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Territorial Behavior in Southern Red-Backed and Ozark Zigzag Salamanders: Effects of Sex, Species, and Ownership

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**TERRITORIAL BEHAVIOR IN SOUTHERN RED-BACKED AND OZARK
ZIGZAG SALAMANDERS: EFFECTS OF SEX, SPECIES,
AND OWNERSHIP**

A Masters Thesis

Presented to

The Graduate College of
Missouri State University

In Partial Fulfillment

Of the Requirements for the Degree
Master of Science, Biology

By

Colton Savage Lynn

August 2018

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**TERRITORIAL BEHAVIOR IN SOUTHERN RED-BACKED AND OZARK
ZIGZAG SALAMANDERS: EFFECTS OF SEX, SPECIES, AND OWNERSHIP**

Biology

Missouri State University, August 2018

Master of Science

Colton Savage Lynn

ABSTRACT

Territorial disputes are common among terrestrial woodland salamanders (genus *Plethodon*). Males and females of both Ozark zigzag (*P. angusticlavius*) and southern red-backed (*P. serratus*) salamanders are territorial, but differing costs and benefits between sexes may influence the expression of territorial behavior. I compared the competitive and exploratory behavior of males and females of both species in laboratory experiments. Competitive behavior was assessed through staged contests between same-sex, same-sized conspecifics. There were no differences between males and females for territory owners (residents). Female intruders were more aggressive than male intruders, spending more time in and performing higher grades of the All Trunk Raised display (an aggressive posture). Females were also significantly more cautious than males about leaving territories during the exploration trials. Overall, *P. angusticlavius* showed more aggressive, submissive, and exploratory behavior, and were less cautious about leaving territories than *P. serratus*. The differences between males and females likely reflect a difference in the costs and benefits of territory ownership for males and females. Females fight harder to gain and hold territories, and are less willing to leave, which may indicate that the cost of not having a territory is greater for females.

KEYWORDS: *Plethodon serratus*, *Plethodon angusticlavius*, territoriality, sex differences, species differences, exploration, aggression, submission, caution, behavior

This abstract is approved as to form and content

Alicia Mathis, PhD
Chairperson, Advisory Committee
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In the interest of academic freedom and the principle of free speech, approval of this thesis indicates the format is acceptable and meets the academic criteria for the discipline as determined by the faculty that constitute the thesis committee. The content and views expressed in this thesis are those of the student-scholar and are not endorsed by Missouri State University, its Graduate College, or its employees.

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INTRODUCTION

The way that territoriality is manifested in males and females can be strongly influenced by the resources that are being defended. Territories are frequently categorized by the primary resource that is defended, with the most common types being (1) feeding and (2) breeding (e.g., chapters from Hardy & Briffa, 2013). When food is the primary resource, both same-sex and opposite-sex individuals are competitors and elicit defensive behaviors from the territory owner (Maher & Lott, 2000). However, for breeding territories, where areas containing one or more mates are defended, only same-sex conspecifics are competitors, with opposite-sex conspecifics eliciting less defensive behavior (Bonadonna et al., 2017). In addition, some territories can serve multiple purposes simultaneously or the primary function (feeding/breeding) can vary seasonally (e.g., Wise & Jaeger, 2016). One example is a territory that functions primarily to sequester food for the defender in the nonbreeding season, mates early in or leading up to the breeding season, and defense of offspring later in the breeding season (Tornick, 2010, Wise & Jaeger, 2016).

When territories extend into the breeding season, the way that territoriality operates for males and females varies widely. For example, in some songbirds, such as the song sparrow, *Melospiza melodia*, the male defends a territory that attracts a female who nests and rears offspring on the territory; males, but not females, defend the territory against male intruders during the female's receptive period (Moser-Purdy et al., 2017). In some cases, mated pairs co-defend territories, splitting the energetic and survival costs of maintaining a territory (e.g., red-backed salamanders, *Plethodon cinereus*, Lang &

Jaeger, 2000; snapping shrimp, *Alpheus angulatus*, Matthews, 2002). In other taxa females defend feeding territories against other females, and males defend larger breeding territories that overlap with the territories of multiple females (e.g., site-blotched lizards, *Uta stansburiana*, Sinervo & Lively, 1996; tigers, *Panthera tigris*, Carter et al. 2015).

Even when multiuse territories ostensibly have the same function—feeding, mating, raising young—for both sexes, differences in costs and benefits for males and females can lead to differences in territorial behavior. Males and females may value resources differently, with, for example, males benefitting more strongly from defense of mates and females benefitting more from defending food for herself or her offspring (e.g., Eikenaar et al., 2008). Differential costs of defense can include, but are not limited to, the higher energetic costs of activity for females laden with eggs (e.g., Cooper et al., 1990).

In some terrestrial salamanders (Family Plethodontidae), territories usually occur beneath cover objects such as rocks or logs on the forest floor that provide food and protection from desiccation during dry periods (Jaeger, 1984) and also can serve as breeding territories (Lang & Jaeger, 2000). Individuals of some species compete for larger cover items which excludes unsuccessful competitors from the highest quality shelter (Mathis, 1990). Within a species, a variety of factors can affect aggressive defense of territories, including body size (Townsend & Jaeger, 1998), ownership (Mathis et al., 2000), age (Anthony & Wicknick, 1993), parasite load (Maksimowich & Mathis, 2000), territorial quality (Nunes, 1988), food quality (Gabor & Jaeger, 1995), and experience (Mathis & Britzke, 1999).

In some species of plethodontid salamanders, at least, both males and females appear to be territorial (e.g., *P. angusticlavius*, Dalton & Mathis, 2014; *P. cinereus*, Wise & Jaeger, 2016; *P. kentucki*, Marvin, 1998; *Desmognathus eschscholtzii*, Wiltenmuth, 1996), but relatively little study has compared territorial behavior of males and females. Most studies of plethodontid territoriality have avoided the question of possible sex differences by testing only males or unsexed individuals (e.g., Anthony & Wicknick, 1993; Anthony et al., 1997; Townsend & Jaeger, 1998; Camp, 1999; Mathis & Britzke, 1999; Kohn et al., 2013). However, in the best-studied species, *P. cinereus*, males and females appear to co-defend feeding territories under cover objects (Mathis, 1990; Lang & Jaeger, 2000) and may also give preferential treatment to their mates in a form of social monogamy (Gillette et al., 2000). In this species, social monogamy may be enforced by punishment of cheaters because males and females are more aggressive toward their partners that have associated with opposite-sex conspecifics (Jaeger et al., 2002; Prosen et al., 2004). Another salamander in this family, *Desmognathus eschscholtzii*, also exhibits behavior that suggests territoriality in both males and females, with more aggressive males (Wiltenmuth, 1996).

Agonistic (aggressive or submissive) territorial behaviors in nature have been well documented in the genus *Plethodon* (Jaeger, 1984; Nunes, 1988; Jaeger & Schwarz, 1991; Staub, 1993; Gabor & Jaeger, 1995; Mathis et al., 1998; Townsend & Jaeger, 1998; Mathis & Britzke, 1999; Lang & Jaeger, 2000; Maksimowich & Mathis, 2000; Mathis et al., 2000; Kohn et al., 2013). Agonistic behavior ranges from relatively low-level behaviors such as aggressive and submissive displays (Jaeger, 1984; Jaeger & Schwarz, 1991), chasing (Anthony & Wicknick, 1993) and escape behaviors (Dalton & Mathis,

2014) to more overt actions including bite-and-release (Jaeger, 1984) and prolonged biting with wrestling (Anthony et al., 1997). Advertisement is via both visual displays (Jaeger 1984) and chemical markings (Anthony, 1993; Anthony & Wicknick, 1993). For detection of chemical cues, plethodontid salamanders have specialized naso-labial grooves ending in cirri that they press to the substrate ('nose tap'), transporting substrate chemicals to their vomeronasal organs (Dawley & Bass, 1989). This chemosensory sampling is relatively easy to quantify during behavioral observations.

In plethodontid salamanders, courtship and mating typically occurs over prolonged periods (e.g., Camp, 1988) and sperm is stored in the spermathecae (Eddy et al., 2015). The prolonged mating system and presence of sperm storage suggests a potential for low paternity assurance (e.g., Liebgold et al., 2006) and an opportunity for males to seek matings with multiple females. Females carry enlarged follicles for several months (e.g., Herbeck & Semlitsch, 2000), guard the eggs post-oviposition (e.g., Tornick, 2010), and may forage less than males and non-brooding females (e.g., Ng & Wilbur, 1995). These differences between males and females may result in differences in territorial defense and in fidelity to the territory which could result in a difference in territoriality between males and females.

Differences in levels of agonistic (aggressive/submissive) behavior have been reported for similarly-sized species of *Plethodon* (Anthony & Wicknick, 1997; Camp, 1999) and even among some populations of the same species (Wise & Jaeger, 2016). In Missouri, *Plethodon serratus* and *P. angusticlavius* have parapatric distributions (Figure 1; Johnson, 2000; Daniel & Edmond, 2018), exhibit behavior that is consistent with territoriality (Mathis et al., 1998; Mathis & Britzke, 1999), and inhabit similar woody,

rocky hillsides (Johnson, 2000). The two species, which are similar in size and general appearance (Johnson, 2000), phylogenetically occupy different clades within the subgenus *Plethodon* (Kozak et al., 2006). Previous studies (Dalton, Reeder, Bortosky & Mathis, personal observations) indicated that *P. angusticlavius* is generally more active/exploratory even though the two species do not differ in temperature-dependent baseline metabolic rates. Their data indicate that the two species differ in their response to disturbance in the field as well, with *P. serratus* being more likely to flee and *P. angusticlavius* more likely to freeze. These two species have qualitatively similar agonistic behaviors (Mathis et al., 1998; Mathis & Britzke, 1999), but it is not known whether the species differ quantitatively in their levels of agonism.

