Original Article

Female anoles display less but attack more quickly than males in response to territorial intrusions

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Fighting to defend a territory can be costly due to the risk of injury associated with physical combat. Therefore, many species rely on displays that allow individuals to assess one another, avoid escalation, and mitigate the costs of physical conflict. Most studies of territorial aggression have been conducted in the context of male–male competition, and although females of many species are also aggressive, direct comparisons of male–male and female–female aggression are rare. Consequently, the relative extent to which males and females of territorial species use behavioral displays and physical aggression to mediate intrasexual competition is generally unknown. To address this question, we experimentally introduced same-sex intruders onto the territories of male and female brown anole lizards (*Anolis sagrei*). We found that, although males were slightly more likely to attack an intruder than were females, males also allowed a greater amount of time to elapse before escalating to an attack, relative to females. Males also exhibited more aggressive display behaviors (dewlap extensions, push-ups, and head-bobs) before engaging in a physical attack. These results are consistent with the idea that, due to a potentially greater risk of injury, males may attempt to avoid escalating to physical conflict. The high rates of attack and low latency to attack that we observed for interactions between females also run counter to the general assumption that males are categorically more aggressive in territorial, polygynous species characterized by extreme male-biased sexual size dimorphism.

Key words: **aggression, *Anolis sagrei*, display behavior, fighting, intrasexual competition, territoriality.**

INTRODUCTION

Competition among males often involves fighting with weapons such as antlers, horns, claws, and jaws (Clutton-Brock 1982; Moczek and Emlen 2000; Gvozdík and Damme 2003; Pratt et al. 2003). Such weapons render fighting dangerous because they can inflict serious and even fatal injuries (Jakobsson et al. 1995; Neat et al. 1998; Watson and Field 2004). Consequently, males often use behavioral displays to avoid escalation to physical aggression, particularly when the potential combatants are mismatched in size or fighting ability (McElligott et al. 1998; López and Martín 2001; Logue et al. 2010). Females of many species also interact aggressively when competing for resources such as food, nest sites, and reproductive opportunities (Slagsvold and Lifjeld 1994; Sandell and Smith 1997; Pruetz and Isbell 2000; Clutton-Brock 2007). However, the extent to which females use behavioral displays to mediate intrasexual aggression is largely unknown (Edwards and Lailvaux 2013; Cain and Rosvall 2014).

Theory predicts that escalation to physical combat occurs when the probable benefits of fighting outweigh the expected costs to an individual (Smith and Parker 1976; Clutton-Brock et al. 1979). Given that the nature and magnitude of these costs and benefits likely differ between males and females owing to differences in their reproductive strategies, it is expected that the sexes will also differ in their use of behavioral displays and/or physical aggression to resolve intrasexual competition. However, due to a historical focus on male–male aggression and its associated behaviors, relatively few studies have directly asked whether the frequency of physical aggression and associated behavioral repertoires differs between conspecific males

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and females (Foote 1990; Albert et al. 1992; Grant and Foam 2002; Arnott and Elwood 2009). To address this question, we conducted an experiment in free-living brown anole lizards (*Anolis sagrei*), a species in which intrasexual aggression has been observed in both sexes (Evans 1938; Edwards and Lailvaux 2013), but heretofore studied primarily in males (but see Driessens et al. 2014). We experimentally quantified and compared the behavioral repertoires of adult males and females when confronted with a novel intruder of the same sex by introducing tethered stimulus animals onto the territories of resident anoles (Vinegar 1972; Cooper 1999).

