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Carl D. Anthony, *John Carroll University*
Jill A. Wicknick
Robert G. Jaeger

SOCIAL INTERACTIONS IN TWO SYMPATRIC SALAMANDERS: EFFECTIVENESS OF A HIGHLY AGGRESSIVE STRATEGY

by

CARL D. ANTHONY[1,2], JILL A. WICKNICK[2] and ROBERT G. JAEGER[3]

(Department of Biology, University of Southwestern Louisiana, Lafayette, LA 70504-2451, USA)

Summary

In terrestrial plethodontid salamanders, aggressive behaviour is thought to function in the spacing of territorial residents among contested cover objects on the forest floor. Such behaviour, when exhibited toward heterospecifics, plays an important role in the competitive interactions between species. We compared levels of aggressive behaviour in intra- and interspecific contexts in two species of sympatric salamanders (*Plethodon ouachitae* and *P. albagula*) that have similar ecological requirements but differ in adult size. We also tested the effectiveness of such behaviour in holding cover objects (territorial foci) in the laboratory and on the forest floor. We predicted that if one species were more aggressive than the other, then that species would have greater success in obtaining and holding cover objects. In laboratory trials, residents of *P. ouachitae* (the smaller species) were extremely aggressive in both intra- and interspecific contexts. Individuals of *P. ouachitae* delivered bites at a rate 14 times that of previously studied species of *Plethodon* and were significantly more likely to escalate to biting when tested as territorial residents (in intra- and interspecific trials) and as intruders (in interspecific trials). *Plethodon albagula* exhibited a lower level of aggression, similar to other species of *Plethodon*. In laboratory trials, in which salamanders

competed for cover objects of differing quality, residents of *P. ouachitae* were effective in expelling conspecific intruders, and they were marginally effective at expelling intruding *P. albagula*. Residents of *P. albagula* were less effective in expelling conspecific intruders and did not expel intruding *P. ouachitae*. We conclude that the extreme aggression exhibited by *P. ouachitae* enabled it to expel intruders from artificial cover objects and to invade cover objects held by larger heterospecific residents. Field data supported intraspecific defence of cover objects by *P. ouachitae*, but results for *P. albagula* were inconclusive. These results are consistent with the geographic distributions of these species (*P. ouachitae* typically outnumbers *P. albagula* in the Ouachita Mountains) and provide an example of a behavioural mechanism overcoming a size-related disadvantage.

Introduction

Territorial behaviour allows individuals to sequester resources from competitors and is exhibited across a broad phylogenetic spectrum. One assumption of territoriality theory is that aggression exhibited by territorial residents functions to exclude intruders from defended areas (Petrie, 1984; Marden & Waage, 1990; Stamps, 1992). Defeated contestants are then thought to join a non-territorial floater population (Brown, 1969), which is characterized by individuals of lower fitness resulting from lack of mates, resources, or a combination thereof. In terrestrial salamanders of the family Plethodontidae, territories and their associated cover objects (rocks and logs on the forest floor) are thought to provide patches of moisture and prey, especially during dry periods when foraging in the leaf litter is not possible (Jaeger, 1971a, b; Jaeger *et al.*, 1995). Aggressive behaviour has been well studied in plethodontid salamanders (*e.g.* Cupp, 1980; Jaeger, 1984; Keen & Sharp, 1984; Nishikawa, 1985a; Ovaska, 1987; Anthony & Wicknick, 1993a; Staub, 1993) and appears to be a crucial component of social interactions. Jaeger *et al.* (1982) provided behavioural evidence that aggressive behaviour in *Plethodon cinereus* can result in expulsion of conspecific intruders in the laboratory. Smith & Pough (1994) showed that, when provided with a single cover object in an experimental chamber, salamanders displaced each other in complex ways; residency status and species' identity were the most important factors determining which individual was displaced.

When they occur in sympatry, terrestrial plethodontid salamanders that have similar ecological requirements are likely to compete for the same territories (Mathis *et al.*, 1995), and exclusion of one species by another

may occur if expression of territoriality is asymmetric (Wrobel *et al.*, 1980; Gergits, 1982; Nishikawa, 1985a). Species exclusion, through interspecific territoriality or interference competition, may evolve through α-selection (Gill, 1974), where traits that increase an individual's interspecific competitive ability are favoured. Interference mechanisms, such as interspecific aggressive behaviour, that can hinder a competitor's access to resources are traits that are thought to be especially sensitive to α-selection (Gill, 1974). Alternatively, interspecific aggressive behaviour may be a form of species misidentification, where aggressive behaviour evolves in an intraspecific context and is then exhibited toward heterospecifics only by fortuitous chance (Murray, 1971; Nishikawa, 1987). In either case, the effectiveness of interspecific aggression can have profound effects on the competitive balance between territorial species.