For both species, males and females have agonistic behaviors consistent with territoriality in males and females (Mathis et al., 2000; Dalton, Reeder, Bortosky & Mathis, personal observations). In *P. serratus* potential sex differences involved in territorial defense have not been studied in detail. In *P. angusticlavius*, though, males and females appear to spend similar amounts of time performing escape behavior in response to chemical cues from conspecifics (Dalton & Mathis, 2014).

In this study, I quantified the differences in territorial competition and exploratory activity between males and females of *P. angusticlavius* and *P. serratus* in two studies:

(1) Competitive (agonistic and chemosensory) behavior. Salamanders were tested in dyad contests of same-sex, same-size conspecifics, with one individual a territory owner ('resident') and one an intruder. As a consequence of their generally higher activity levels (Dalton, Reeder, Bortosky & Mathis, personal observations) I predicted that *P. angusticlavius* would spend more time performing all behaviors than *P. serratus*. I

predicted that *P. serratus* would compensate for their predicted lower time in agonistic behaviors by exhibiting more intense levels of aggression. Because feeding territories may be more valuable to gravid females due to their higher energetic demands, I predicted that they would spend more time in aggressive defense of their territories than males. Lastly, I predicted that residents of territories would spend more time in aggressive behavior than intruders.

(2) Exploratory behavior: I tested males and females of both species individually in an arena with concentric rings that formed surmountable barriers around a central territory. Individuals were tested as either residents (on own-marked territories) or intruders (on conspecific-marked territories). I predicted that *P. angusticlavius* would be generally more exploratory than *P. serratus*, which would verify the preliminary results of Dalton, Reeder, Bortosky & Mathis (personal observations). I also predicted that males would be more exploratory than females because males typically have greater motivation to seek mates, and females may incur a greater energetic cost if they lose their territories while exploring. Lastly, I predicted that intruders would be more exploratory than residents because they should benefit by finding unclaimed areas.

METHODS

Collection and Care of Lab Animals

Plethodon angusticlavius were collected from Bull Shoals Field Station, Taney County, MO, and *P. serratus* were collected from Reis Biological Station, Crawford County, MO (Figure 1). Salamanders were collected in the fall of 2015 and spring of 2016 for the competition experiment and the spring of 2018 for the exploration experiment; fall and spring encompass the breeding season for both species (Wilkinson et al., 1993; Herbeck & Semlitsch, 2000). Only adult salamanders were tested (snout-vent length ≥ 32 mm). I housed the salamanders on moistened filter paper substrates in individual petri dishes (13 cm diameter \times 1.5 cm height) that were kept in an environmental chamber at $15^{\circ} \pm 2^{\circ}$ C. I fed all individuals 10 *Drosophila hydei* once a week, and changed their filter-paper substrates as needed (every 7-14 days). After each trial, the individuals that were tested were returned to their home dishes and replaced in the environmental chamber.

In the summer of 2016, before any trials began, there was an outbreak of the pathogenic chytrid fungus (*Batrachochytrium dendrobatidis*) in the lab. All salamanders were treated with Itraconazole (a fungicide) and tested negative following treatment. Salamanders were given 3 wk to recover from the stress of infection and treatment before behavioral trials began. At the end of each experiment, all salamanders were re-tested for the presence of chytrid fungus and all samples tested negative. All methods gained prior approval by the Missouri State University IACUC (2/14/2014, renewed 2/14/2017; protocol #17-012.0).

Competition

Individuals ($n = 40$ *P. angusticlavius* and 51 *P. serratus*) were paired for size (± 2 mm) and one individual in each pair was randomly designated as the resident. Four days prior to testing, residents were removed from their home dishes in the environmental chamber and placed in separate arenas ($24 \times 24 \times 2$ cm) with fresh substrates (moistened paper towel) so that they could establish their territories with scent marks (Mathis et al., 2000) and acclimate to temperatures (21-26.5 °C) of the testing room. The intruders were removed from the environmental chamber at the same time as the resident and were given new filter-paper substrates but were left in their home dishes for 4 d. I fed each individual (residents and intruders) 5-10 *D. hydei* (based on the number of days since the last feeding) at the beginning of their acclimation period to control for hunger levels. Any *D. hydei* remaining on the day of trials were removed.

Trials were performed 4 July 2016 through 24 November 2016 between the times of 0800 and 1800 h. The resident for each pair was determined randomly. Dyad pairs were removed from the experiment if one of the individuals exhibited poor body quality or died; 11 pairs were removed from testing over the course of the experiment. Individuals were tested once as an intruder and once as a resident, with a minimum of 1 wk (maximum = 17 wk) between trials of the same individuals. Different individuals were paired together in the second block of trials to avoid recognition of each other which could lead to reduced levels of aggression (Kohn et al., 2013).

At the beginning of each trial, I placed a small dusting of fluorescent pigment (either green or orange, randomly assigned to individuals in each pair) on each salamander's dorsal surface, posterior to the pectoral girdle, to allow for easier

identification. I then placed the resident under an opaque habituation dish (8.5 cm × 1 cm) on either the west or east (determined randomly) end of its territory and then introduced the intruder, which was immediately covered by a second habituation dish on the opposite end of the arena from the resident. After a 10-min habituation period, I recorded the following behaviors for both the resident and intruder, as described by Jaeger (1984) and Mathis (1990): (1) time, in seconds, with all of the trunk raised above the substrate (All Trunk Raised or ATR: aggressive display), (2) the number of times each individual tapped its nasolabial grooves against the substrate or to another salamander (nose taps: chemosensory behavior), (3) time, in seconds, that each individual spent with its head and body spent pressed to the side walls of the arena (EDGE: submissive or escape behavior).

In addition, the most extreme grade of ATR achieved by each individual, as described by Jaeger & Schwarz (1991), was also recorded. The five grades of ATR are: (0) no ATR was performed; (1) the lowest ATR grade where the body, excluding the tail, is lifted slightly off the substrate; (2) the same as ATR 1 but the trunk is higher off the substrate; (3) the same height above the substrate as ATR 2 but the tail is also lifted; (4) the tail is still resting on the substrate but the back is arched up; and (5) the back is arched and the tail is lifted.

Exploration

Individuals (n = 54 *P. angusticlavius* and 90 *P. serratus*) were paired for size (\pm 2mm) and one individual in each pair was randomly designated as the resident. As in the competition experiment, individuals were removed from the environmental chamber 4 d

prior to testing and provided with new filter paper substrates so that they could establish their territories with scent marks (Mathis et al., 2000) and acclimate to room temperature (19-21 °C). Unlike in the competition experiment, salamanders were tested individually; “residents” were tested on own-marked substrates and “intruders” were tested on substrates marked by a resident. For each resident/intruder pair, residents were tested first to ensure that only its scent marks were present. Two intruders (1 male and 1 female of *P. serratus*) died prior to testing. Trials were conducted 12 March 2018 through 21 April 2018 between 0900 and 1630 h.

The testing arena for this experiment was an exploratory ring apparatus lined with damp paper towels (Figure 2) that was developed by Reeder (2013). Before each trial, residents were removed from their home dish and placed in a holding chamber while a circular patch of the resident’s home substrate was cut out and placed in a smaller central dish (8.5 cm × 1.5 cm) that formed the core of the ring apparatus; this dish simulated the resident’s home territory. The central dish (Zone 1) was surrounded by four concentric stainless-steel rings (1.5 cm tall × 18.5, 28.5, 38.5, and 48.5 cm in diameter) that created four additional zones that were unmarked and thus served as unclaimed areas. For each trial, the resident was placed in the central dish and covered with an opaque habituation cover (8.5 cm × 1 cm) which fit over the central dish for 10 min of acclimation. The habituation cover was then removed and the central dish was left uncovered so that the salamander could exit its marked area. The behavior of each individual was recorded for 15 min. Intruders were tested similarly except that they began the trial in a central dish that had been marked by the assigned resident.

The behaviors recorded were (1) the time in seconds it took the individual to move after the habituation cover was removed (latency to move), (2) the time in seconds it took the individual's pelvic girdle to cross the edge of the experimental dish into the second zone (latency to cross), (3) the farthest zone reached from the experimental dish (farthest zone), and (4) the number of times an individual lifted its head above the edge of a ring or returned to a zone before the pelvic girdle crossed into the next zone (reversals).

Statistical Analysis

Data in both experiments were not normally distributed and were align-rank transformed (Higgins & Tantoush, 1994) for statistical analyses. For both experiments, each of the 4 response variables was analyzed separately using a three-way Analysis of Variance (ANOVA) with sex, species, and ownership status (residency) as factors (Figure 3). For the competition data, although each salamander was tested once as a resident and once as an intruder, we treated these as independent replicates; this approach is generally more conservative than a repeated-measures analysis because it does not control for individual variation (Charness et al. 2012). All factors were crossed to show how interactions affected the results (e.g., sex*species, sex*residency, sex*species*residency). For p -values $0.10 > p > 0.05$ that were not explained by a significant interaction effect, I also calculated effect sizes (eta-squared or η^2) (Olejnik & Algina, 2003). The 3-way ANOVAs were performed using the GLM function in Minitab 17.1.0.

RESULTS

Competition

Time spent in the aggressive posture (ATR) was significantly affected by the main effect of species ($F = 12.65, p < 0.001$; Table 1), with *P. angusticlavius* spending more time in ATR than *P. serratus* (Figure 4). The intensity or grade of ATR was significantly affected by species ($F = 11.12, p = 0.001$; Table 2) as well, with *P. angusticlavius* reaching higher grades of ATR than *P. serratus* (Figure 5). Species also significantly affected time spent in EDGE ($F = 49.92, p < 0.001$; Table 3), and *P. angusticlavius* spent more time in EDGE than *P. serratus* (Figure 6). The only behavior not affected by species was Nose Taps ($F = 1.36, p = 0.245$, Table 4, Figure 7).

