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MOVEMENT RATES OF THE LIZARD *ANOLIS CAROLINENSIS* (SQUAMATA: DACTYLOIDAE) IN THE PRESENCE AND ABSENCE OF *ANOLIS SAGREI* (SQUAMATA: DACTYLOIDAE)

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ABSTRACT. Shifts in a species' habitat can be precipitated by co-occurring with a closely related, ecologically similar species, to avoid negative interspecific interactions. Such shifts in habitat may also cause a change in movement behavior in sympatric populations compared with allopatric populations. *Anolis carolinensis* lizards are known to shift their habitat to higher perches in the presence of *Anolis sagrei*, and we examine whether movement rates differ between populations of *A. carolinensis* that are allopatric and sympatric with recently arrived *A. sagrei*. We find an interaction between the effects of sex and the presence of *A. sagre*i on movement rates, indicating that males and females respond differently in their movement rates to the presence of a congener. We suggest that variation in the motivation for movement between the sexes may explain intraspecific relationships between movement and habitat.

KEY WORDS: foraging; Florida; spoil islands; invasive species

INTRODUCTION

Habitat use can differ among populations of a species that are either sympatric or allopatric with closely related, ecologically similar species (e.g. Schoener, 1975; Medel *et al.*, 1988; Schluter and McPhail, 1992; Dietrich and Werner, 2003). Interspecific interactions often have negative fitness consequences (Polis *et al.*, 1989; Gronig and Hochkirch, 2008; Grether *et al.*, 2009; Hendry *et al.*, 2009), and shifts in the habitat used by one or both species when they co-occur can reduce the frequency of such interactions.

Although sympatric habitat shifts themselves have been frequently documented (Schluter, 2000; Stuart and Losos, 2013), the behavioral consequences of such shifts are not well studied. One behavior, movement, is important to organisms for a variety of reasons, including foraging, territory defense,

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intersexual interactions, and escape from predators (Losos, 1990; Jayne and Irschick, 2000; Anderson, 2007; Huey and Pianka, 2007). Movement behavior can be influenced by the habitat in which individuals occur. For example, individuals occupying habitats that differ in prey type, location, and density (e.g., Bottom and Jones, 1990; Ives *et al.*, 1993) may vary in the number of movements made while foraging (Eifler and Eifler, 1999; Greef and Whiting, 2000; Barahona and Navarrete, 2009). The ecological consequences of variation in movement rates are also diverse and may include effects on foraging success, predation risk, and energy expenditure. Nevertheless, to our knowledge, only a few studies have shown that changes in habitat use can result in altered movement rates within species (e.g., Barahona and Navarrete, 2009; Hovel and Wahle, 2010).

Anolis lizards offer an excellent opportunity for studying the effects of intraspecific variation in habitat use on movement rates. These arboreal, insectivorous lizards are known to vary in habitat use between sympatric and allopatric populations; in many *Anolis* species, the average perch height of individuals in populations sympatric with other anoles differs from the average perch height of individuals in allopatric populations (Jenssen, 1973; Schoener, 1975; Jenssen *et al.*, 1984; Losos *et al.*, 1993; Losos and Spiller, 1999; Kolbe *et al.*, 2008; Stuart *et al.*, 2014). Moreover, both interspecific and intraspecific variation in movement rates in anoles suggest that movement rates are related to habitat. In the Greater Antilles, *Anolis* lizards have repeatedly evolved to specialize on particular microhabitats within the arboreal habitat, and anole species that perch low on tree trunks (trunk-ground ecomorphs) have lower movement rates than lizards perching higher on tree trunks and in the canopy (trunk and trunk-crown ecomorphs; Cooper, 2005; Johnson *et al.*, 2008). Within species, however, the relationship between movement rates and perch height differs among different microhabitat specialists (Cooper, 2005) and may co-vary with changes in season (Lister and Aguayo, 1992; Jenssen *et al.*, 1995). In general, the ecological forces shaping the associations between habitat and movement rates remain unknown (Johnson *et al.*, 2008). In particular, we do not know whether a habitat shift due to the presence of a congener can affect movement rates.

Almost all previous research on movement rates in anoles has been conducted on males (Moermond, 1979; Cooper, 2005; Johnson *et al.*, 2008); indeed, research on female anoles has often lagged behind research on male anoles (Butler *et al.*, 2007; Losos, 2009). Male and female lizards spend a majority of their time engaged in different activities during the breeding season (Jenssen *et al.*, 1995; Nunez *et al.*, 1997), but we do not know if this difference causes males and females to move at different rates or if the presence of a congener can affect male and female movement behavior in different ways.

In the southeastern United States, the native *Anolis carolinensis* co-occurs widely with the invasive *Anolis sagrei*, and these two ecologically similar species interact strongly with one another. Closely related and morphologically similar to high-perching trunk-crown anoles in Cuba (Williams, 1969; Glor *et al.*, 2005; Campbell-Staton *et al.*, 2012), *A. carolinensis* perches at low heights in the absence of other *Anolis* lizards but shifts to higher perches in the presence of the larger, also low-perching *A. sagrei* (Collette, 1961; Edwards and Lailvaux, 2012; Stuart *et al.*, 2014). In this study, we assess the effect of the presence of *A. sagrei* on the movement rates of male and female *A. carolinensis* by comparing populations of *A. carolinensis* where they are the only anoles present to populations of *A. carolinensis* where they co-occur with *A. sagrei*.

