



Do interspecific interactions between females drive shifts in habitat use? A test using the lizards *Anolis carolinensis* and *A. sagrei*

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An important goal in evolutionary ecology is to understand how and why coexisting closely related species partition habitat among themselves. Although studies of interspecific interactions typically focus on males, interactions between females may also play an important role in shaping habitat use within multi-species communities. The green anole (*Anolis carolinensis*) exhibits a wide range of habitat use in south-eastern Louisiana, but its observed habitat use is restricted and altered in areas where it occurs with the introduced *Anolis sagrei*. We staged interactions between these two species in the laboratory to test the hypothesis that *A. sagrei* dominate *A. carolinensis* in contests over shared habitat. We examined whether species identity, bite force, dewlap size, and body size affected the outcome of interspecific interactions between both males and females, and tested the prediction that bite force and size would be the most important determinants of interaction outcomes in both sexes. In male interspecific interactions, we found that individuals with relatively larger dewlaps tended to score higher on aggressive behaviours regardless of species identity, and that interactions consisted of signalling and rarely escalated to physical combat. However, we found that *A. sagrei* females achieved higher aggressive scores than *A. carolinensis* females in almost all cases, lending support to the notion that female interspecific behaviour is probably more important than male behaviour in driving changes in habitat use. © 2013 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2013, 110, 843–851.

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INTRODUCTION

In areas where two or more ecologically similar species exploit a range of common resources, selection may drive each species to specialize on part of that range, thereby constraining each species' niche width and reducing potentially costly competitive interspecific interactions (Andrewartha & Birch, 1954; Schluter, 1994). For instance, in the well-known adaptive radiation of Galapagos finches, each of at least 13 species possesses particular characteristics (e.g. specialized beaks), allowing them to partition their resource use so that competition is minimized (Schluter, 2000). Similarly, the adaptive radiation of cichlid fish is also thought to be driven in part

by specialization of the feeding apparatus to specific resource niches (Fryer, 1996; Sturmbauer, 1998; Takahashi & Koblmüller, 2011). This notion of ecological character displacement has undergone a revival in recent years (Stuart & Losos, 2013), but despite a great deal of interest in the evolutionary implications of such interspecific interactions, the proximate behavioural competitive mechanisms, such as aggressive behaviours, leading to specialization on key resources have received relatively little attention (Grether *et al.*, 2009; but see Adams, 2004; Peiman & Robinson, 2007; Laiolo, 2013 for some examples).

The nature of the competitive interactions driving such resource specialization may vary among taxa or with the contested resource. In the case of direct interspecific competition over habitat use, aggressive signalling and physical confrontations are likely to be important in governing access to desirable habitat

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(Brawn, 1990). While aggression within a species generally arises as a result of male competition over resources or mates, interspecific aggression is often triggered by common resource overlap in sympatric species or poor species recognition (Nishikawa, 1987). Repetitive aggressive interspecific interactions over time, however, can result in almost complete separation of resource use, such that a given species may be asymmetrically constrained and consistently dominated by another (Robinson & Terborgh, 1995; Peiman & Robinson, 2010). This can make interpretations of observed current-day interactions (if any) difficult, because the historical factors leading to such ecological outcomes are often unclear (the 'ghost of competition past'; Connell, 1980). Indeed, a common hurdle facing researchers interested in studying the development of specialization within ecological communities is that they are often forced to start with complete species assemblages and reason backwards (Schluter, 2000; Losos & Mahler, 2010).