Anolis sagrei is found at population densities of nearly 1 lizard/m² and frequently engages in social interactions (Schoener and Schoener 1980). Both sexes are territorial, but males are 2–3 times more massive than females (Cox and Calsbeek 2010) and typically hold larger territories from which they aggressively exclude other males, and within which females hold smaller territories overlapping those of other females (Schoener and Schoener 1982; Jenssen and Nunez 1998; Paterson 2002). Individuals frequently engage in social displays (Tokarz 1985; Tokarz and Beck 1987), and both sexes communicate with a similar repertoire of visual signals, including head-bobs, push-ups, and extensions of the dewlap, a brightly colored flap of skin that extends from the throat (Orrell and Jenssen 2003; Simon 2007). However, *A. sagrei* males tend to use these behavioral displays to a greater degree than females in a variety of social contexts (Driessens et al. 2014). Male anoles frequently engage in fights that involve biting and can result in serious injuries, but less is known about female aggression (Greenberg and Noble 1944; McMann 1993; Stamps and Krishnan 1997; Stamps and Krishnan 1998; Jenssen et al. 2000). Successful territory defense is likely to confer fitness benefits for both sexes through increased mating success for males and increased food availability to support egg production for females (Trivers 1976; Stamps 1977). Therefore, we predicted that males and females would both respond aggressively toward territorial intruders. Because males have more powerful jaws capable of inflicting serious injury and more conspicuous displays, (i.e., 10-fold larger dewlaps, dorsal and nuchal crests that are absent in females), we predicted that males would be more likely than females to use these elaborate displays, but also show a greater latency than females to escalate to a physical attack (Edwards and Lailvaux 2013; Driessens et al. 2014). The latter prediction runs counter to the simplistic expectation that males of a polygynous, territorial species with extreme male-biased sexual size dimorphism should generally exhibit a greater propensity toward physical aggression, relative to females.

METHODS

We conducted our experiment on 2 spoil islands within the Guana Tolomoto Matanzas Estuarine Research Reserve in northern Florida (29°63′N, 81°21′W). We conducted all behavioral observations between 9:00 and 18:00 from 29 July to 2 August 2015. This period is during the middle of the lengthy reproductive season, which spans from approximately March to October in other Florida populations of *A. sagrei* (Lee et al. 1989). At the time of our study, females are expected to be producing eggs at near peak levels, and males have enlarged testes and elevated plasma testosterone levels (Lee et al. 1989; Tokarz et al. 1998).

We staged a total of 85 territorial intrusions by introducing a tethered stimulus male onto the territory of a focal male (n = 43 individual focal males), or a tethered stimulus female onto the territory of a focal female (n = 42 individual focal females). We use the

term "territory" with the reasonable assumption that focal individuals (which were alert, visually conspicuous, and stationary when first encountered) were challenged on their actual territories. For each introduction, we used a stimulus animal collected that same day from the other island, thereby ensuring that the focal animal had never previously encountered the stimulus animal. We measured each stimulus animal for snout-vent length (SVL, nearest mm) and body mass (nearest 0.01 g), deployed it for up to 3 successive trials, then released it on the same day at its location of capture on its home island. Before release, we gave each stimulus animal a paint mark on its dorsum to prevent its inadvertent use in a subsequent trial.

We tethered the stimulus animal to a 3 m telescoping fishing pole with a 1 m length of the braided fishing line (Spiderwire 30lb test, Pure Fishing, SC), then gently placed it within 1 m of an otherwise undisturbed focal animal of the same sex. We attempted to place each stimulus animal at the same perch height as the focal animal. If this was not possible due to the spatial configuration of available perches, we placed the stimulus animal slightly below, but never above, the focal animal. After introducing the stimulus animal, the observer set the fishing pole on the ground, backed away to a distance of 10 m, and conducted a focal observation through binoculars. Each trial lasted 15 min, or until (1) physical contact occurred between the focal and stimulus animals, or (2) the focal animal fled. During each trial, we recorded in sequence for the focal animal (1) any movement toward or away from the stimulus animal, (2) each extension of the dewlap, and (3) each head-bob (vertical nodding of the head) or push-up (elevation of the anterior portion of the body using the forelimbs). For analysis, we combined head-bobs and push-ups into a single category of behavior due to difficulty discerning between the 2 in some trials, particularly for females. We recorded the end time of each trial and categorized its outcome depending on whether the focal animal attacked (charged the intruder and initiated physical contact), fled (left the vicinity and ceased interacting with the intruder), or reached the end of the 15 min period without attacking or fleeing. We excluded trials in which the focal animal interacted with an individual other than the stimulus animal. At the end of a trial, we captured the focal individual, measured its SVL and body mass, and painted a unique numeral on its flank to avoid unknowingly testing the same focal animal in multiple trials.