METHODS

This study was carried out from June to August 2010 in Mosquito Lagoon, Florida, on small dredge-spoil islands that are home to either only *A. carolinensis* (one-species islands) or both *A. carolinensis* and *A. sagrei* (two-species islands). Three one-species islands (Crescent, Hornet, South Twin) and two two-species islands (Line of Cedars, Lizard) were sampled here. One- and two-species islands did not differ in geographic or environmental characteristics apart from the presence of *A. sagrei* (Kamath *et al*., 2013; Stuart *et al*., 2014). Therefore, differences in *A. carolinensis* behavior between one- and two-species islands are most likely attributable to the presence of *A. sagrei* rather than to environmental differences among islands with and without *A. sagrei.* Previous research has confirmed that both male and female *A. carolinensis* move to higher perches on two-species islands compared with one-species islands in Mosquito Lagoon (Campbell, 2000; Stuart *et al*., 2014).

Focal observations lasting up to 20 minutes or until the lizard disappeared from view were conducted on undisturbed male and female lizards between 0700 and 1700 hours from 22 June to 6 August, 2010. A single observer (AK) watched individual lizards through binoculars, noting the number of movements made by the lizard in the time observed. Observations were only conducted in relatively open habitats, to ensure that a distance of at least 2 m was maintained between the lizard and the observer. If possible, lizards were caught and temporarily marked with a Sharpie® marker after the observation period to ensure that lizards were not re-sampled during subsequent visits.

For each lizard, we calculated the number of movements per minute (MPM), a movement rate index often used for lizards, including anoles (Cooper, 2005; Johnson *et al*., 2008). Observations that lasted less than five minutes or observations where MPM < 0.25 were excluded from subsequent analyses to exclude lizards potentially disturbed by the observer's presence (following Johnson *et al*., 2008; mean length [± standard deviation] of observations included: 15.6 ± 5.1 minutes). We square root–transformed MPM before statistical analysis to improve the normality of model residuals. We compared MPM for males and females between island types using a linear mixed effects model in R (*nlme* package; Pinheiro *et al.*, 2013) with *A. sagrei* presence and sex as fixed effects, the interaction term *A. sagrei* presence × sex, and a random effect of island. Next, we split the data set by *A. carolinensis* sex and used a mixed effects model with a fixed effect of *A. sagrei* presence and a random effect of island to assess the effect of *A. sagrei* presence on MPM for males and females separately. Statistical significance was assessed by comparison with a null model in which the term of interest was dropped, using a likelihood ratio test. Statistical analyses were conducted in R version 3.0.2 (R Core Team, 2013).

RESULTS

A total of 204 *A. carolinensis* individuals were observed for this study, including 42 females and 68 males from one-species islands and 36 females and 58 males from two-species islands. Across all observations with MPM > 0.25, the mean and standard deviation of MPM was 1.29 ± 0.75, which is comparable in magnitude to previous estimates of movement rates of trunk-crown anoles (Johnson *et al*., 2008). Movement rates varied substantially across individual observations, with coefficients of variation of MPM within islands ranging from 41% to 74%; the coefficient of variation of island means of MPM was 25%.

A significant interaction between *A. sagrei* presence and *A. carolinensis* sex on MPM ($\chi^2_{(1)} = 7.11$, $P = 0.007$; Fig. 1) suggests that the sexes differ in how MPM varies with the presence of *A. sagrei*. Upon splitting the dataset by *A. carolinensis* sex, we found that males have lower MPM on two-species islands than on one-species islands ($\chi^2_{(1)} = 6.58$, $P = 0.01$), whereas MPM does not differ between females on one- and two-species islands ($\chi^2_{(1)} = 1.39$, $P = 0.24$; Fig. 1).

DISCUSSION

Despite substantial variation among individuals and across islands in movement rates, we found an interaction between the effect of *A. sagrei* and the sex of *A. carolinensis* on MPM, suggesting that movement rates in male and female *A. carolinensis* are affected differently following a shift to higher perches in the presence of *A. sagrei*. In particular, male *A. carolinensis* move less often in the presence of *A. sagrei*, whereas the movement rates of female *A. carolinensis* are unchanged in the presence of *A. sagrei*.