For ATR, there was a significant 3-way interaction between species, sex and residency ($F = 5.47, p = 0.018$; Table 1). For residents, males and females spent similar amounts of time in ATR, but female intruders spent more time in ATR than their conspecific male counterparts (Figure 4). The difference between males and females was somewhat stronger for *P. angusticlavius* than for *P. serratus*. The significant main effect of sex on time spent in ATR ($F = 14.74, p < 0.001$; Table 1) is largely driven by the difference between the sexes for intruders (Figure 4). The intensity of ATR was influenced by a significant sex*residency interaction ($F = 8.03, p = 0.006$; Table 2), with females showing similar levels of intensity as both residents and intruders, and male exhibiting more intense ATR as residents (Figure 5).

Although there were no significant effects on nose taps, two borderline results showed trends. Overall, intruders tended to perform more nose taps than residents

(residency effect $F = 3.47$, $p = 0.064$, Table 4, Figure 7), with females tending to perform more nose taps than males when they were intruders (sex*residency effect, $F = 3.36$, $p = 0.068$, Table 4, Figure 7). However, the effect size calculations for residency ($\eta^2 = 0.019$) and sex*residency ($\eta^2 = 0.018$) indicated that the differences between means were weak (η^2 ranges from 0–1, with 0 being the smallest effect and 1 being the largest).

Exploration

Species significantly affected all exploratory behaviors. Individuals of *P. angusticlavius* were faster to move ($F = 16.35$, $p < 0.001$; Table 5, Figure 8), faster to cross the first barrier ($F = 252.91$, $p < 0.001$; Table 6, Figure 9), and reached a more distant zone ($F = 110.06$, $p < 0.001$; Table 7, Figure 10) than *P. serratus*. In contrast, *P. serratus* performed more reversals ($F = 39.07$, $p < 0.001$; Table 8, Figure 11) than *P. angusticlavius*.

There was a significant interaction of sex and species on furthest zone reached ($F = 6.03$, $p = 0.015$; Table 7). Female *P. angusticlavius* reached more distant zones than males, but male *P. serratus* reached more distant zones than females (Figure 10). The number of reversals was significantly affected by sex ($F = 5.73$, $p = 0.018$; Table 8), with females of both species reversing more often than males (Figure 11). Residency did not significantly affect any exploratory behaviors for either species (Table 5, 6, 7, 8).

DISCUSSION

Both male and female residents showed relatively high levels of aggression (ATR) in defending their territories, which is consistent with predicted residency effects for salamanders (e.g., Mathis et al., 1998, Mathis et al., 2000; Reiter et al., 2014) and other species (e.g., crabs, Fayed et al., 2008; fish, Nijman & Heuts, 2011; rodents, Stokes et al., 2012). However, for intruders, both the amount and intensity of aggression were influenced by sex, with female intruders displaying more frequent and more intense ATR than males. This difference may suggest that females without territories place a higher value on gaining a territory than males. The access to food provided by a territory may be particularly important for gravid females because of the high energetic costs of brooding for female plethodontid salamanders (Ng & Wilbur, 1995). Male intruders may benefit more by acting as floater males (Mathis, 1991) who do not defend a territory but wander in search of females rather than attempting to take over a territory from another male, particularly during the breeding season. However, this pattern may not apply to all species of terrestrial salamanders. For example, male intruders of *Ensatina eschscholtzii*, were more aggressive than females, which the authors attributed to stronger territorial or mate competition for males than females (Wiltenmuth, 1996).

Female intruders, but not residents, showed a weak and nonsignificant ($p = 0.068$, $\eta^2 = 0.018$) tendency to perform more nose taps than males. Wiltenmuth (1996) also found that female intruders of *E. eschscholtzii* performed more nose taps than male intruders/residents and female residents. In addition, female and male intruders showed a weak and nonsignificant ($p = 0.064$, $\eta^2 = 0.019$) tendency to perform more nose taps than

residents. Functionally, nose taps appear to be involved in collecting a variety of information, including detection of prey (Placyk & Graves, 2002), and predators (Cupp, 1994) in addition to attributes of other salamanders, such as, sex of pheromone donor (Dawley, 1984; Dalton & Mathis, 2014), condition of the donor (Maksimowich & Mathis, 2001; Dalton & Mathis, 2014), and the quality of the donor's territory (Walls et al., 1989). Therefore, it is difficult to determine the specific function of sex differences in nose-tapping behavior. Direct comparisons of my data with those of other studies are complicated by differences in study design, such as the inclusion of opposite-sex pheromones; for example, males of *P. shermani* nose-tapped more than females when exposed to chemical cues from females (Schubert et al., 2008).

Exploratory behavior was not influenced by residency, but the furthest zone reached was affected by a species*sex interaction. For *P. serratus*, males explored farther than females, a result that was also reported for this species by Reeder (2013). Long-term mark-recapture studies of other species also showed longer distance movements by males than females (*P. cinereus*: Liebgold et al., 2011; *E. eschscholtzii*: Staub et al., 1995). In contrast, *P. angusticlavius* females explored further than males. The reason for this sex difference between the two species is unclear. For both species, females were more cautious than males, with females exhibiting a significantly higher number of reversals (extending the snout over the barrier, but returning to the previous zone). Sex differences in caution may be a result of gravid females experiencing increased vulnerability to predation due to decreased locomotor ability (e.g., Seigel et al., 1987) or males having more to gain from being bold because of the benefits of securing additional mates (Han et al., 2015). The difference in cautiousness also suggests that females may be more hesitant

to leave a territory (the central ring) because the risk of losing a feeding territory to an intruder is great for females (Ng & Wilbur, 1995). Reeder's (2013) study of exploratory behavior in *P. serratus* did not find reversal differences between the sexes; however, his definition of a reversal was more conservative, requiring the salamander to touch the substrate of the next zone before returning to the previous zone.

The results of the exploratory study verified the personal observations of Dalton, Reeder, Bortosky, & Mathis. *Plethodon angusticlavius* consistently moved faster, left the first zone faster, and moved further than *P. serratus*. Because *P. angusticlavius* is more active, I predicted that they would also spend more time performing each behavior in the competition trials. This prediction was supported for time spent in ATR and EDGE behavior, with *P. angusticlavius* spending over twice as much time in these behaviors as *P. serratus*.

I predicted that *P. serratus* would compensate for their lower time spent in ATR by escalating to higher intensity levels of ATR more quickly. However, this compensation did not occur, and *P. angusticlavius* had higher mean intensity levels of ATR than *P. serratus*. In *P. cinereus*, Jaeger & Schwarz (1991) found that intruders, but not residents, responded to increasing intensity of ATR with more submissive behavior. I, therefore, hypothesize that the lower intensity of ATR exhibited by *P. serratus* could lead to contests being settled less quickly than in *P. angusticlavius*.

There was also a difference between *P. angusticlavius* and *P. serratus* in the frequency of cautious behavior (reversals). If this difference was an artifact of the difference in activity levels between the two species, then *P. angusticlavius* should have performed more reversals. However, although *P. angusticlavius* was about twice as

active, *P. serratus* performed about three times as many reversals. Qualitatively, the *P. serratus* population that we sampled appears denser than that of the *P. angusticlavius* population. The cautious behavior by *P. serratus* may be a hesitancy to risk losing the territory to a nearby salamander. Mathis (1990) observed that when territorial residents of *P. cinereus* from a dense population were removed from their territories, new salamanders invaded and quickly took over residency. Dalton, Reeder, Bortosky & Mathis (personal observations) observed a difference in collection efficiency between *P. angusticlavius* and *P. serratus* at the same sites I collected from which may be an indication of a difference in population density. The *P. serratus* population yielded a greater average capture rate (9.5 salamanders/h/person) than the *P. angusticlavius* population (3.9 salamanders/h/person) (data collected between 2015 and 2018).

I hereby hypothesize that the difference in activity between the two species is due in part to environmental influences, potentially including competitor density (Shonfield et al., 2012), prey availability (Maerz & Madison, 2000), or climatic conditions (Ovaska, 1988). A few other studies have reported population differences in behavior of territorial salamanders, even within a species (e.g., Wiltenmuth & Nishikawa, 1998; Maerz & Madison, 2000; Wise & Jaeger, 2016). The difference in activity between the two species could also be a result of phylogeny. These two species belong to distantly related clades of the genus *Plethodon*, with *P. angusticlavius* being in the *P. welleri* group and *P. serratus* in the *P. cinereus* group (Kozak et al., 2006). However, Camp (1999) found that geographically-close populations of distantly-related species (*P. websteri* and *P. serratus*) were behaviorally more similar than geographically-distant populations of closely-related species (*P. serratus* and *P. cinereus*). Therefore, phylogeny may not be the most

important explanation for population differences among species of terrestrial salamanders.

While the cause of the species/population differences between *P. angusticlavius* and *P. serratus* are still unclear, the results are consistent with the hypothesis that both males and females of these species are territorial. Overall, sex appears to influence behavior of intruders more than residents. Whereas both male and female residents strongly defended their territories, female intruders appeared to fight more strongly than males to gain territories, and are more cautious when leaving the territory. These results suggest that these species may be good models for understanding different costs and benefits of territoriality between males and females and among populations.

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Table 1. ANOVA table for time spent in ATR.