Lizards lack a corpus callosum integrating right and left hemispheres of the brain, and can therefore exhibit a bias toward increased aggression when viewing rivals from their left field of view, reflecting lateralization of aggressive behavior controlled by the right hemisphere of the brain (Deckel 1995; Hews and Worthington 2002; Hews et al. 2004). For this reason, we alternated the field of view (right or left) into which the stimulus animal was introduced at the beginning of each trial. During each trial, we recorded all changes in the field of view and classified each individual behavior (dewlap extension, head-bob, push-up, attack) according to the field of view through which the focal animal was observing the intruder at the time when that behavior was expressed. We found no effect of field of view on any aspect of aggression, including the probability of attack, latency to attack, and the frequency of display behaviors, irrespective of whether we separated or combined males and females for analysis (Supplementary Table S1). Consequently, we did not consider the field of view in any subsequent analyses testing for sex differences in behavioral responses.

Statistical methods

To test for a sex difference in the probability of attack, we used logistic regression with the outcome of each trial (1 = attack,

0 = flee or time out) as the response variable and sex as the main effect. To test for a sex difference in the latency to attack, we restricted our analysis to the subset of trials that ended in attack (37 of 43 male; 29 of 42 female) and used generalized linear models with latency to attack (time in seconds) as the dependent variable and sex as the main effect. To test for sex differences in the number of behaviors preceding an attack, we conducted similar analyses using counts of dewlap extensions, head-bobs + push-ups, or total behaviors (dewlap extensions + head-bobs + push-ups) as dependent variables. Because any differences in count data could potentially be explained by differences in the length of trials due to differences in the latency to attack, we also conducted analogous tests for sex differences in the rate (behaviors per minute) of each behavior. Latency to attack, behavioral counts, and behavioral rates were not normally distributed, so we used generalized linear models with a Poisson distribution, a log link, and an overdispersion parameter estimated as the chi-square value divided by the degrees of freedom.

Because body size can affect aggressive interactions in anoles, we ran separate iterations of each of our models including both body size (SVL) of the focal animal and the difference in body size between focal and stimulus individuals (SVL focal–SVL stimulus) as covariates. To make male and female measures of body size equivalent for inclusion in the same model, SVL was standardized to a mean of zero and converted to units of standard deviation. Additionally, we also tested for effects of body size (SVL and mass) or body size difference on the probability of attack, latency to attack, or on the number and rate of display behaviors (Supplementary Tables S2–S5).

Because temperature can influence the behavior of ectotherms, we tested for effects of time of day on aggressive behaviors. Time of day was found to have no effect on probability of attack ($\chi^2 = 2.35$; $P = 0.13$), latency to attack ($F_{1,64} = 0.02$; $P = 0.88$), rate of display behaviors ($F_{1,67} = 1.16$; $P = 0.28$), or number of display behaviors ($F_{1,83} = 1.07$; $P = 0.30$). Therefore, we do not include time of day in any of our analyses.

RESULTS

Sex difference in frequency of attack

Most trials (66 of 85; 77.6%) ended in an attack of the intruder by the focal animal within 15 min (Figure 1). The remaining trials ended with the focal animal fleeing (10 of 85; 11.8%) or with 15 min elapsing without the focal animal fleeing or attacking (9 of 85; 10.6%). In all trials scored as attacks, the focal animal charged, bit, or initiated physical contact with the stimulus animal. We never observed the stimulus animal attacking the focal animal. Although a greater percentage of male-male trials ended in attack (37 of 43; 86%) than did female–female trials (29 of 42; 69%), this difference was marginally nonsignificant ($\chi^2 = 3.60$; $P = 0.058$; Figure 1a). This difference remained nonsignificant when including a covariate for the body size of the focal animal ($\chi^2 = 2.08$; $P = 0.15$) or for the difference in size between focal and stimulus animals ($\chi^2 = 2.11$; $P = 0.15$).