That males and females differ behaviorally in their response to *A. sagrei* is not surprising, because males and females have different motives for movement during the breeding season. Male anoles, including *A. carolinensis*, spend a majority of their time in the breeding season engaged in social interactions (Andrews, 1971; Fleming and Hooker, 1975; Lister and Aguayo, 1992; Jenssen *et al.*, 1995). Females, on the other hand, spend most of their time foraging in both the breeding and the non-breeding seasons (Lister and Aguayo, 1992; Nunez *et al.*, 1997). This difference between the sexes in their reasons for moving suggests that even though MPM is usually considered an index of foraging behavior for lizards, it is better interpreted in a context-specific manner (Perry, 2007; Reilly *et al.*, 2007). In studies conducted during the breeding season, such as this one, MPM should be interpreted as an index of sit-and-wait foraging vs. active foraging only for females. The absence of a change in MPM in sympatric females relative to allopatric females suggests that lizards do not forage more actively in the presence of *A. sagrei*, despite shifting to higher perches. Nevertheless, it seems unlikely that females move solely to forage (Nunez *et al.*, 1997). Although it will always be challenging to determine the motivation for a given individual's movement, repeated observations of individuals in different seasons, at different times of day, and in different social and ecological contexts might lend further insight into variation in movement rates of lizards.

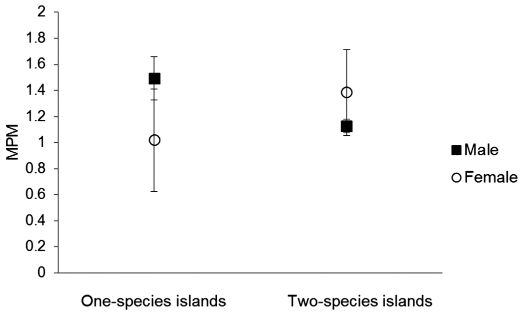

Figure 1. Movements per minute (MPM) of male and female *Anolis carolinensis* on one- and two-species islands (i.e., in the absence and presence of *Anolis sagrei*). Points represent the mean of island means for males (closed squares) and females (open circles) on each type of island, with error bars showing the standard deviation in island means.

In contrast to females, male *A. carolinensis* move less often in the presence than in the absence of *A. sagrei*. Decreased movement rates in anoles can be related to increased perch height, as has been documented in males in the trunk-crown anole *Anolis stratulus* as well as several grass-bush anoles (Cooper, 2005). The shift of male *A. carolinensis* to higher perches in the presence of *A. sagrei* (Stuart *et al.*, 2014) may thus drive the decrease in movement rates in male *A.*

carolinensis observed here. Although changes in habitat visibility with perch height have long been considered to underlie these relationships (Moermond, 1979; Cooper, 2005), the precise mechanisms that lead movement rate and habitat to be associated with one another remain unknown, and the opposite relationship between perch height and movement rates has also been observed previously (Johnson *et al.*, 2008). Such contradictions can be seen within our data set as well—females, who tend to perch lower than males (Schoener, 1968; Perry, 1996), have a lower movement rate than males on one-species islands (Fig. 1).

Male anoles spend a majority of their time in the breeding season engaged in social interactions and territory defense (Andrews, 1971; Fleming and Hooker, 1975; Lister and Aguayo, 1992; Jenssen *et al.*, 1995), and decreased movement rates in male *A. carolinensis* on two-species islands might result from changes in territory size and social interactions due to the presence of *A. sagrei*. Territory size decreases with increasing lizard density in anoles (Schoener and Schoener, 1982), and *A. sagrei* reaches high densities on small islands even in the presence of other anoles (Losos and Spiller, 1999, Campbell and Echternacht, 2003). If male *A. sagrei* and *A. carolinensis* territories do not overlap to avoid interspecific interactions, *A. carolinensis* territories may be smaller on two-species islands due to the increased combined population density of *A. carolinensis* and *A. sagrei* on two-species islands. Territory size may also decrease at higher perches due to reduced visibility in the canopy because of the challenges of preventing intruders from entering a large territory in a visually cluttered environment (Eason and Stamps, 1992). Sympatric males might therefore require fewer movements to defend these potentially smaller territories than allopatric males. Alternatively, because the population densities of *A. carolinensis* decrease in the presence of *A. sagrei* (Campbell, 2000), male *A. carolinensis* on two-species islands might encounter fewer conspecific male rivals and may therefore need to move less often to display to conspecifics and defend their territories against intruders.

Much more attention has been paid to the behavioral ecology of male anoles than to that of female anoles (Butler *et al.*, 2007; Losos, 2009). Our results suggest that male and female anoles can differ in their behavioral responses to ecological pressures. Understanding the mechanisms leading to behavioral and ecological variation within a species will therefore depend upon documenting this variation in both males and females, a conclusion that is hardly surprising. It is disappointing that research on fundamental aspects of the biology of even organisms as well-studied as *Anolis* lizards remains largely focused on males.

Although we do not know the mechanisms driving changes in movement behavior, our study indicates that novel interaction with a congeneric competitor has further behavioral consequences for *A. carolinensis* individuals beyond a shift in habitat. However, some behaviors of *A. carolinensis*, such as the partitioning of feeding and displaying into different microhabitats, remain unchanged in the presence of *A. sagrei* (Kamath *et al.*, 2013). The behavioral consequences of strong ecological interactions are therefore complex and not easily predicted, and intensive observations of individuals in the field will be central to fully understanding how co-occurring with an ecologically similar congener can shape intraspecific variation in behavior.

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