The flipside of specialization is ecological release, whereby a species entering a new environment is able to exploit a wider range of resources than in its native range (Cox & Ricklefs, 1977; Bolnick *et al.*, 2010). Invasive species often experience such release as a result of introduction into a new ecological milieu, allowing them to make use of new or different resources, often at the expense of native species (e.g. Petren & Case, 1996; Shine, 2010). In doing so, invasive species can alter the resource use of natives, thereby imposing strong selection pressure for specialization upon those native species. These interactions between species may result in niche partitioning and/or ecological character displacement (Tynkkyne, Rantala & Suhonen, 2004; Peiman & Robinson, 2007, 2010; Grether *et al.*, 2009; Anderson & Grether, 2010; Pearce, Pryke & Griffith, 2011), and could ultimately play a very important role in shaping ecological communities. Competitive interactions between invasive and native species that have occurred in sympatry for only a short period of time and that compete for shared resources therefore offer a unique opportunity to observe the proximate behavioural origins of specialization on a small scale (Hess & Losos, 1991; Losos & De Queiroz, 1997; Bolnick *et al.*, 2010).

The invasion and advance of the lizard *Anolis sagrei* throughout the south-eastern United States has the potential to greatly impact the ecology and behaviour of both *A. sagrei* and the native green anole lizard, *Anolis carolinensis*. *Anolis carolinensis* is the only anole native to the United States and, locally, to New Orleans. The species is morphologically adapted to exploit the trunks and crown areas of trees, and thus is nominally a trunk–crown ecomorph. However, when no other anoles are present, *A. carolinensis* will frequently expand its niche to

include crown–trunk–ground habitat (Echternacht, 1999). By contrast, *A. sagrei* is a trunk–ground eco-morph and is known to adapt very well to new habitats, especially disturbed habitats (Marnocha, Pollinger & Smith, 2011). Although native to Cuba and the Bahamas, *A. sagrei* has been introduced multiple times to the US (Kolbe *et al.*, 2004), including New Orleans. In New Orleans, *A. sagrei* and *A. carolinensis* are both relatively abundant, but the *A. sagrei* population appears to be on the rise in recent years (Lailvaux, unpublished data). Both species share a similar diet, are similarly sized, and experience slight spatial niche overlap even when naturally present together (Campbell, 2000). However, when *A. sagrei* is introduced into an environment previously dominated by *A. carolinensis*, *A. carolinensis* commonly exhibits shifts in habitat use and often becomes rarer within a period of a few years (Echternacht, 1999; Campbell, 2000). Indeed, several studies, including a recent study of anoles in New Orleans, have found that *A. carolinensis* perches significantly higher when *A. sagrei* are present, suggesting that *A. sagrei* are actively displacing the native green anoles (Collette, 1961; Losos & Spiller, 1999; Edwards & Lailvaux, 2012). The factors behind this shift in habitat are currently unclear, but the population in New Orleans offers an ideal study situation to address this question.

We staged male–male and female–female interactions between *A. carolinensis* and *A. sagrei* to investigate the nature of the interspecific interactions that are likely to be driving shifts in habitat use by *A. carolinensis*. Males of both species are highly territorial, and use similar displays consisting of push-ups, bobbing, and dewlap extensions to advertise territory ownership and gain mates. Furthermore, previous studies have shown that bite force is an important determinant of intraspecific male combat outcomes in both of these species (Lailvaux *et al.*, 2004; Lailvaux & Irschick, 2007b). A previous study of staged interactions between *A. carolinensis* and *A. sagrei* demonstrated that both species display more vigorously at conspecifics rather than at been heterospecifics, and suggested that male–male interactions are unlikely to be a key component of competition (Tokarz & Beck, 1987). However, male interspecific interactions have previously been reported in nature (Collette, 1961; Losos, Marks & Schoener, 1993), and so we tested how bite force and relative dewlap size may affect the outcome of fights between these heterospecifics. Finally, while most studies of both inter- and intraspecific aggression focus on males, there is also evidence that females of some *Anolis* species may defend resources and demonstrate territoriality towards similarly sized congeners more so than males (Rand, 1967a, b). The

documented *A. carolinensis* mating system is that of female defence polygyny (Ruby, 1984; Nunez, Jenssen & Ermland, 1997; Jenssen, Lovern & Congdon, 2001), whereby males defend territories containing females or resources that females require. If female green anoles are forced to alter their habitat use by the presence of *A. sagrei*, then the observed shift in green anole male habitat use may simply reflect males following females to their new habitat. We therefore investigated the outcome of female interspecific interactions in a similarly staged setting. However, while females of both species have significantly lower bite forces than males (Herrel, Mcbrayer & Larson, 2007; S. P. Lailvaux, unpubl. data) it is unclear whether females can bite hard enough to inflict significant injury, and bite force might therefore not be expected to be important to female contest resolution. We therefore tested the following specific hypotheses:

