

Context Dependent Territory Defense: The Importance of Habitat Structure in *Anolis sagrei*

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Abstract

Territoriality is a potentially costly endeavor, and several mechanisms for mitigating the costs of territoriality have been investigated in the wild. For example, territory owners can reduce the costs of defending territory boundaries by prioritizing defense of the most valuable areas within territories, investing less energy in low quality areas. We staged pairwise encounters between adult male lizards on natural territories in the wild, to test whether male brown anoles, *Anolis sagrei*, would differentially defend certain regions of their territories over others. Based on our observations that male *A. sagrei* spend most of their time on elevated perches on tree trunks or branches compared with sites on the ground, we predicted that territory residents would respond more aggressively to territory invasions that took place on elevated perches than to invasions on the ground. We measured significant differences in the behavior of residents following invasion on the ground vs. on the elevated perches, and results partially supported our hypothesis. Males performed more displays and approached intruders more often when territory invasion took place on the ground, but were quicker to attack intruders that entered territories on elevated perches. Our hypothesis was only partially supported, potentially indicating that elevated perches are preferred as outposts to monitor valuable sites on the ground. Our study provides evidence that territory defense varies not just among individuals, but also within individuals at different locations in a territory.

Introduction

Territory defense can be a costly activity (Marler & Moore 1987, 1988; Moore & Marler 1987) that may result in physical injury, and can detract time away from other activities that affect fitness (e.g. foraging, mating) (Pyke 1979; Nolet & Rosell 1994). This has raised the question of why some individuals are willing to invest more resources in territory defense than others, and why some territory disputes escalate to physical fighting while others do not (Fretwell & Lucas 1969; Høglund et al. 1993). Variation in the intensity of aggression used to defend territories is most often measured among individuals, some being more likely to defend resources than others. This variation may arise due to several factors, inclu-

ding differences in fighting ability (Dugatkin & Biederman 1991), the perceived value of a resource (Maynard Smith & Parker 1976), or prior residency on territories (Olsson & Shine 2000). By contrast, variation in territoriality may also arise within individuals, and this aspect of variation is less well understood (Riechert 1979, 1984; Johnsson et al. 2000). For example, individuals may defend particularly valuable regions of their territory more intensely than other areas (Riechert 1979; Baird & Sloan 2003), thereby restricting costs of defense to certain regions of the habitat.

Previous work on the territorial behavior of juvenile *Anolis* lizards has revealed much about patterns of settlement behavior (Stamps & Krishnan 1994b, 1995) and social interactions (Stamps & Krishnan

1994a, 1998) among territory residents. Juvenile *A. aeneus* have shown evidence of individual recognition and dominance relationships that remain stable between territorial dyads (Stamps 1984; Stamps & Krishnan 1994b). In this study, we use adult brown anoles, *Anolis sagrei*, to investigate the importance of site preferences to territory defense.

Anolis sagrei is a member of the 'trunk-ground' class of Caribbean ecomorphs (Williams 1983; Losos 1990). As its name implies, the trunk-ground ecomorph tends to occupy perching sites on the ground or at slightly elevated sites on tree trunks or low branches [mean perching height = 0.41 m taken from (Losos 1990)]. Perching data (records of males not foraging, interacting with other lizards, or otherwise in motion at first sighting) indicate an apparent preference for elevated perching sites. For example, at our study sites in the Bahamas, preliminary observations indicated that 96.8% ($n = 448$) of initial perch sightings occurred at perches elevated off the ground, and sightings on the ground were of lizards in motion between adjacent perching sites or foraging for food. More frequent use of elevated perches may be due to the presence of terrestrial lizard species (e.g. *Ameiva* spp.) that prey on anoles (R. Calsbeek, personal observation). Alternatively, elevated perches may be used as vantage points to scan other parts of the territory while foraging or defending territory boundaries (Baird & Sloan 2003).

Adult male *A. sagrei* are seasonally territorial, defending territories during the breeding season (Tokarz et al. 1998, 2002). Male *A. sagrei* are known to court females in adjacent territories (Tokarz 1998), and will opportunistically take over territory space following removal of rival males (Paterson 2002). The goal of this study was to test whether the intensity of territory defense differed between elevated perching sites and sites on the ground. Using a wild population, we staged encounters to test whether intruders would elicit varying levels of aggression from resident male *A. sagrei* in response to invasion into different portions of a territory. We mapped territory boundaries for lizards and staged encounters between territory residents and unfamiliar strangers. We varied the locations of territory invasion between trials to test whether resident males would respond more aggressively to invasions on elevated perches compared with invasions on the ground. Based on our observation that males spend more time on elevated perching sites over those on the ground, we hypothesized that territory residents would respond more aggressively to invasion on elevated perches compared with invasion on the ground.

