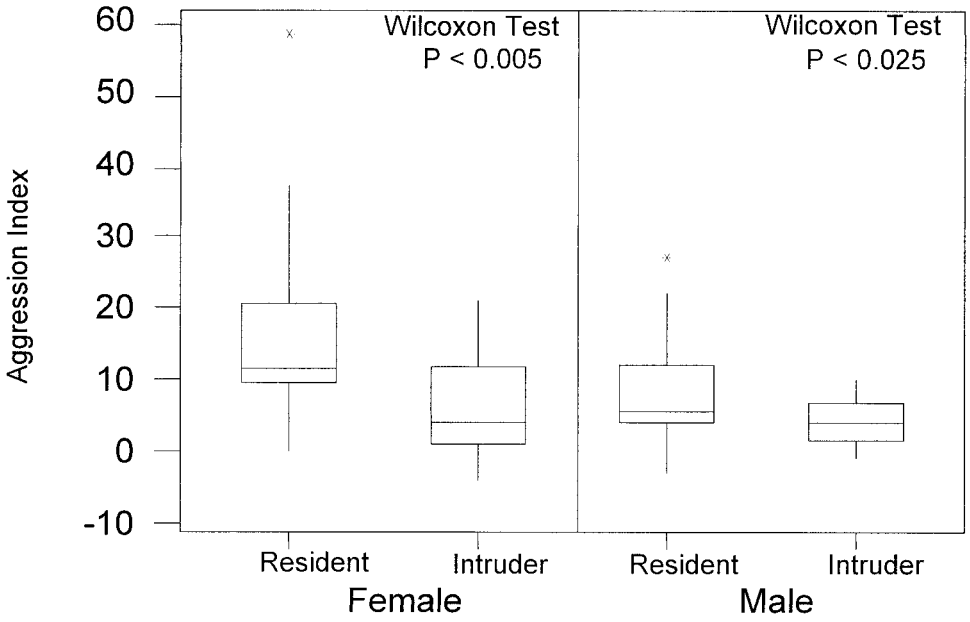

FIG. 1.—Comparison of aggressive behavior of residents and intruders. Aggression indices of female and male residents and intruders of *Plethodon angusticlavius*. Indices are number of aggressive moves (MOVE TOWARD, LOOK TOWARD) minus the number of submissive moves (MOVE AWAY, LOOK AWAY). Data are presented as boxplots with the horizontal lines in the boxes indicating medians, the boxes representing interquartile ranges and the asterisks indicating outliers

conditions, the difference between residents and intruders is independent of RHP. Similar advantages of prior residency have been reported for other taxa (*e.g.,* Barnard and Brown, 1982; Waage, 1988), including some plethodontid salamanders (Wiltenmuth, 1996; Anthony *et al.,* 1997; Mathis *et al.,* 1998).

Differences in levels of aggression between residents and intruders were found for both males and females, supporting the hypothesis of territoriality for both sexes. Studies of plethodontid salamanders often focus on aggressive behavior of males (*e.g.,* Cupp, 1980; Gabor and Jaeger, 1995; Anthony *et al.,* 1997; Townsend and Jaeger, 1998), but aggression by females also has been reported for several species (*e.g.,* Horne, 1988; Staub, 1993; Dahlgren, 1996; Wiltenmuth, 1996). Intersexual variation in aggression ranges from no apparent differences (*e.g.,* Jaeger *et al.,* 1982; Nishikawa, 1987; Selby *et al.,* 1996) to males being more aggressive than females (Staub, 1993; Wiltenmuth, 1996) to aggression being largely limited to breeding males (Ovaska, 1987). In our study males clearly were not more aggressive than females. Seven of the eleven individuals that performed bites were females and the most bites were by a female resident that bit an intruder 19 times in one trial. The relationship between courtship and defense of feeding territories by both males and females remains an interesting puzzle. There is some evidence that males and females of *Plethodon cinereus* occupy intersexually overlapping territories (Mathis, 1991), but it remains to be seen whether a similar situation occurs in *P. angusticlavius*.

Plethodontid salamanders appear to use three lines of territorial defense (Jaeger, 1986; Mathis *et al.,* 1995). First, pheromones are indiscriminately broadcast to inform an intruder that a resident is present in the area. Second, visual agonistic postures are performed. When these "identifying acts" fail to deter the intruder, the third step is escalation to the dangerous biting stage. All three stages of defense are present during same-sex contests between adults of *Plethodon angusticlavius*. Adults of both sexes can respond to chemical stimuli produced by conspecifics (Maksimowich, 1998), and both males (Maksimowich, 1998; Mathis and Britzke, 1999; current study) and females (current study) use visual postures and biting during staged contests in the laboratory.

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