The Rich Mountain salamander, *Plethodon ouachitae*, occurs on the north slopes of Winding Stair, Spring, Rich, Kiamichi, and Blackfork mountains in Oklahoma and Arkansas (Blair & Lindsay, 1965; Duncan & Highton, 1979; Anthony & Wicknick, 1993b). Adults of *P. ouachitae* are considered territorial because they aggressively defend areas (Thurow, 1976; Anthony & Wicknick, 1993a), distinguish between their own odours and those of conspecifics (Anthony, 1993), home to cover objects on the forest floor and exhibit site fidelity (Anthony, 1995), and are seldom found together under cover objects in same-sex pairs (Anthony, 1995). The western slimy salamander, *Plethodon albagula*, also occurs on the above mountains, as well as within the shallow valleys between the ranges. Little is known about the behavioural ecology of this species, but it is generally assumed that individuals behave much like other members of the *P. glutinosus* group, some of which are considered territorial (Thurow, 1976). Adults of *P. ouachitae* reach a mean size of 58 mm snout-vent length (SVL) while adults of *P. albagula* reach a mean size of 70 mm SVL (Pope & Pope, 1951; Duncan & Highton, 1979). These size differences may not be great enough to preclude competition for resources, such as cover sites and their associated prey populations, but the differences may be large enough to affect the outcome of that competition, especially if interference mechanisms are involved. Game theory models (Maynard Smith & Parker, 1976) predict that when opponents are disparate in size, then size alone may determine the outcome of an interaction; larger salamanders are expected to

have a size-related advantage when competing for cover objects and territories (Mathis, 1990). Nonetheless, within its range, *P. ouachitae* (the smaller species) typically outnumbers *P. albagula* by at least 5:1 and often by as much as 50:1 or more (Pope & Pope, 1951; Blair & Lindsay, 1965; Duncan & Highton, 1979). If *P. ouachitae* is excluding *P. albagula* from areas through interference, it must be utilizing some mechanism that circumvents its initial size-related disadvantage. In an attempt to clarify this mechanism, we devised a series of experiments to examine variation in territorial behaviour between these two sympatric salamanders.

In experiment 1, we compared levels of aggressive behaviour in intra- and interspecific contests in *P. ouachitae* and *P. albagula*. Based on field distributions and on previous studies indicating high levels of aggression in *P. ouachitae* (Thurow, 1976; Anthony & Wicknick, 1993a), we predicted that *P. ouachitae* would be more aggressive than *P. albagula*. In experiment 2, we tested these species for their ability to expel conspecific and heterospecific intruders from cover objects in the laboratory. We predicted that the more aggressive species would be more successful at defending cover objects as a resident and obtaining cover objects as an intruder. In experiment 3, we examined the ability of *P. ouachitae* and *P. albagula* to expel conspecifics from cover objects on the forest floor through a manipulation of resident salamanders (Mathis, 1990; Griffis, 1993). Because size has been shown to be important in determining the outcome of territorial contests (Mathis, 1990; Griffis, 1993), we predicted that when a resident salamander was removed, smaller individuals (from the floater population) would invade, but when the resident was left in place, either fewer, or similarly sized, individuals would invade.

Methods

General

We collected adult males of *Plethodon ouachitae* on Winding Stair Mountain, Le Flore Co., Oklahoma (34°42′57″ north latitude, 94°40′33″ west longitude; elevation = 550 m) in May, September, and October 1991. We collected adult males of *P. albagula* from Coon Mountain, Le Flore Co., Oklahoma (34°42′03″ north latitude, 94°38′00″ west longitude; elevation = 450-550 m) in September and October 1991. Sex was determined by the presence or absence of the male's mental gland. Both collecting localities are on north-facing slopes and they are separated by a distance of approximately 4 km.

We transported the salamanders to our laboratory in individually marked containers. Prior to testing, salamanders were housed individually in 13×18 cm clear plastic containers at 15°C under a natural (Lafayette, Louisiana) photoperiod. The containers were filled with 2 cm of potting soil; salamanders were fed 50-60 *Drosophila virilis* every seven days. All tested salamanders remained in healthy condition and gained mass and body length while in captivity.