1. Outcomes of interspecific interactions between male *A. sagrei* and *A. carolinensis* would be predicted by larger body size and stronger bite force;
2. Outcomes of interactions between female *A. sagrei* and *A. carolinensis* will be predicted by larger body size.

MATERIAL AND METHODS

Adult male and female *A. carolinensis* and *A. sagrei* lizards (55 male and 38 female *A. sagrei*, 56 male and 40 female *A. carolinensis*) were captured from City Park in New Orleans, Louisiana, during April/May 2012. Because both species are present in City Park, location of capture of each individual was noted to avoid staging interactions between potentially familiar animals. Lizards were captured either by hand or with a noose attached to a pole by walking through the habitat during normal activity hours (09.00–17.00 h), and capturing any lizard present. Lizards were then transported to the University of New Orleans to measure morphology, maximum bite force, and staged interactions.

MORPHOLOGY

On the day of capture, we measured body mass to the nearest 0.01 g with a digital balance (Mettler Toledo PR8002 DeltaRange), and snout–vent length (SVL) to the nearest 0.01 mm with digital calipers. After staged interactions, we measured SVL, forelimb length, hind limb length, and head morphology with digital calipers. We measured dewlap size by first extending the dewlap, using forceps to grasp the ceratobranchial near the articulation with the basihyoid, and then photographing the extended dewlap using a Canon Rebel T1i SLR digital camera.

The images were analysed using TPSDIG v. 2.15 to calculate dewlap area (Vanhooydonck *et al.*, 2005; Huyghe *et al.*, 2007; Lailvaux & Irschick, 2007b; Rohlf, 2010).

BITE FORCE

We measured *in vivo* bite force using an isometric Kistler force transducer (type 9023, Kistler) connected to a type 5058a Kistler charge amplifier (see Herrel *et al.*, 1999, 2001 for a detailed description) using standard methods. Lizards were induced to bite a force plate by tapping their cheek until their mouth opened, then lining up the mouth with the centre of the force plate until the lizard bit forcefully. Bite trials were repeated every hour for a total of five trials per animal, and the largest bite force obtained was taken as the maximal bite force for that animal (Adolph & Pickering, 2008; Losos, Creer, & Schulte II, 2002). All lizards were placed in an incubator at 33 °C (approximately the preferred field body temperature for both species; see Huey & Webster, 1976; Lailvaux & Irschick, 2007a) for 1 h prior to trials, and during rest periods in between trials.

STAGED ENCOUNTERS

We staged interactions following methods consistent with those used in previous studies (Lailvaux *et al.*, 2004; Perry *et al.*, 2004; Henningsen & Irschick, 2012). We used a large 38-litre glass aquarium as a test arena, with the sides and back covered with opaque paper. Each end of the arena contained a brick to provide a raised platform for the displays, and each aquarium was initially divided with a clear plastic perforated aquarium divider. *Anolis carolinensis* lizards were paired randomly with *A. sagrei* lizards of the same sex, and one of each pair was placed randomly on either side of the divider. This allowed the animals to see and display to each other, but prevented them from physically interacting. After a 15-min acclimatization period, the divider was removed and we added one perch site beneath a suspended heat lamp (Henningsen & Irschick, 2012). The lizards were free to move throughout the arena for an additional 60 min. Sixty minutes of behaviour was scored for each interaction, not including the acclimatization period, and encounters were recorded with a Sony Handycam digital camera and tripod. Each animal was used in only a single interaction.