Sex difference in latency to attack

Across both sexes, trials that concluded with an attack usually (53 of 66; 80%) ended in less than 5 min. When a trial did end in the attack, females displayed a much shorter latency to attack (median/mean: 104/119 s) than did males (median/mean: 186/226 s), and this difference was highly significant ($\chi^2 = 9.63$; $P = 0.002$;
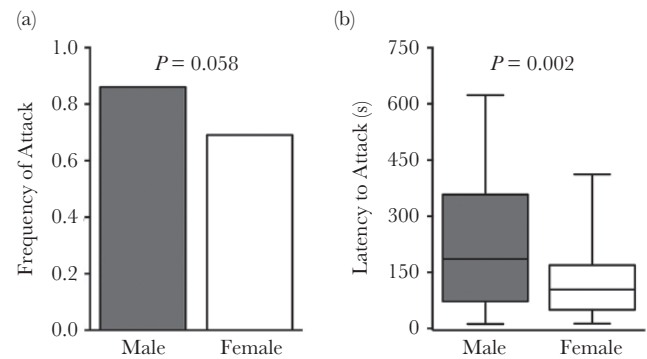

Figure 1
Sex differences in (a) frequency of attack and (b) latency to attack between focal males and females challenged with a same-sex territorial intruder. (a) The proportion of trials that ended in an attack of the intruding animal, shown separately for $n = 43$ and 42 focal males and females, respectively. (b) Median (bar), 25–75% interquartiles (box), and 5–95% percentiles (whiskers) for elapsed time until the attack in the subset of trials that ended in the attack. See text for statistical details.

Figure 1b). This sex difference remained significant when including a covariate for the body size of the focal animal ($\chi^2 = 12.35$; $P < 0.001$) or for the difference in size between focal and stimulus animals ($\chi^2 = 12.62$; $P < 0.001$).

Nearly half (48%) of the attacks by resident females occurred within 90 s of our staged territorial intrusions, and nearly all (97%) of the attacks by females occurred within 5 min. By contrast, less than a third (30%) of attacks by males occurred within 90 s, and only two-thirds (68%) of the attacks by males occurred within the first 5 min.

Sex difference in display behavior preceding attack

For trials that ended in the attack, females performed display behaviors in 23 of 29 trials while males displayed in 34 of 37 trials. In these trials that ended in attack, females performed fewer head-bob and push-up behaviors ($\chi^2 = 12.95$; $P < 0.001$; Figure 2a), fewer dewlap extensions ($\chi^2 = 22.86$; $P < 0.001$; Figure 2c) and fewer total display behaviors (dewlap extensions + head-bobs + push-ups) than did males before attacking the intruding stimulus animal ($\chi^2 = 23.53$; $P < 0.001$; Figure 2e). When body size of the focal animal was included in these models as a covariate, sex differences remained similar for head-bobs and push-up behaviors ($\chi^2 = 12.75$; $P < 0.001$), dewlap extensions ($\chi^2 = 17.39$; $P < 0.001$), and total behaviors ($\chi^2 = 21.20$; $P < 0.001$). When the difference in body size between focal and stimulus animals was used as the covariate, sex differences also remained similar for head-bobs and push-ups ($\chi^2 = 11.70$; $P < 0.001$), dewlap extensions ($\chi^2 = 18.75$; $P < 0.001$), and total behaviors ($\chi^2 = 19.45$; $P < 0.001$).