Experiment 1: Level of intra- and interspecific aggressive behaviour

We performed tests of behavioural interactions in February and March 1992. Salamanders were housed and tested in $22.9 \times 15.7 \times 5.4$ cm plastic trays with transparent lids. The floors of the trays were covered with sterile, moistened soil to a depth of 2 cm. We fed salamanders approximately 75 *Drosophila virilis* once weekly during the testing period and kept them on a natural (Lafayette, Louisiana) photoperiod at 15°C.

To allow salamanders maintenance of residency status for an extended period, all salamanders were housed in their home chambers for 28 days before testing began. We did not change the soil substrates between tests. We fed salamanders 72 h prior to each test and, in an effort to standardize hunger levels, we removed excess flies 24 h prior to testing. Each resident salamander ($N = 27$) was paired once each with an intraspecific, an interspecific, and a non-salamander control (moistened paper toweling rolled into the general size and shape of a salamander) intruder. The control intruder was used to control for disturbance (*i.e.* removal of tray lid and introduction of the acclimation dish) and as a focal point for movements such as move toward and look toward. Each salamander was also used as an intruder in one intraspecific and in one interspecific trial. At least one week elapsed between use as either a resident or as an intruder and no salamander was paired with the same animal more than once. We randomly paired conspecific salamanders by size to minimize size related asymmetries in fighting ability (Maynard Smith & Parker, 1976). Paired individuals of *P. ouachitae* differed by a mean of 0.4 mm SVL ($\pm$ 0.3 mm, SE); paired individuals of *P. albagula* differed by a mean of 0.9 mm SVL ($\pm$ 0.8 mm). Interspecific pairs were also randomly paired by size and differed by a mean of 9.9 mm SVL ($\pm$ 2.3 mm), with *P. albagula* always being the larger animal. We determined SVL with vernier calipers, measuring from the snout to the anterior angle of the vent.

We randomized the order in which residents were paired with intraspecific, interspecific, and control intruders. The order in which an individual was used as a resident and as an intruder was also randomized. Intruders and residents were gently picked up and placed in separate covered, opaque acclimation dishes. The dishes were lowered into the resident's home chamber. We allowed both animals 5 min to acclimate to the new situation and then removed the lids to the acclimation dishes.

We recorded the number of bites delivered by resident salamanders for 15 min after the onset of interactive behaviour — always look toward (Jaeger, 1984) or move toward (Wrobel *et al.*, 1980) — by either resident or intruder. Time to first interactive behaviour ranged from 295-1039 s (mean = 471.3). Total bites per trial were compared among trial types using either Wilcoxon's signed-ranks tests (when data were paired) or Mann-Whitney U-tests (Sokal & Rohlf, 1981). We also compared the time from first interactive behaviour to first bite by resident and intruding salamanders among trial types using the above tests. The bite targets of residents (head, body, or tail) were compared to an expected distribution (derived from relative sizes of those body parts) using Chi-square tests. All tests were

two-tailed with $\alpha = 0.05$ except where data were used more than once in analyses; α was then appropriately reduced using the sequential Bonferroni's correction (Siegel & Castellan, 1988; Rice, 1989).

Experiment 2: Effectiveness of aggression by salamanders in the laboratory

We placed 30 adult males of *P. ouachitae* and 30 adult males of *P. albagula* singularly into 45×32 cm opaque, plastic, rectangular chambers. Nylon screening was affixed to each chamber lid with duct tape. Each chamber floor was covered with 1 cm of sterile potting soil. Cover objects (Color Tile®: unglazed prairie tan quarry tile) measuring $15 \times 15 \times 1$ cm and $15 \times 7.5 \times 1$ cm were placed in opposite, but otherwise random, ends of the chambers. The cover objects were set on an angle (a 1.5-cm diameter marble was placed under one end of each) so that salamanders could fit easily beneath them. Each cover object was watered daily with spring water, but the larger cover object received twice as much moisture as the smaller one (32 *vs* 16 ml). Salamanders were fed 15-20 *D. virilis* every third day; the flies were placed at the raised edge of the larger cover object. We chose this lower food level (approximately one-half that of the maintenance level) to increase the probability of area defence and to insure that excess flies did not associate with the smaller cover object.

Trials were run in January and February 1995. We allowed each salamander 8 days to establish residency under a 12L : 12D photoperiod at 14-16°C. After 8 days, we transferred an intruder from its original home chamber (see general methods) into the center of a resident's chamber between 16:00 and 17:30 h. Each intruder was placed into a chamber with a conspecific, a congeneric, and a control (no) resident, in random order, for a total of 180 trials. To increase the probability of area defence, residents were not handled. Each salamander was used three times as an intruder and twice as a resident (once in each treatment). No salamander was paired with the same individual twice. We randomly paired conspecific salamanders within size-classes to minimize size differences. Pairs of *P. ouachitae* differed by a mean of 0.68 mm SVL ($\pm$ 0.65 mm, 1 SE); pairs of *P. albagula* differed by a mean of 1.30 mm SVL ($\pm$ 1.83 mm). Interspecific pairs were also randomly paired by size and differed by a mean of 12.05 mm SVL ($\pm$ 2.03 mm), with *P. albagula* always being the larger animal.