We scored behaviour using methods similar to those of Lailvaux *et al.* (2004). All observed agonistic behaviours were assigned positive scores using the following system: head bobs and push-ups, defined as a bout of rapid up-and-down movement of the head or body,

and dewlap display bouts scored as 0.5. Lateral displays, chases, and bites were scored as 1. Lateral displays were defined as an animal turning its body perpendicular to the line of sight of the other animal combined with lateral compression and dorso-ventral expansion. Chases were defined as running towards an opponent. Retreats, defined as running away from an opponent, were scored as -1. Submissive nodding, as described for *A. sagrei* (Simon, 2011), was awarded -0.25. Scores were also awarded for first to perch and longest on perch (0.25 each) and hiding (-0.25). The member of the pair that has the higher cumulative score at the end of the observation period was considered the 'winner'.

ANALYSIS

Male-male interactions

To analyse the effects of morphological characteristics (dewlap, head measurements, mass, SVL) and bite force differences on determining outcomes of staged male interactions, we selected one of the two individuals in each contest at random as the focal individual. If the focal individual exhibited the highest aggressive score, the outcome of the contest was coded as 1, and outcomes for focal males with the lowest score in a dyad were coded as 0. This coding was then entered into a generalized linear model as a binary dependent variable with a logit link (Hardy & Field, 1998; Lailvaux & Irschick, 2007b), using software R v. 2.13.2. Quasibinomial errors were used to correct for over-dispersion identified in the model. The independent variables were the differences in morphological measurements and bite force between the focal individual and the other competitor, plus the interactions between each variable. We also included quadratic terms in the initial models to test for non-linear effects. Model simplification based on deletion tests using log-likelihood ratios allowed the creation of a

'minimum adequate model' to describe the data (Crawley, 1993; Hardy & Field, 1998). To visualize the interactions among variables, we used the *fields* package in R v. 2.13.2 to create three-dimensional response surfaces.

Female-female interactions

Due to the nature of the outcomes of the female-staged interactions (see Results), we did not perform similar modelling analyses on the female data. To test for differences between species in dewlap size, maximum bite force and SVL, we used a one-way MANOVA with species as a factor for both males and females.

RESULTS

MALE-MALE INTERACTIONS

We filmed 55 male-male staged interactions. In five of these interactions, no behaviours were observed during the testing period; consequently, these bouts were excluded from analyses (Lailvaux & Irschick, 2007b). Of the 50 remaining matches, there were 30 *A. sagrei* 'winners' and 20 *A. carolinensis* 'winners'. None of the staged interactions escalated to physical combat. After randomly selecting a focal male from each pair for GLM analysis and removing non-significant terms from the saturated model, our simplest model had two significant two-way interactions, namely SVL/relative dewlap size and bite force/relative dewlap size (Table 1). Because species identity did not explain a significant amount of variation in male contest outcomes in the overall model, either alone or in conjunction with other factors, we pooled data from the two species and estimated the response surface for winning or losing based on dewlap size, SVL, and bite force for all individuals. The resulting three-dimensional response surfaces reveal that

Table 1. Results of the best-fitting minimum adequate model describing the outcomes, in terms of aggressive scores, of staged interactions between male *A. sagrei* and *A. carolinensis*

Variable	Est. coefficient	SE	Z value	P-value
Intercept	-0.825	0.453	-1.824	0.075
SVL	0.058	0.101	0.579	0.565
Bite	-0.160	0.179	-0.891	0.378
Dewlap	0.641	1.275	0.503	0.618
SVL:dewlap	0.910	0.405	2.248	0.030
Bite force:dewlap	-1.268	0.671	-1.891	0.065