Methods

Study Site

We conducted field studies on the island of Great Exuma, Bahamas (23°31'N 75°49.5'W) from 17 May to 22 June 2003, a time period corresponding with the middle of the breeding season (Tokarz 1998). *Anolis sagrei* at this study site perch on the broad trunks of palm trees (*Pseudophoenix* spp.) and Australian pine trees (*Casuarina equisetifolia*) (mean perch diameter = 230 mm), or on the branches of scrubby vegetation including sea-grape (*Coccoloba uvifera*), sea hibiscus (*Hibiscus tiliaceus*), and buttonwood (*Conocarpus erectus*) (mean perch diameter = 25 mm). Occasional hurricane disturbance (Spiller et al. 1998) has rendered most of the lizard habitat sufficiently open that an observer may pass through an area and observe all active marked lizards on any given day. *Anolis sagrei* are rarely seen at rest on the ground, but they do forage there for food, and occasionally move between perches by dropping to the ground and running to an adjacent perch.

We captured 132 male lizards either by hand or using a noose tied from silk thread (Sinervo & Adolph 1994) and attached to a telescoping pole. We recorded mass (g), and snout-vent-length (SVL, mm) for all individuals, and applied a small dorsal paint-mark for individual identification. Paint-markings are visible for about 10 d before they are shed. Therefore, all individuals also received a unique combination of colored elastomer markings (information available at <http://www.nmt-inc.com>) that were injected to the underside of their hind- and forelimbs for permanent identification. The elastomer was injected as a liquid that polymerizes within 2 hours. Permanent tags were necessary to identify lizards that had shed paint marks and to monitor survival throughout this study. The tags are preferable to toe-clipping in anoles, because removal of the specialized toe-pads, which are an adaptation for arboreality in this species, can have adverse consequences for locomotor performance (R. Calsbeek, personal observation).

Territory Maps

We recorded territory data for all individual lizards by making multiple passes over the entire study site for a period of 2 wk. We mapped 1134 unique locations ($\bar{x} = 7.2$ unique locations/male and 5.2 unique locations/female) using compass bearings and distance measurements from known landmarks

or relative to their initial site of capture. The minimum convex polygon (Tinkle et al. 1962) that circumscribed locations for each individual defined its territory. Territories in our study population are small (approx. 10 m²) and typically include a single preferred perch (R. Calsbeek, unpublished data). Lizards were often seen at the same location in their territory, and the 1134 data points do not include multiple sightings at the same location.

We found that home-ranges and territories of most males in this study were synonymous (Maher & Lott 1995), given the consistent defense of these areas in response to invaders (see below). Our territory data were not intended to quantitatively estimate male territory size (Stone & Baird 2002), but the number of territory sightings per individual in this study was sufficient to roughly delineate territory boundaries and to identify males that would likely have interacted previously. As a conservative approach, we captured strangers from at least 75 m away (approx. 25 territory diameters), who were unlikely to have previously interacted with the focal male they were paired with in our experiment. Because the actual boundaries of each territory were not measured with a high degree of precision (Rose 1982), we can only be sure that introductions were made within the territories of focal males, but do not report on the distance from territory borders from which males were introduced.

Experimental Design

We tested the degree to which territorial males would defend different regions of the territory by staging encounters between territory residents and an intruding stranger. Intruder males were captured and held in a small covered container (e.g. picnic cooler) for 8–10 min prior to introduction. Males were tethered around their waist to a 1-m length of silk thread attached to a fishing pole, and were gently lowered into the territory of a focal-resident male. All intruder males were lowered into the territories of residents at a distance of approx. 1.5 m from the resident male. The tether did not constrain the behavior of intruders except to prevent them from moving further than the 1-m length of silk. We lowered intruders into one of two sites on the resident male's territory: either on the ground ($n = 20$) or onto an elevated perch ($n = 11$). The location of intruders (ground vs. elevated perches) was determined randomly for each trial. Intruder males were never involved in consecutive trials and were never used more than twice.