During the morning following introduction of the intruder, between 09:30 and 10:30 h, we recorded the time in seconds during a 10-min trial that each salamander spent beneath the superior (larger, wetter, with prey) cover object. We used a combination of written descriptions and pictograms of the unique dorsal spotting patterns of each salamander for individual identification. The data were not normally distributed, so we analyzed them using Wilcoxon's signed-ranks tests for paired data. We incorporated the sequential Bonferroni adjustment (Rice, 1989) when data were used more than once in an analysis. We made one-tailed comparisons between experimental treatments and controls because we knew from observing salamanders during the setup period that they preferred the larger cover object. Comparisons between intra- and interspecific trials were two-tailed.

Experiment 3: Effectiveness of aggression by salamanders on the forest floor

In April 1994, in collecting areas for *P. ouachitae* and for *P. albagula* (see general methods), we randomly designated cover objects to control and experimental groups. The cover objects

(naturally occurring rocks) were those used in an earlier study on site fidelity and homing in these species (Anthony, 1995) and were known to have been occupied by adult male or female salamanders. In the area of allopatry for *P. ouachitae* on Winding Stair Mountain, we designated 27 cover objects to the control group and 27 to the experimental group. In the area of allopatry for *P. albagula* on Coon Mountain, we designated 12 to the control group and 12 to the experimental group. A larger sample size on Coon Mountain was not possible due to difficulty in finding resident salamanders.

When a salamander was discovered beneath a cover object designated as an experimental, it was photographed, measured, and removed from the site. We released these salamanders 300 m away in an area still within each respective allopatric population. Control animals were photographed and measured, but not removed. Photographs were used in lieu of toe clipping as a method of individual identification of salamanders (Loafman, 1991; Donnelly *et al.*, 1994). We checked cover objects eight times between 12 April and 30 May 1994.

We made statistical comparisons between the sizes (SVL) of original residents and the sizes of the invading salamanders in the control and experimental (resident displaced) groups. We used paired tests (Wilcoxon signed-ranks tests) for analyses of these data because the SVL of the original resident is compared to the SVL of an invading salamander at the same rock. We also compared the number of invading salamanders under control and experimental rocks with a Chi-square test for independence.

Results

Experiment 1: Level of intra- and interspecific aggressive behaviour

When paired with conspecifics, residents of *P. ouachitae* bit in 25 of 27 trials (93%; 909 total bites). When paired with *P. albagula*, residents of *P. ouachitae* bit in 23 of 27 trials (85%; 466 total bites). Residents of *P. albagula* bit in 13 of 27 conspecific trials (48%; 78 total bites) and in 9 of 27 heterospecific trials (33%; 73 total bites). Residents of *P. ouachitae* bit conspecific intruders an average of 33.7 times per 15-min trial, the highest rate of biting reported for any species of *Plethodon* (Jaeger, 1981, 1984; Nishikawa, 1985b; Ovaska, 1987). Bites were rapidly exchanged until one opponent was able to grasp and hold the other in its jaws in a prolonged bite (Fig. 1A-C). These prolonged bites were similar to the 'gripping' behaviour reported by Ovaska (1987) for *P. vehiculum*. In *P. ouachitae*, however, prolonged bites were often followed by rapid lateral rolling on the part of the biter, which forced the opponent into a contorted, knot-like position (Fig. 1C) (Anthony & Wicknick, 1993a).