AIC = NA

Null deviance = 66.406 on 49 d.f

Residual deviance = 49.262 on 44 degrees of freedom

Number of Fisher scoring iterations: 6

Dispersion parameter for quasibinomial family taken to be 1.291

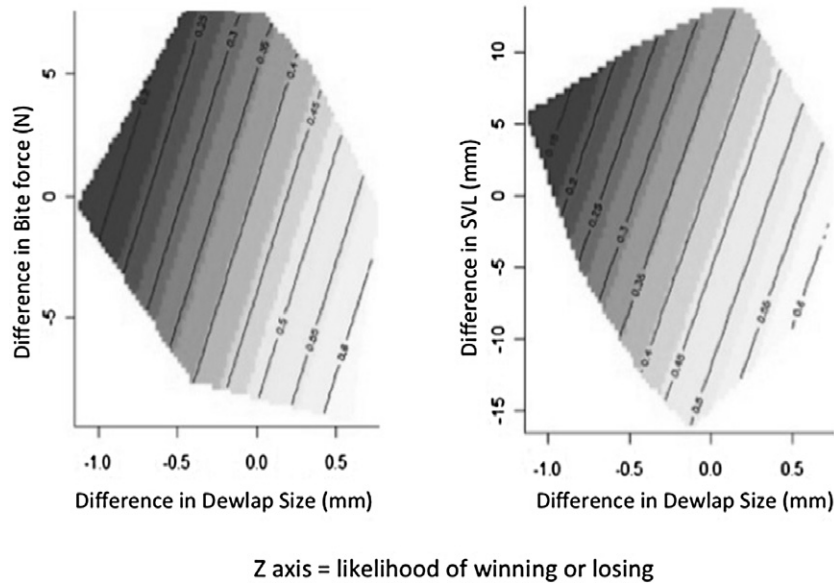


Figure 1. Non-parametric response surfaces of male interactions. These two models are three-dimensional response surfaces of the two significant two-way interactions. The z -axis represents the likelihood of winning a fight, where light colours are peaks, and the dark areas are valleys. Surface A shows the interactions between difference in maximum bite force (N) and difference in dewlap size (mm^2), while surface B demonstrates interactions between difference in snout–vent length/SVL (mm) and difference in dewlap size (mm^2).

individuals with large dewlaps relative to both maximum bite force (Fig. 1A) and SVL (Fig. 1B) accrued higher aggressive scores, regardless of species identity. These results are very robust, and hold whether *A. sagrei* and *A. carolinensis* are analysed together in a global model or in separate models.

FEMALE–FEMALE INTERACTIONS

We filmed 38 female–female staged interactions. In 36 of these *A. sagrei* scored higher based on observed behaviour, again with no escalated combat occurring (Fig. 2).

We also compared body size, dewlap size, and maximum bite force for both males and females between the two species, *A. carolinensis* and *A. sagrei*, using a one-way MANOVA (Table 2). Differences in SVL, dewlap size, and bite force were all significantly different (Pillai's trace = 0.9974; SVL: $F_{1,100} = 97.75$, $P < 0.001$; dewlap size: $F_{1,100} = 15.56$, $P < 0.001$; bite force: $F_{1,100} = 97.72$, $P < 0.001$) between males of each species, while SVL and bite force were significantly different between females of each species (Pillai's trace = 0.9975; SVL: $F_{1,74} = 249.28$, $P < 0.001$; bite force: $F_{1,74} = 133.89$, $P < 0.001$). *Anolis sagrei* females have a larger relative dewlap size than *A. carolinensis* females in relation to SVL, although the difference was not statistically significant (Pillai's trace = 0.9975; $F_{1,74} = 0.867$, $P = 0.354$).

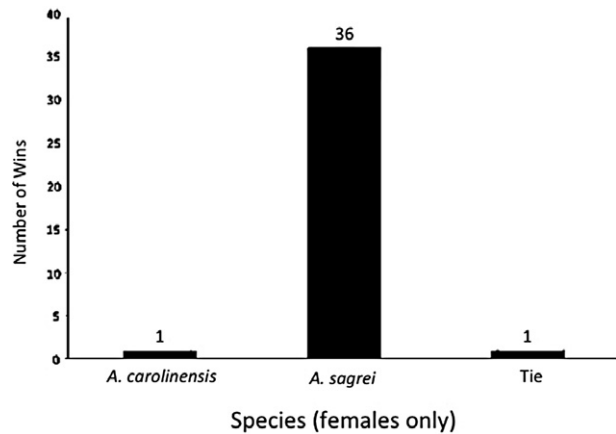


Figure 2. Of 38 female–female interactions, one was a tie, one was won by an *A. carolinensis* female, and the other 36 were won by *A. sagrei* females.