Source	DF	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Species	1	31994	31994.0	12.65	<0.001
Sex	1	36348	36348.1	14.74	<0.001
Residency	1	4427	4426.7	1.68	0.197
Species*Sex	1	8180	8180.5	3.17	0.077
Species*Residency	1	14	13.7	0.01	0.943
Sex*Residency	1	6708	6707.7	2.58	0.110
Species*Sex*Residency	1	14884	14883.6	5.74	0.018

Table 2. ANOVA table for ATR grade.

Source	DF	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Species	1	5426.7	5426.72	11.12	0.001
Sex	1	1527.2	1527.24	2.69	0.105
Residency	1	1904.0	1903.95	3.41	0.069
Species*Sex	1	760.6	760.60	1.36	0.248
Species*Residency	1	608.5	608.51	1.07	0.304
Sex*Residency	1	4366.8	4366.85	8.03	0.006
Species*Sex*Residency	1	596.6	596.65	1.05	0.308

Table 3. ANOVA table for time spent in EDGE.

Source	DF	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Species	1	109855	109855	49.92	<0.001
Sex	1	6791	6791.38	2.42	0.121
Residency	1	1774	1773.98	0.62	0.431
Species*Sex	1	241	240.9	0.09	0.771
Species*Residency	1	1702	1702.0	0.60	0.440
Sex*Residency	1	4608	4607.71	1.63	0.203
Species*Sex*Residency	1	2309	2308.7	0.82	0.367

Table 4. ANOVA table for number of Nose Taps.

Source	DF	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Species	1	3774	3773.89	1.36	0.245
Sex	1	4149	4149.05	1.49	0.224
Residency	1	9659	9658.5	3.47	0.064
Species*Sex	1	237	236.61	0.08	0.771
Species*Residency	1	495	494.78	0.18	0.673
Sex*Residency	1	9154	9153.9	3.36	0.068
Species*Sex*Residency	1	58	58.3	0.02	0.885

Table 5. ANOVA table for latency to move.

Source	DF	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Species	1	26597	26597.2	16.35	<0.001
Sex	1	2838	2838.02	1.64	0.203
Residency	1	136	136.28	0.08	0.781
Species*Sex	1	214	213.67	0.12	0.728
Species*Residency	1	705	705.27	0.40	0.527
Sex*Residency	1	218	217.75	0.12	0.725
Species*Sex*Residency	1	1318	1317.77	0.75	0.387

Table 6. ANOVA table for latency to cross.

Source	DF	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Species	1	159935	159935	252.91	<0.001
Sex	1	575	574.62	0.33	0.568
Residency	1	18	17.70	0.01	0.921
Species*Sex	1	2820	2819.55	1.63	0.204
Species*Residency	1	1208	1207.7	0.69	0.408
Sex*Residency	1	734	734.2	0.42	0.519
Species*Sex*Residency	1	609	608.52	0.34	0.558

Table 7. ANOVA table for farthest zone reached.

Source	DF	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Species	1	109988	109988	110.06	<0.001
Sex	1	1392	1392.29	0.80	0.372
Residency	1	1585	1585.36	0.90	0.344
Species*Sex	1	9987	9987.0	6.03	0.015
Species*Residency	1	95	95.20	0.05	0.816
Sex*Residency	1	1067	1066.67	0.61	0.438
Species*Sex*Residency	1	4	4.09	0.00	0.962

Table 8. ANOVA table for number of reversals.

Source	DF	Adj SS	Adj MS	<i>F</i>	<i>p</i>
Species	1	42352	42351.8	39.07	<0.001
Sex	1	7729	7729.10	5.73	0.018
Residency	1	217	216.81	0.15	0.695
Species*Sex	1	607	607.16	0.44	0.508
Species*Residency	1	365	365.39	0.26	0.610
Sex*Residency	1	209	208.9	0.15	0.701
Species*Sex*Residency	1	549	549.01	0.39	0.532

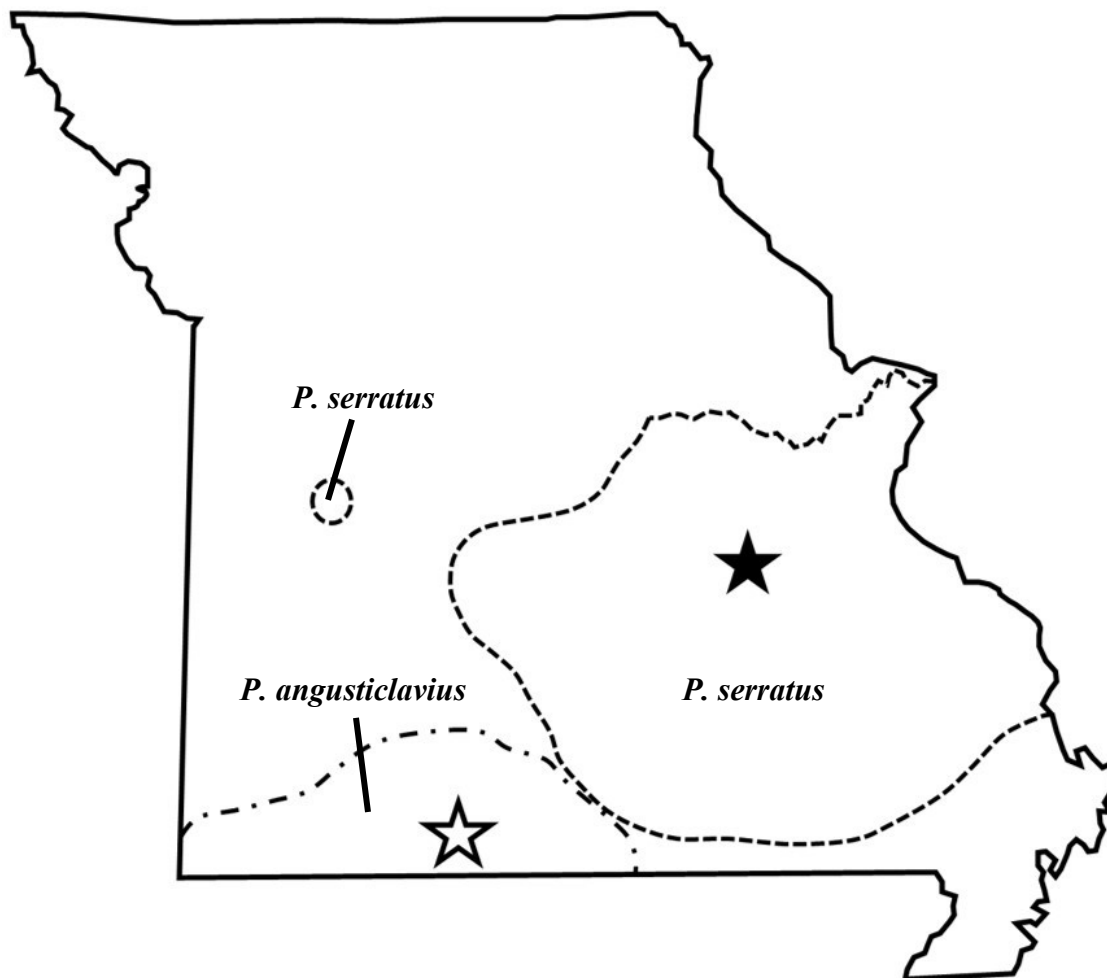


Figure 1. Distributions and collection sites of *P. angusticlavius* and *P. serratus* in Missouri. Distributions were estimated from Johnson (2000) and Daniel & Edmond (2018). The solid star marks the *P. serratus* collection site (Reis Biological Station) and the open star marks the *P. angusticlavius* collection site (Bull Shoals Field Station). At the closest point, the two species come within 7.5 km but do not appear to overlap in current distribution.