When these data were expressed as rates of behavior rather than numbers of behaviors, females also exhibited lower rates of head-bobs and push-ups ($\chi^2 = 5.48$; $P = 0.019$; Figure 2b), dewlap extensions ($\chi^2 = 32.29$; $P < 0.001$; Figure 2d), and total display behaviors ($\chi^2 = 9.24$; $P = 0.002$; Figure 2f). Again, these results were qualitatively similar when body size of the focal individual was included as a covariate; females exhibited lower rates of head-bobs and push-ups ($\chi^2 = 11.70$; $P < 0.001$), dewlap extensions ($\chi^2 = 18.15$; $P < 0.001$), and total display behaviors ($\chi^2 = 19.45$; $P < 0.001$). When the difference in body size between focal and stimulus animals was the covariate, results remained significant for effects of sex
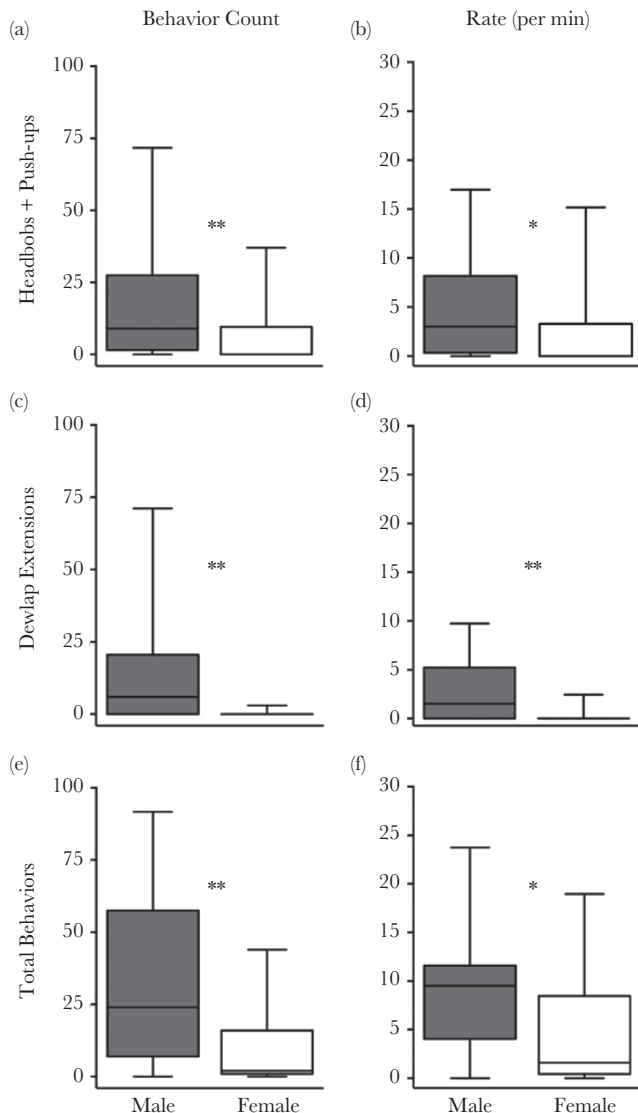
Figure 2
Sex differences in the number (a–c, left column) and rate (d–f, right column) of aggressive behaviors for trials that ended in an attack of the same-sex terriorial intruder. Data are medians (bar), 25–75% interquartiles (box), and 5–95% percentiles (whiskers). Total behaviors (lower panels) represent the sum of behavioral categories reported separately in the upper and middle panels. **$P < 0.001$; *$P < 0.02$. See text for statistical details.

on head-bobs and push-ups ($\chi^2 = 6.12$; $P = 0.012$), dewlap extensions ($\chi^2 = 21.77$; $P < 0.001$), and total display behaviors ($\chi^2 = 7.82$; $P = 0.002$).

DISCUSSION

Our experimental introductions revealed that both male and female brown anoles use a combination of visual displays and physical attacks to defend their territories against same-sex intruders. Although male–male interactions were slightly more likely to result in physical attacks (86%) than were female–female interactions (69%), this difference was not significant, such that most trials in each sex culminated in an attack of the novel intruder. However, males did exhibit an increased latency to attack, which was accompanied by an increased rate and duration of signaling using dewlap extensions,

head-bobs, and push-ups. Although females also signaled to intruders using these same behaviors, notably head-bobs, they tended to instigate physical attacks more quickly and with less behavioral preamble than males. These results are consistent with the hypothesis that male anoles, which sometimes engage in prolonged and costly fights involving wrestling and harmful biting with their enlarged jaws (Cooper 1977; Lailvaux and Irschick 2007), have an expanded morphological and behavioral repertoire (e.g., enlarged dewlap, dewlap extensions) which they use as a primary response to territorial intrusion before resorting to physical attacks. More broadly, our results are consistent with a game-theory view of animal combat, which predicts that individuals will benefit from assessing the ability of rivals and avoiding dangerous contests when costs are likely to outweigh benefits (Emlen 2008). Although this view has often been applied to male contests involving weaponry, it is equally applicable to predictions about female behavior even if sex differences dictate that the potential costs and benefits will be different than in a male contest.