DISCUSSION

Multiple factors can play a role in driving apart habitat use in sympatric species. Here we tested two specific hypotheses to investigate whether interspecific interactions between now-sympatric *A. sagrei* and *A. carolinensis* in south-eastern Louisiana were a possible cause of observed shifts in habitat use by *A. carolinensis*. We found that in male–male interactions, individuals with the higher aggression scores were those with larger dewlaps relative to both

Table 2. Average body size (snout–vent length) and average dewlap size by sex and species; despite the shorter average body size of male *A. sagrei*, *A. carolinensis* males have a smaller average dewlap size

Species	Average SVL \pm SE (mm)	Average dewlap size \pm SE (mm ²)	Average bite force \pm SE (N)
<i>A. sagrei</i> (male)	56.662 \pm 0.393	1.943 \pm 0.039	5.850 \pm 0.163
<i>A. carolinensis</i> (male)	63.318 \pm 0.555	1.693 \pm 0.051	9.827 \pm 0.372
<i>A. sagrei</i> (female)	42.021 \pm 0.326	0.270 \pm 0.010	1.369 \pm 0.010
<i>A. carolinensis</i> (female)	50.426 \pm 0.450	0.286 \pm 0.010	2.936 \pm 0.101

dewlap size and body size, regardless of species identity (Fig. 1). The results for females, however, were strikingly different, with *A. sagrei* females scoring higher in almost every interspecific interaction with *A. carolinensis* females, despite female green anoles being larger, with stronger bite forces. Thus, our first hypothesis (i.e. that outcomes of aggressive interactions between male *A. sagrei* and *A. carolinensis* would be predicted by stronger bite forces among species) was not supported. Furthermore, our second hypothesis was also not supported, as our results indicate that species identity is the most important factor driving female–female interaction outcomes as opposed to size.

MALES

Although *A. sagrei* scored higher in a majority of the staged interactions in this study (30 out of 50), they did not ‘win’ significantly more bouts than *A. carolinensis*, and indeed species identity was not a significant factor in the model (Table 1, Fig. 1). Instead, the response surfaces for males indicate that large dewlaps in combination with both small body size and low bite force relative to those of an opponent predict outcomes in interspecific interactions, strongly suggesting that relative dewlap size is the key trait in such competitive situations (Fig. 1). Although the ecology of anole dewlaps is poorly understood, previous studies have posited a role for the dewlap in interspecific recognition and signalling contexts (reviewed by Losos & Chu, 1998; Losos, 2009; Vanhooydonck *et al.*, 2009); nonetheless, direct measures of the value of dewlap size in competitive interspecific contexts are few. Another possibility to be taken into account for future work is differences in dewlap colour or brightness, as several studies have shown that UV reflectance can influence either intraspecific contest outcomes (Bajer *et al.*, 2011) or the likelihood of being challenged by rivals (Stapley & Whiting, 2006) in male *Lacerta viridis* and *Platysaurus broadleyi* lizards, respectively. Our results differ from those obtained for intraspecific anole male combat, which tend to show that dewlap