Two observers, seated quietly approx. 5 m away, scored male–male interactions simultaneously. One recorded the numbers and types of display behaviors, while the other recorded the latency (time from start of the trial) of the focal male to approach and attack intruders. We scored behaviors as follows: a push-up was the vertical lifting of the torso by extension of the forelimbs, push-up bouts were sets of push-ups performed in succession with no more than a 2-s pause between displays, dewlap extensions were displays of the colored throat fan (both partial and full extension), dewlap bouts were sets of dewlap displays performed in succession as above for push-ups, arched back displays involved lateral compression of the abdomen followed by the displaying male walking in circles around an intruder, and an attack was any escalation to physical contact between males (e.g. bites) perceived by the observer to endanger the other male (Table 1).

The push-ups scored in this study were similar (but not necessarily identical) to 'bobs' described by others (McMann 2000; McMann & Paterson 2003a,b). We differentiate between push-ups and bobs because others (McMann 2000; Paterson 2002; Tokarz et al. 2003) further note that some 'bobs' are actually 'nodding displays' that we did not observe in the field. Therefore, we take a cautious approach and assume that we have pooled both 'nods' and 'bobs' into one behavior called push-ups. The maximum length of each pairwise interaction was limited to 15 min. Any encounter that escalated to physical contact (e.g. biting) was terminated immediately to prevent injury to either animal. None of the study animals were injured beyond the superficial abrasion of one male, and all study animals were still alive 2 wk following the termination of our experiments.

Statistical Analysis

We staged 31 total encounters between pairs of males. The distributions of count data (e.g. push-up

Table 1: Factor loadings for the two principal components that summarize the behaviors scored in this study

Behavior	Loadings PC1	Loadings PC2
Push-ups	0.861	−0.297
Push-up bouts	0.887	−0.350
Dewlap displays	0.522	0.798
Dewlap bouts	0.480	0.834
Approaches	0.808	−0.108
Arched back displays	0.835	−0.693
Percentage of variance explained (%)	56.40	26.60

and dewlap displays) were skewed, and we used non-parametric tests of all of our hypotheses concerning these variables (Sokal & Rohlf 1995). We used Mann–Whitney U -tests to measure differences in response to the location of the invasion site (ground vs. elevated perch). All other data were normally distributed and were tested using parametric statistics. Because dominance interactions are often influenced by differences in body size (Maynard-Smith & Brown 1986; Chellappa et al. 1999; Calsbeek & Sinervo 2002), including interactions between *A. sagrei* lizards (Tokarz 1985), we tested for the role of body size prior to all analyses. We tested for a relationship between differences in male snout-vent-length ($SVL_{\text{focal male}} - SVL_{\text{intruder}}$) and behaviors scored in our study using ANOVA. Finally, because many of the behavioral responses by resident males were correlated, we combined the behaviors into principal components (PC) for further analysis (following Hyman 2002). Latency scores were not included in the PC analyses owing to high multicollinearity with other traits. We tested whether composite behavioral scores differed as a function of the perching location of intruders using ANOVA.

Results

Body size of interacting males did not differ significantly (mean difference in male SVL = 1.23 ± 1.01 ; paired t -test $t_{30} = 1.11$, $p = 0.28$). Relative male body size (difference in SVL) had no significant effects on any of the behaviors scored in this study (for example: latency to approach intruders; linear regression $r^2 = 0.075$, $p = 0.14$, $n = 31$; all other p -values > 0.36).

We found support for our first hypothesis that territorial males would differentially defend elevated

perches compared with sites on the ground. The site of intrusion had significant effects on the response by residents. Resident males displayed significantly more towards intruders that were lowered onto the ground compared with those that were lowered onto elevated perches in terms of push-ups (Mann–Whitney $U = 208$, $p < 0.0001$; Fig. 1a), push-up bouts (Mann–Whitney $U = 219$, $p = 0.0001$), dewlap extensions (Mann–Whitney $U = 56$, $p < 0.02$; Fig. 1b) and dewlap bouts (Mann–Whitney $U = 53$, $p < 0.02$). Residents approached intruders on the ground more frequently (Mann–Whitney $U = 186$, $p < 0.001$; Fig. 1c), and performed more arched back displays at intruders on the ground (Mann–Whitney $U = 62.5$, $p < 0.01$; Fig. 1d). However, residents attacked intruders on elevated perches nearly twice as fast compared with intruders on the ground ($\bar{x} = 247$ vs. 497 s, respectively; Mann–Whitney $U = 46.5$, $p = 0.01$ Fig. 1e). The difference in time to attack reported above helps explain the large differences in the number of display behaviors exhibited towards individuals on the ground. While residents tended to approach and display at intruders on the ground, they were much quicker to attack intruders on elevated perches.