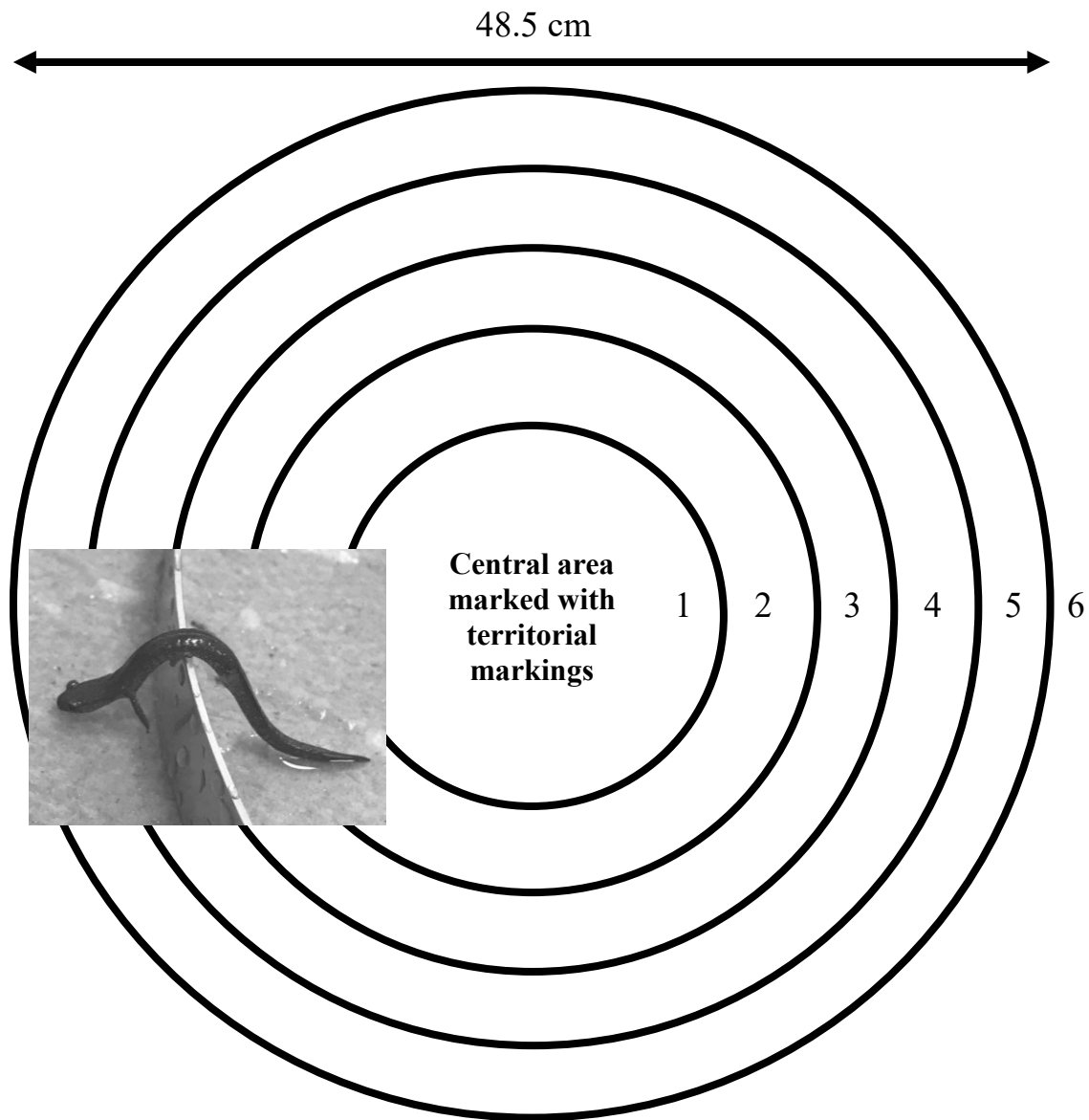


Figure 2: Concentric Ring design. Zones are labeled (1–6). Zone 1 is a territory marked by a resident. Zones 2–6 are unmarked territory. Stainless-steel rings (1.5 cm tall \times 18.5, 28.5, 38.5, and 48.5 cm in diameter) surround the central dish (1.5 cm tall \times 8.5 cm in diameter). The rings and the edge of the central dish act as surmountable barriers to outward exploration.

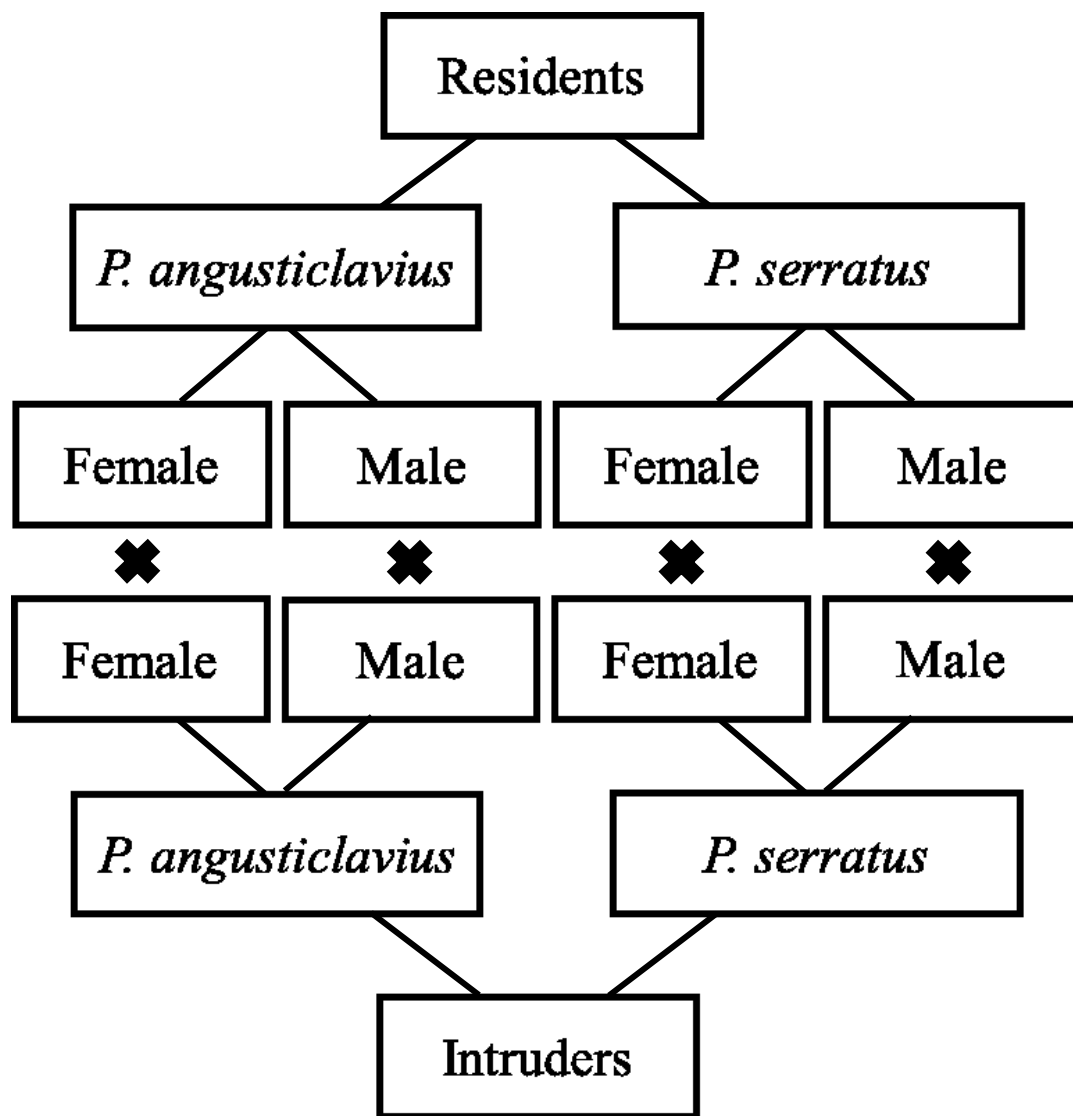


Figure 3: Experimental design including three factors (ownership status, species, and sex). Residents for both experiments were paired (x) with conspecific, same-sex intruders for testing.

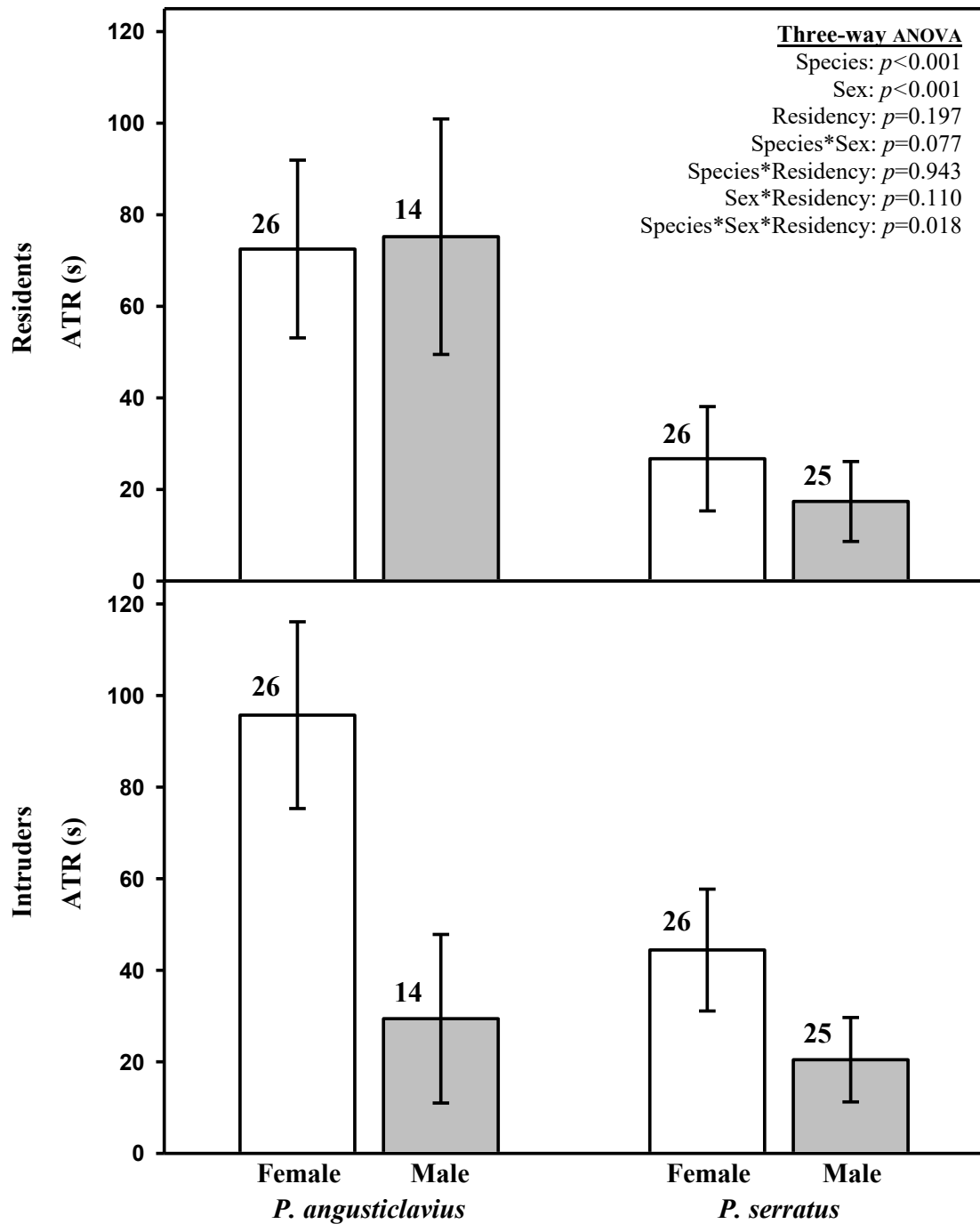


Figure 4. Time spent in the aggressive display All-Trunk Raised (ATR) (mean \pm 1 SE) for males and females of *Plethodon angusticlavius* and *P. serratus*. The top graph is for territorial residents and the bottom is for intruders. Sample size (N) for each group is listed above each corresponding column.