Residents of *P. ouachitae* were more aggressive in intraspecific trials than they were in interspecific trials (Fig. 2A; $p = 0.0004$, Wilcoxon test) while residents of *P. albagula* showed no significant difference in biting
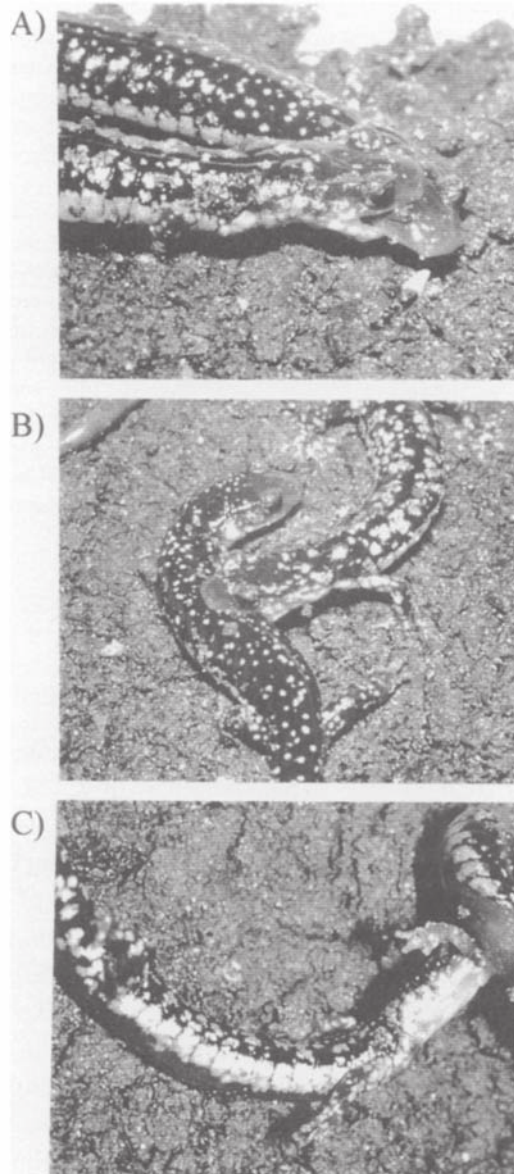
Fig. 1. Photographs depicting biting in *Plethodon ouachitae*. (A) Bite to head, *Plethodon ouachitae* intraspecific trial. Bites to the head can be prolonged. In one *ouachitae/ouachitae* trial, the intruder held the resident's head for over 9 min. (B) Bite to body, *P. ouachitae* intraspecific trial. (C) Lateral roll following bite to limb, *P. ouachitae* intraspecific trial. The resident (animal on the left) has grasped the intruder's forelimb and then rotated its own body rapidly, resulting in the contorted position of the intruder.
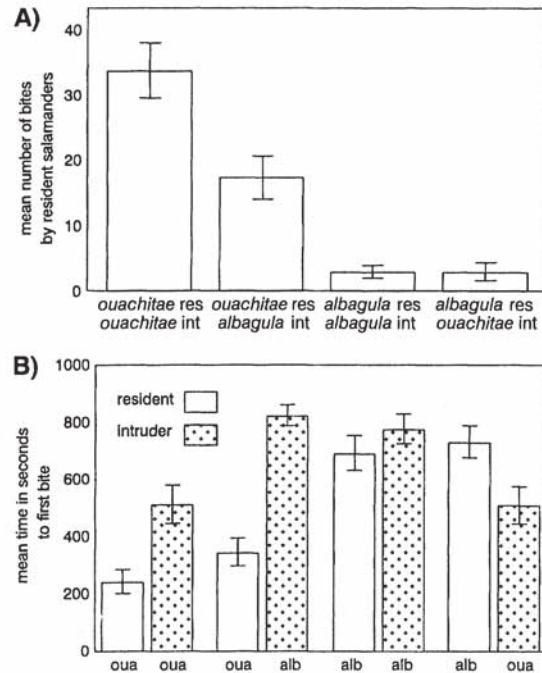
Fig. 2. (A) Mean number of bites by the residents (res) and (B) time to first bite by residents and intruders (int) of *Plethodon ouachitae* (oua) and *P. albagula* (alb) in intra- and interspecific behavioural pairings.

between intra- and interspecific trials (Fig. 2A; $p = 0.94$, Wilcoxon test). Residents of *P. ouachitae* bit significantly more often in intraspecific trials than did resident *P. albagula* (Fig. 2A; $p < 0.0001$, Mann-Whitney test) and also bit significantly more often in interspecific trials than did residents of *P. albagula* (Fig. 2A; $p < 0.0001$, Mann-Whitney test).