Our results are noteworthy in demonstrating that female anoles attack more quickly and with less visual signaling than males. Nearly all (97%) of the attacks by resident females occurred within 5 min of a territorial intrusion. By contrast, only two-thirds (68%) of the attacks by males occurred within the first 5 min. These data are consistent with the idea that the risk of intense combat and serious injury may be relatively lower for females, lessening their reliance on elaborate behavioral displays to avoid physical aggression (Stamps 1977). Reports of prolonged combat involving wrestling and biting are generally restricted to male anoles (Vanhooydonck et al. 2005), and males of many *Anolis* species have larger jaws that are capable of exerting greater bite force than those of females (Herrel et al. 2006, 2007). In *A. sagrei*, males produce a bite force that is more than 400% greater than that produced by females, and it is not clear whether females generally create enough bite force to inflict significant injuries (Edwards and Lailvaux 2013). The presumably lower risk of injury in female–female combat may therefore explain why females in our study were quicker to attack a same-sex intruder. The fitness benefits of successful territory defense are likely greater in male anoles (e.g., increased mating opportunities and reproductive success) than in female anoles (e.g., preferred basking or retreat sites, access to prey), given the elaborate behavioral displays of males and their propensity to engage in prolonged wresting and biting (Jenssen et al. 2000). However, the fact that females in our study quickly and consistently defended their territories against intruding females implies that territory defense confers fitness benefits in both sexes. These results add to the expanding body of work demonstrating that strong predictions about female–female aggression can often be made when its costs and benefits are considered together (Rosvall 2011; Cain and Ketterson 2013).

Female–female aggression has been documented in several *Anolis* species, but it is generally unknown how frequently females fight in the wild. The relative frequency with which females in our study engaged in intrasexual aggression suggests that by some metrics (e.g., the frequency of and latency to attack), females of polygynous species can be as aggressive as males in territorial defense. It is conceivable that rates of aggression in our study may have been artificially high because stimulus animals were tethered and unable to avoid escalation, and because they were novel intruders without any prior history of social interactions with the focal individuals. The "dear enemy" phenomenon suggests that for many animal species, fighting between neighbors decreases after dominance or territorial boundaries are established (Fisher 1954; Jaeger 1981). This has been shown in lizards generally and anoles specifically (Qualls and Jaeger 1991; Fox and Baird 1992; Paterson and McMann 2004). This decrease in fighting

between neighbors could be particularly important for female anoles because their territories tend to overlap one another more than those of males overlap one another (Jenssen and Nunez 1998). Our focal animals may have been much more likely to escalate conflicts against these novel intruders than they would have been against a familiar intruder from a neighboring territory. However, each of these explanations applies similarly to males and females, so any upward bias in aggression under our experimental design is unlikely to account for the sex differences we observed. An additional caveat to our experiment is that we directly compared males and females in their use of a behavioral repertoire that is shared by both sexes, but it is possible that the signals we measured are not equivalent for each sex. Although push-ups and head-bobs have the same amplitude in males and females of other anole species (Jenssen et al. 2000), the dewlap itself is sexually dimorphic in *A. sagrei* (8–10× larger in males; Cox et al. 2015) and in many other anoles (Harrison and Poe 2012). The larger dewlap of males implies a greater functional significance relative to females and likely allows for signaling across greater distances (Jenssen et al. 2000). Despite any sex differences in use of and information conveyed by behavioral displays, our data clearly show that *A. sagrei* females provide fewer displays before escalating to physical conflict.

Collectively, our data show that both male and female brown anoles typically respond to same-sex territorial intruders with behavioral displays and overt physical aggression. Although males exhibited significantly more aggressive behavioral displays before the attack, they were not significantly more likely to attack intruders than were females, and females were significantly quicker than males to attack an intruder. These results are broadly consistent with the hypothesis that females will escalate to physical conflict more quickly because the risk of injury is relatively low, though further study is required to test this hypothesis directly. Taken together, our results run counter to the assumption that males are categorically more aggressive than females in territorial, polygynous species characterized by male-biased sexual size dimorphism.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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