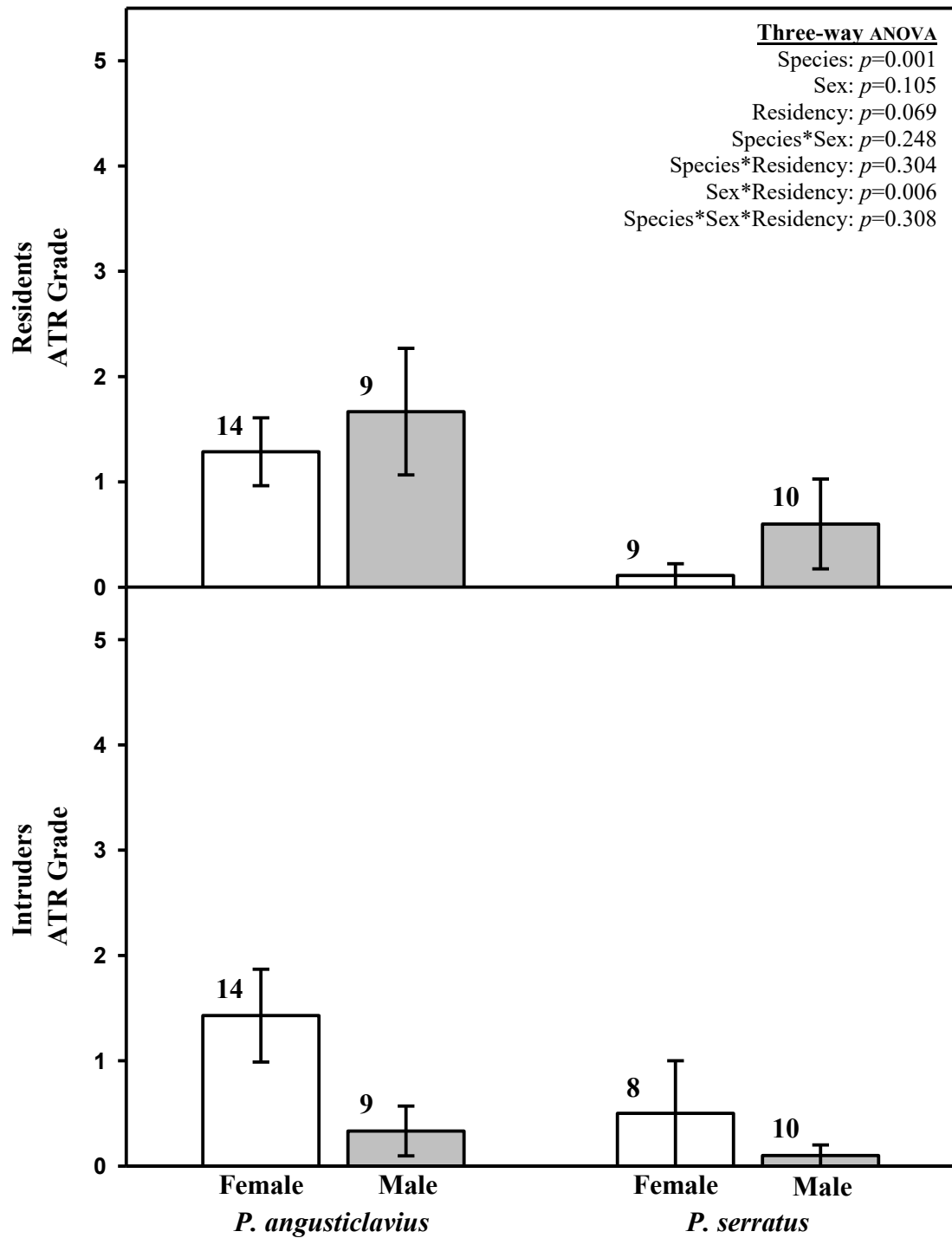


Figure 5. Greatest intensity (grade) of aggressive display All-Trunk Raised reached (ATR) (mean \pm 1 SE) for males and females of *Plethodon angusticlavius* and *P. serratus*. The top graph is for territorial residents and the bottom is for intruders. Sample size (N) for each group is listed above each corresponding column.

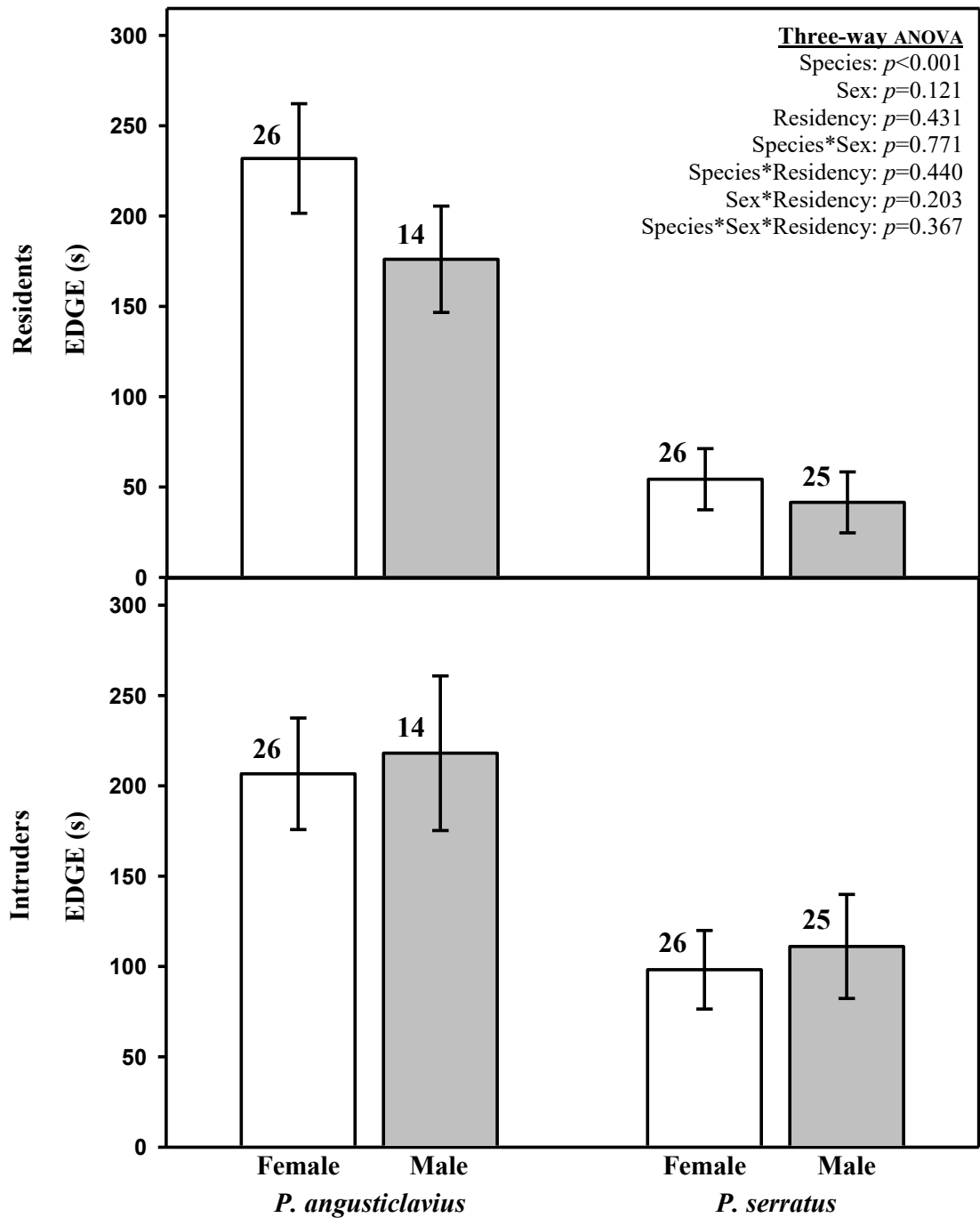


Figure 6. Time spent in the submissive display (EDGE) (mean \pm 1 SE) for males and females of *Plethodon angusticlavius* and *P. serratus*. The top graph is for territorial residents and the bottom is for intruders. Sample size (N) for each group is listed above each corresponding column.