Time to first bite was recorded for both resident and intruding salamanders; this provides a rough measure of propensity to enter into and escalate a contest. In intra- and interspecific trials, residents of *P. ouachitae* were significantly quicker to bite than were intruders (Fig. 2B; $p < 0.0013$, Wilcoxon test). In intraspecific trials, residents of *P. albagula* showed no significant difference in time to first bite when compared to intruders (Fig. 2B; $p = 0.196$, Wilcoxon test). When paired with intruding *P. ouachitae*, however, residents of *P. albagula* were significantly slower to bite first (Fig. 2B; $p < 0.032$, Mann-Whitney test). We also compared time

TABLE 1. *Number of trials where the resident bit the head, body, or tail (A) most frequently or (B) first*

Trial type Resident/Intruder	Bite target			χ^2	p
	head	body	tail		
(A)					
ouachitae/ouachitae	9	11	3	21.65	0.00002***
	(2.83)	(7.87)	(12.29)		
ouachitae/albagula	3	16	0	24.18	0.00001***
	(2.34)	(6.51)	(10.15)		
albagula/albagula	2	6	0	9.19	0.0101*
	(0.99)	(2.74)	(4.27)		
albagula/ouachitae	4	4	0	14.06	0.0009***
	(0.99)	(2.74)	(4.27)		
(B)					
ouachitae/ouachitae	14	6	6	41.77	< 0.00001***
	(3.21)	(8.90)	(13.89)		
ouachitae/albagula	7	8	8	7.61	0.022*
	(2.84)	(7.88)	(12.33)		
albagula/albagula	7	4	1	25.17	< 0.00001***
	(1.48)	(4.11)	(6.41)		
albagula/ouachitae	6	2	2	21.11	0.00003***
	(1.23)	(3.42)	(5.34)		

Expected number of trials based on body proportions are shown in parentheses. Multinomial test, df = 2, $\alpha = 0.05$.

to first bite between residents in intra- and interspecific trials. Residents of *P. ouachitae* bit sooner when paired with conspecifics than when paired with heterospecifics (Fig. 2B; $p < 0.05$, Wilcoxon test). For resident *P. albagula*, there was no significant difference in time to first bite between intra- and interspecific trials (Fig. 2B; $p = 0.55$, Wilcoxon test).

By calculating the mean lengths of head, body, and tail of the salamanders used in this study, bites made to those areas can be compared to an expected distribution to determine if resident salamanders preferentially bit certain areas (Jaeger, 1981; Jaeger *et al.*, 1982; Keen & Sharp, 1984; Ovaska, 1987). Using frequencies of bites to specific areas as observed values results in pseudoreplication (Hurlbert, 1984), so we adopted a more conservative approach that treated each trial as one datum. We compared the number of trials where each target area was bitten most frequently to the expected values (Table 1A) and the number of trials where each body part was bitten first to the expected values (Table 1B). In all treatments,

there was a significant difference in the number of bites among body areas. Residents of *P. ouachitae* and *P. albagula* bit the head and body of intruding salamanders more frequently than expected by chance (Table 1A). There was also a significant difference in the time to first bite among body areas. The head was bitten first more often than expected by chance in all treatments (Table 1B).

Experiment 2: Effectiveness of aggression by salamanders in the laboratory

Intruders of *P. ouachitae* spent significantly more time under superior cover objects in control trials (no resident present) than when paired with conspecific residents, indicating active expulsion of conspecifics by residents of *P. ouachitae* (Fig. 3A; Wilcoxon $t = 84$, N' (non-tied scores) $= 13$, $p = 0.0071$). No significant difference was found in time spent under superior objects by intruders of *P. ouachitae* between controls and congeneric trials (Fig. 3A; $t = 17.5$, $N' = 6$, $p = 0.142$), suggesting that residents of *P. albagula* were ineffective at expelling intruding *P. ouachitae*.

Intruders of *P. albagula* did not differ significantly in time under the superior object in control trials than when paired with either conspecifics or residents of *P. ouachitae* (Fig. 3A; $t = 15.0$, $N' = 5$, $p = 0.043$, $\alpha = 0.025$). Even with the reduction of α required by Bonferroni's adjustment, however, the results approached significance. This suggests that residents of *P. albagula* may be marginally effective at expelling conspecifics and that residents of *P. ouachitae* may be marginally effective at expelling congenerics.