size is less important than bite force for winning fights in territorial anoles (Lailvaux & Irschick, 2007b). However, in this study, as in previous studies using *A. sagrei* and *A. carolinensis* species (e.g. Tokarz & Beck, 1987), staged interactions consisted almost entirely of signalling and rarely escalated to physical combat. This result is in contrast with documented staged interspecific interactions between some other anole species where escalated aggression was observed (e.g. Losos, 1985). The lack of escalated physical interactions between male *A. carolinensis* and *A. sagrei* is perhaps surprising given that each of these dimorphic, territorial species engages in physical confrontations with conspecific males (Lailvaux *et al.*, 2004; Lailvaux & Irschick, 2007b). Furthermore, the shift in habitat use and lower population densities of *A. carolinensis* in the presence of *A. sagrei* (Losos & Spiller, 1999; Edwards & Lailvaux, 2012) is consistent with what one might expect if these species are competing over habitat resources. On the other hand, theory also predicts that interspecific interactions are likely to be less intense and physically aggressive than intraspecific interactions, especially in situations where mistaken identity and interbreeding are unlikely (Brunswick, 1979; but see Lailvaux, Huyghe & Van Damme, 2012). Both anole species exhibit female-defence polygyny, but given that male green and brown anoles are unlikely to mistake each other for the same species, and that the rate of inbreeding between these species is probably extremely rare if it occurs at all (Losos, 2004), our results therefore suggest that habitat separation between these two species is not driven by interspecific aggression between males, despite the appearance of competitive exclusion based on male habitat data (Hess & Losos, 1991).

FEMALES

In contrast to the results from the male–male trials, where species identity was found not to be a significant factor predicting interspecific outcomes, we found that outcome of female interspecific interactions were heavily asymmetric in favour of *A. sagrei*.

In fact, of the 38 female–female interactions staged, *A. sagrei* females received the highest aggressive score in all but two trials (Fig. 2). *Anolis sagrei* females appeared to have larger dewlaps relative to body size, as found in the male staged interactions, but due to the one-sided outcomes of the female–female trials, there is insufficient variation in contest outcomes to estimate the relative importance of dewlap size and species identity statistically (see Table 2, with female dewlap/SVL).

Based on our results, aggressive female interspecific outcomes appear to be based almost entirely on species identity rather than phenotypic trait values, with female *A. sagrei* scoring consistently more aggressive behaviour than *A. carolinensis* regardless of differences in body size, dewlap size, or bite force. If this is true in natural settings as well, the observed shift in green anole habitat use is likely to be driven by *A. carolinensis* females moving higher in response to aggressive *A. sagrei* females with males following them in order to base their territories around female positions. Furthermore, *A. carolinensis* males also generally perch higher than females (Irschick *et al.*, 2005), probably contributing further to the observed habitat shift.

It is not surprising that female interspecific behaviour may be more important than male behaviour in driving these changes in habitat use given the *A. carolinensis* and *A. sagrei* female defence polygyny mating system. In general, *Anolis* female territories are based around food availability, and territory size does not change seasonally like those of males (Losos, 2009). Females also maintain consistent levels of aggressive interactions and displays year-round in other anole species (Andrews, 1971; Schoener & Schoener, 1982; Nunez *et al.*, 1997). As females are defending resources such as food and egg-laying sites, it would make sense for them to defend these resources against all intruders whenever possible. Note that many anoline species use communal egg-laying sites (Rand, 1967c), and it is possible that females may be trying to exclude other females for reasons other than egg-laying. What is surprising, however, is that the ‘winning’ species in these female interactions, *A. sagrei*, exhibits smaller body size, and a weaker maximum bite force than *A. carolinensis*, whereas in males body size and bite force are important combat outcome predictors in dimorphic, territorial anoles (Lailvaux & Irschick, 2007b). Unlike male–male combat, however, female combat has received very little attention, and the morphological and physiological factors that mediate the outcomes of female aggressive interactions are not understood [but see While, Sinn & Wapstra (2009), and Langkilde & Shine (2007), who showed that female aggression is unrelated to body size in the lizard *Egernia whiteii*].

Further studies investigating the nature of female combat would be useful for understanding these interactions. It would be particularly useful to examine female–female interspecific interactions year-round, and not just during breeding periods.

In conclusion, we found evidence that female interspecific behaviour may possibly be more important than male behaviour in driving the well-documented changes in habitat frequently occurring following introduction of *A. sagrei* into areas formerly occupied solely by *A. carolinensis*. This result offers potential insight into the factors driving apart species that use similar habitat resources in the early stages of ecological habitat displacement. However, further studies are required to test whether these behaviours observed in the lab are indicative of behaviour that occurs during interactions between these two species in nature.

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