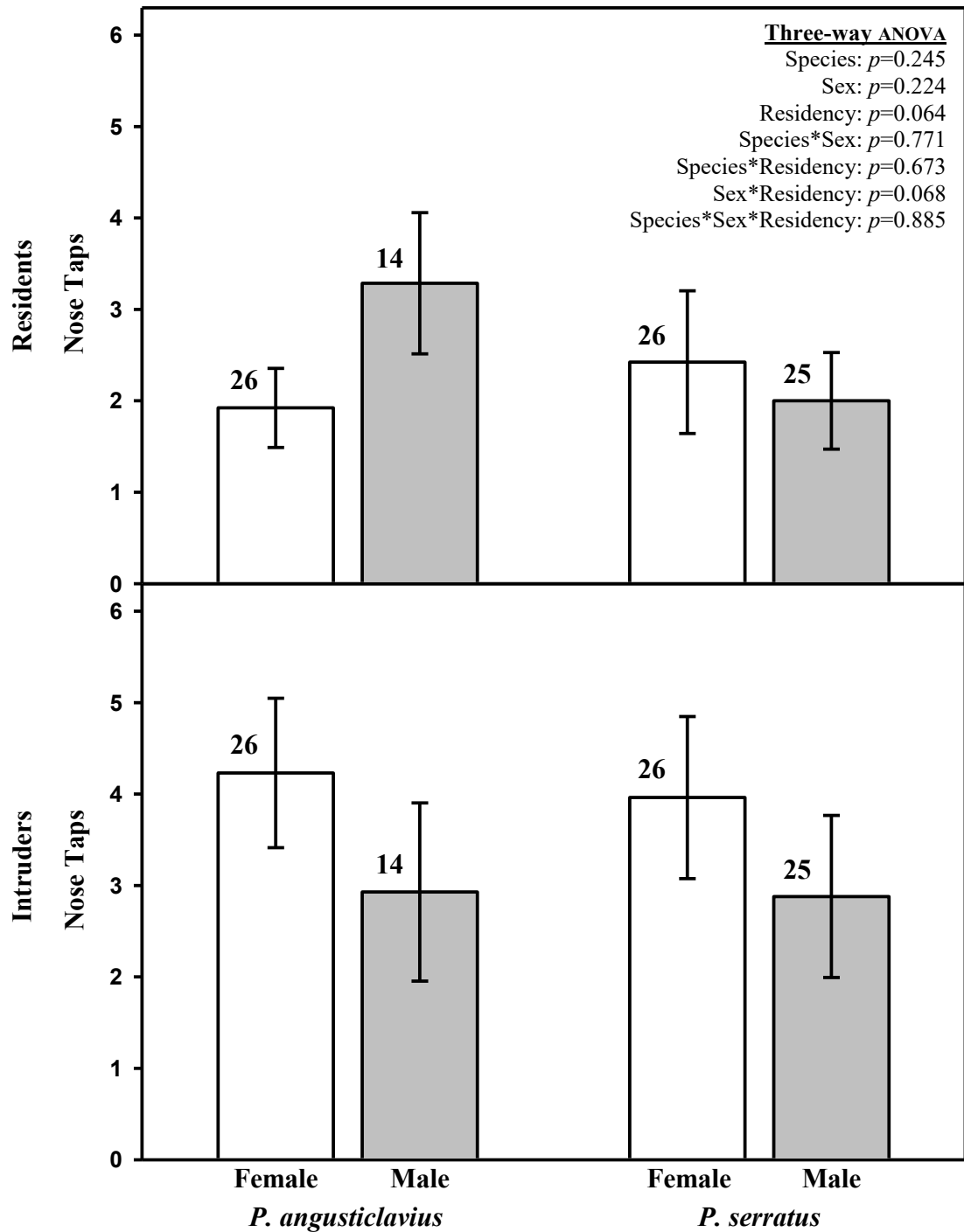


Figure 7. Number of chemosensory Nose Taps (mean \pm 1 SE) for males and females of *Plethodon angusticlavius* and *P. serratus*. The top graph is for territorial residents and the bottom is for intruders. Sample size (N) for each group is listed above each corresponding column.

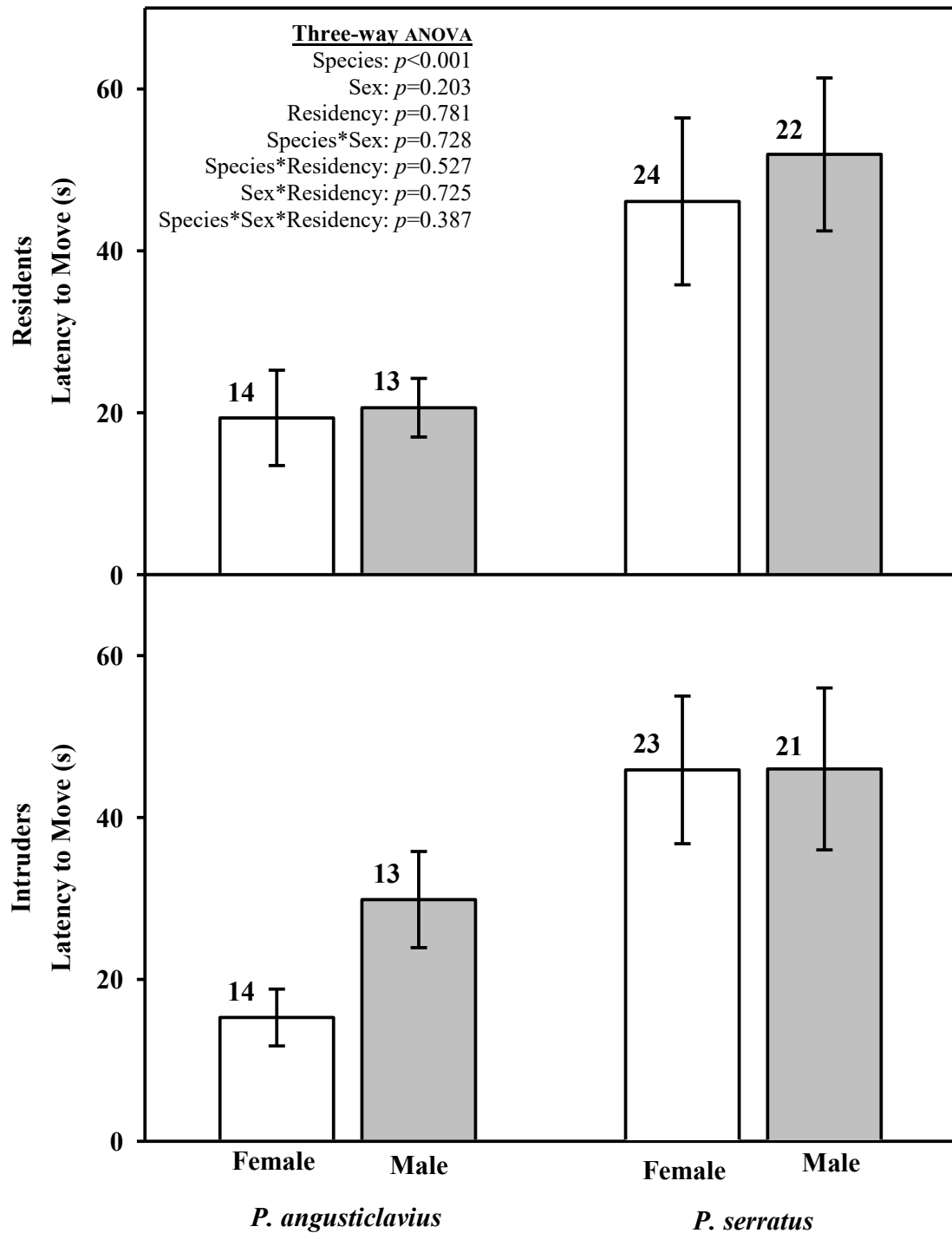


Figure 8. Latency to move (mean \pm 1 SE) for males and females of *Plethodon angusticlavius* and *P. serratus*. The top graph is for territorial residents and the bottom is for intruders. Sample size (N) for each group is listed above each corresponding column.