Tail damage occurred in three (2.5%) of the trials. Two intruders of *P. ouachitae* lost tail tips overnight when paired with conspecifics. In both cases, these animals spent zero seconds under the superior cover object during the morning trial (the residents, in each case, spent the entire trial under the superior cover object). The tails were presumably ingested by the residents, as tail tips were not present in the test chambers. One resident of *P. ouachitae* lost its entire tail to an intruding *P. albagula*. The tail was not ingested and was found intact in the test chamber following the trial. The tailless resident of *P. ouachitae* was not displaced by the intruder; both salamanders occupied the superior cover object during the trial. No other damage or injury was noted in any other trials.
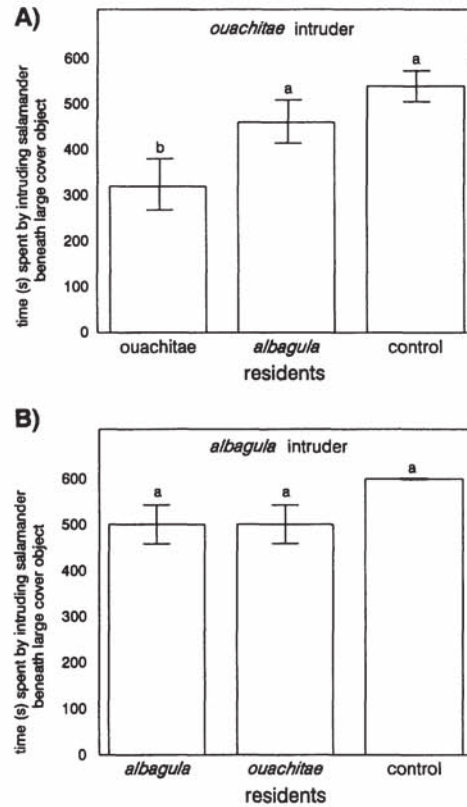
Fig. 3. Time spent under the superior cover object by intruding salamanders when paired with conspecific, heterospecific, and no residents. (A) *P. ouachitae* as intruders. (B) *P. albagula* as intruders. Bars differing in letters (a and b) differed significantly at $\alpha = 0.05$.

Experiment 3: Effectiveness of aggression by salamanders on the forest floor

No significant difference was found in the number of *P. ouachitae* invading control compared to experimental (resident displaced) territories ($\chi^2 = 0.25$, df $= 1$, $p = 0.62$). In the control condition, the SVLs of invading salamanders were not significantly different from those of the original residents (Table 2). In the experimental condition, where residents were removed, significantly smaller salamanders invaded (Table 2). Because of the low number of *P. albagula* found at Coon Mountain, only one designated experimental cover object was invaded by a salamander

TABLE 2. *Mean (± 1 ṠE) snout-vent length (SVL) of* P. ouachitae *that invaded control and experimental cover objects on the forest floor compared to the size of the original residents*

	Original resident SVL (mm)	Invader SVL (mm)	N	z	p
Control	55.8 (1.17)	51.7 (2.74)	7	1.36	0.17 NS
Experimental	53.3 (0.47)	45.6 (2.62)	9	2.19	0.028*

Wilcoxon signed-ranks test, two-tailed. Asterisk indicates significant difference at $\alpha = 0.05$.

(a conspecific smaller than the original resident). Original residents were recaptured in the two control cover objects that yielded salamanders.

Discussion

Individuals of *P. ouachitae* often outnumber *P. albagula* in areas of quality plethodontid habitat and dense, pure populations of *P. ouachitae* are common (Pope & Pope, 1951; Duncan & Highton, 1979; Anthony, 1995). The observed effectiveness of the highly aggressive behavior exhibited by *P. ouachitae* in intra- and interspecific contexts is consistent with these species distributions and provides an example where a size-advantage inherent in one species is overridden by the behavioural strategy of another.

In experiment 1, where aggressive behaviour of the two species was compared, *P. ouachitae* bit at a rate 14 times that of other species of *Plethodon* (Jaeger *et al.*, 1982; Nishikawa, 1985b) and was significantly more aggressive than *P. albagula* in all trials. In contrast, *P. albagula* bit at rates comparable to other species of *Plethodon* previously studied. A territorial resident is expected to act more aggressively than an intruder due to the benefits inherent in holding a territory (Parker, 1976; Davies, 1978; Maynard Smith, 1982; Figler & Einhorn, 1983). Thus, it is not surprising that residents of *P. ouachitae* were quicker to bite than intruders, in both intra- and interspecific trials. The lack of significance in time to bite between residents and intruders in intraspecific trials of *P. albagula* suggests that this species may not be territorial. In interspecific trials, intruding individuals of *P. ouachitae* were quicker to bite than residents of *P. albagula*. The highly aggressive strategy adopted by *P. ouachitae* appears to have two components. (1) Individuals of *P. ouachitae* have a high probability of entering into biting contests regardless of residency

status. (2) These salamanders bite many times in rapid succession during aggressive encounters. In both species, in intra- and interspecific trials, bites by the residents tended to be concentrated on the head and body (Table 1). This is in contrast with results of other studies where bites were concentrated on the head and tail (Jaeger *et al.*, 1982; Ovaska, 1987). In *P. cinereus*, bites to the head sometimes result in nasolabial scarring, which can reduce the foraging ability of a salamander (Jaeger, 1981). The snouts of the animals used in this study were not examined after interactions (because the animals were not sacrificed for microscopic examination), so it is not known if any scarring to the nasolabial grooves occurred.