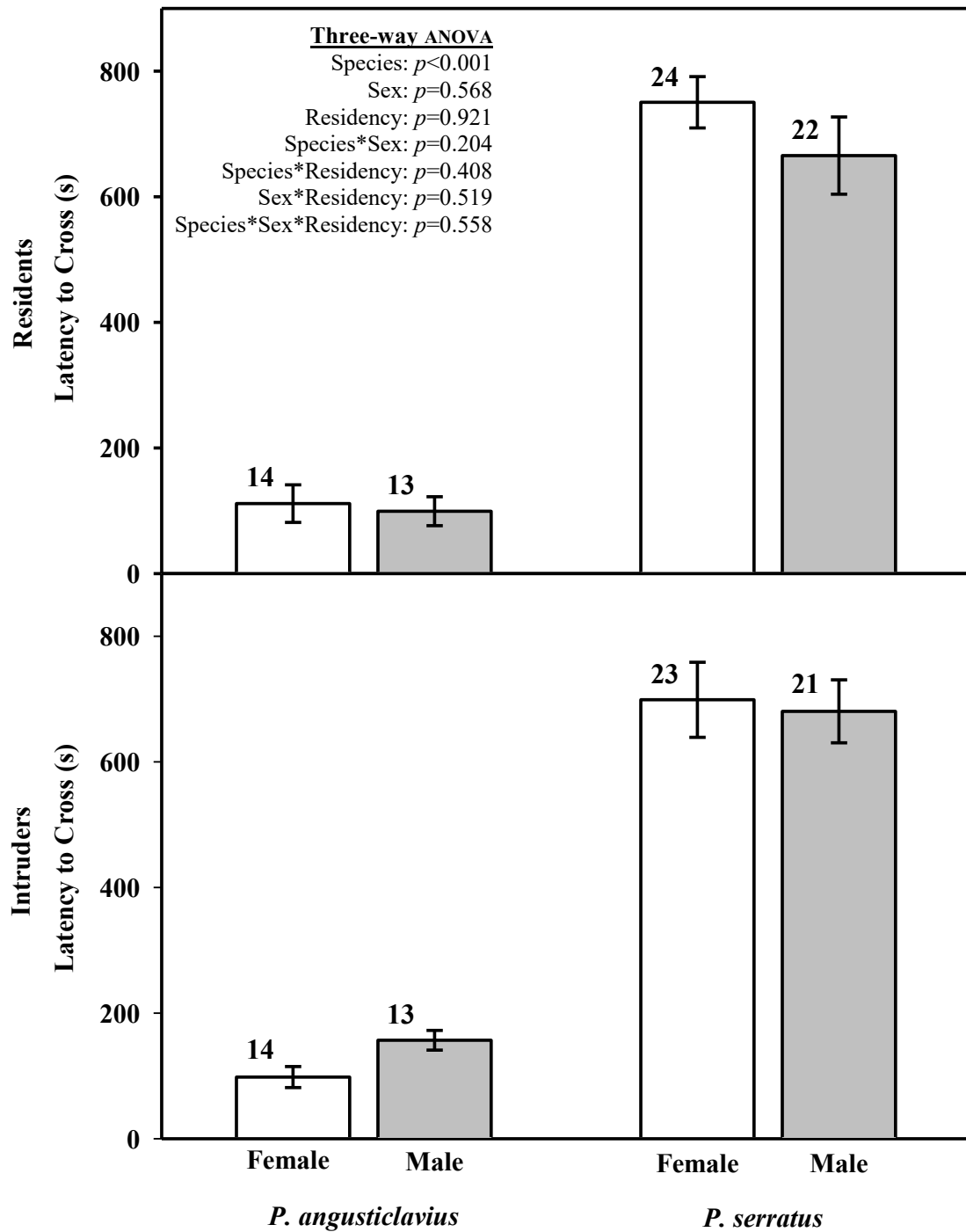


Figure 9. Latency to cross (mean \pm 1 SE) for males and females of *Plethodon angusticlavius* and *P. serratus*. The top graph is for territorial residents and the bottom is for intruders. Sample size (N) for each group is listed above each corresponding column.

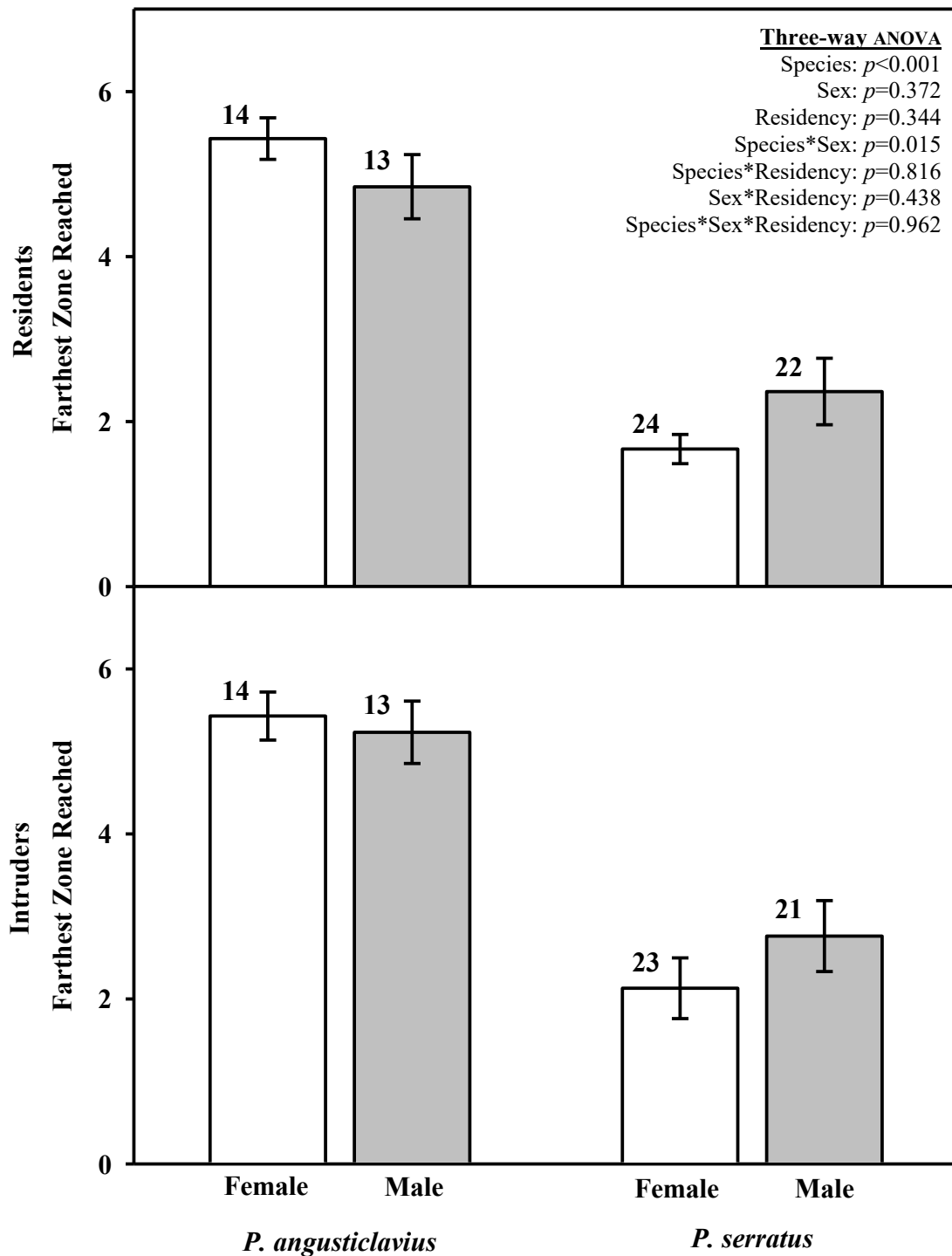


Figure 10. Farthest Zone reached (mean \pm 1 SE) for males and females of *Plethodon angusticlavius* and *P. serratus*. The top graph is for territorial residents and the bottom is for intruders. Sample size (N) for each group is listed above each corresponding column.

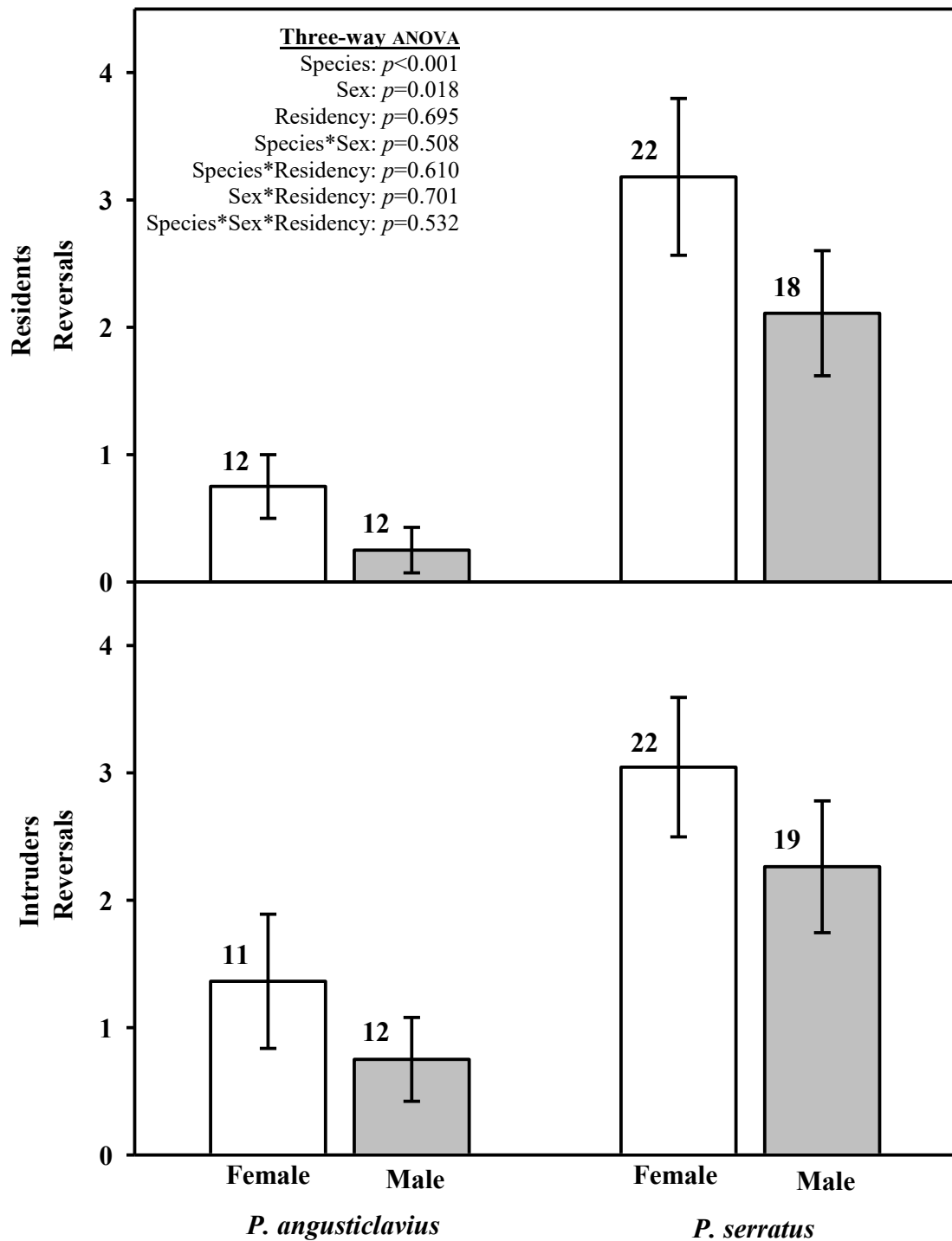


Figure 11. Number of Reversals (mean \pm 1 SE) for males and females of *Plethodon angusticlavius* and *P. serratus*. The top graph is for territorial residents and the bottom is for intruders. Sample size (N) for each group is listed above each corresponding column.