The effectiveness of the extreme level of aggressive behaviour exhibited by *P. ouachitae* was most evident in experiment 2, where resident salamanders were tested for their ability to exclude intra- and interspecific intruders from preferred cover objects. Residents of *P. ouachitae* were successful in excluding conspecifics from preferred cover objects and were somewhat successful at excluding intruding *P. albagula*. Residents of *P. albagula* were marginally effective in excluding conspecifics but were unable to exclude intruding *P. ouachitae*. The aggressive behaviour patterns exhibited by both resident and intruding *P. ouachitae* appear to be effective in defending and obtaining territories. In interspecific trials, intruding individuals of *P. ouachitae* were doubly disadvantaged by their small size and by their non-resident status. Yet despite these handicaps, they were able to obtain space from a larger, resident-advantaged competitor. If this reflects what occurs in nature, it places *P. ouachitae* at a distinct advantage in a territorial context.

Although larger size is usually correlated with territorial success (Mathis, 1990; Roff, 1981), Zamudio *et al.* (1995) showed that, in *Drosophila*, small males (which had been raised at high temperature) successfully defended territories against large males (which had been raised at a lower temperature). This result was independent of testing temperature and the authors concluded that large size may be less important than physiological and behavioural vigour. Our results are similar. Behavioural vigour in the form of the highly aggressive strategy exhibited by *P. ouachitae* appears to negate the size-advantage held by *P. albagula*.

In experiment 3, field results supported area defence in *P. ouachitae* as well. As predicted, individuals of *P. ouachitae* that invaded cover objects

where the resident had been removed were significantly smaller than those found under control cover objects (resident not removed) (Table 2). In contrast, individuals invading control cover objects were not significantly different in size than the original residents. These results are suggestive of defence of cover objects in the field, where a floater population of smaller conspecifics will invade vacant territories if given the opportunity. Mathis (1990) drew similar conclusions from a population of *P. cinereus* that was similarly manipulated.

We hypothesize that either α-selection has forced *P. ouachitae* to adopt a highly aggressive strategy as a means of competing with a larger congener or, alternatively, that the highly aggressive behaviour exhibited by *P. ouachitae* is a consequence of intense intraspecific competition. We have noted dense populations of this species with up to 45 salamanders per search hour found under cover objects in diurnal surveys. If a highly aggressive strategy evolved in this context, its utility as an interspecific interference mechanism may only be coincidental, even though it functions in excluding interspecific competitors from contested resources (Nishikawa, 1987). The significantly higher level of aggressive behaviour in intraspecific trials of *P. ouachitae*, and its effectiveness in excluding conspecifics from cover, supports this latter scenario. Additional support for evolution of aggressiveness in an intraspecific context comes from the nature of the contact zones that currently exist between *P. ouachitae* and *P. albagula*. Areas of true overlap are rare. We have encountered occasional individuals of *P. albagula* on Winding Stair Mountain. *Plethodon ouachitae* occurs on Coon Mountain on both sides of the allopatric site for *P. albagula* in low densities. It is likely, then, that the current effects of interspecific competition, and hence α-selection, at these sites are negligible. Although α-selection may not be important in the maintenance of a highly aggressive behavioural strategy, we cannot discount its role in the origin of such a strategy. For example, both species occupy similar habitats (Pope & Pope, 1951; Anthony 1995) and both are generalist feeders (Black, 1974: *P. ouachitae*; Pfingsten & Downs, 1989: *P. glutinosus* complex). The effects of past competitive events ('the ghost of competition past'; Connell, 1980) and the effects of dispersal and gene flow from other populations where interspecific competition may be more prevalent are not known. Regardless of the selective pressures leading to increased aggressiveness in *P. ouachitae*,

the high frequency of biting and its effectiveness in this species are consistent with the observed species distributions in that *P. ouachitae* outnumbers *P. albagula* within the restricted range of *P. ouachitae*.

We draw three conclusions from the results of these studies. (1) The high intensity of aggressive behaviour exhibited by *P. ouachitae* may help to explain the apparent parapatric distributions of these two species. (2) Size alone may not always be the best predictor of territorial success; in our study, the smaller, more aggressive species had greater success. (3) Because the aggressive behaviour exhibited by *P. ouachitae* is more effective against conspecifics, and because current interspecific competition between these two species is low at the sites studied, the elevated levels of aggressive behaviour most likely evolved in an intraspecific context and not from α-selection.

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