When we combined all of the behaviors into composite scores, we found evidence for two principal components, which collectively explained 83% of the variation in behavior (Table 1). Push-up displays loaded heavily onto the first axis (PC1) along with approaches and arched back displays, while dewlap displays loaded onto the second axis (PC2). There was a significant difference in PC1 related to perching location that was consistent with the results outlined above (Fig. 2). Residents had greater PC1 scores in response to invasion on the ground compared with invasion on elevated perches (ANOVA

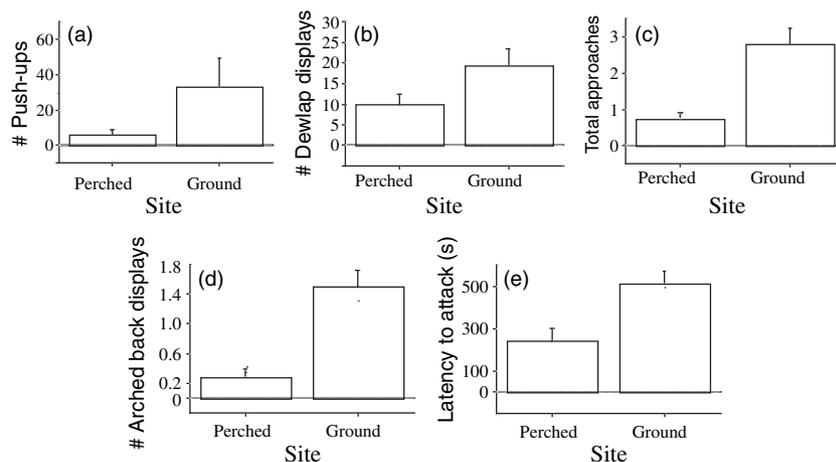


Fig. 1: Differences in behaviors exhibited towards intruders on elevated perches vs. sites on the ground. Resident males signaled significantly more, but waited significantly longer to attack intruders on the ground compared with intruders on elevated perches. Results are based on $n = 20$ pairwise interactions on elevated perches and $n = 11$ pairwise interactions on the ground. Histogram bars in panels (a–e) represent mean values (+ SE)

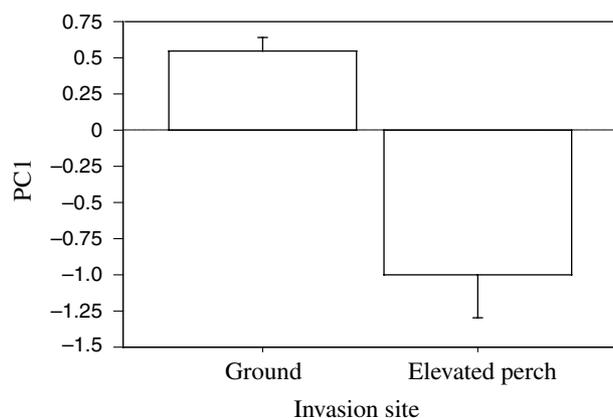


Fig. 2: Principal component analysis showing that variation in push-up and dewlap displays was highly correlated (PC1), and that males that invaded territories on the ground could be distinguished from those that invaded on elevated perches on the basis of this variation. Males invading on the ground received significantly more push-up and dewlap displays compared with males that invaded territories on elevated perches ($p < 0.001$). Results are based on all 31 pairwise interactions. Histogram bars show the mean (+ SE)

$F_{1,29} = 36.86$, $p < 0.0001$). There was no significant difference in PC2 as a function of invasion site (ANOVA $F_{1,29} = 0.79$, $p = 0.38$). Together, these results indicate that variation in some signaling behaviors (push-ups, approaches, and arched back displays) was highly correlated and these behaviors were more likely to be directed at intruders on the ground than those on elevated perches.

Discussion

Variation among individuals in defensive behavior of territories has been explored at great length over many decades (Davies 1978; Kaufman 1983; Maher & Lott 1995; Calsbeek & Sinervo 2002). However, less attention has been paid to variation in defense of different regions of a territory by single individuals (Riechert 1979; Johnsson et al. 2000; Calsbeek et al. 2002; Baird & Sloan 2003). Male spiders in the genus *Agelenopsis* invest more resources in territory defense at high-quality sites compared with lower quality sites (Riechert 1979), and brown trout, *Salmo trutta*, increase aggression and decrease their latency to attack intruders when experimentally given high quality territories in the laboratory (Johnsson et al. 2000). Side-blotched lizards, *Uta sansburiana*, not only vary in the degree to which they defend territories (Sinervo & Lively 1996), but levels of dominance and aggression expressed by individual males change over very short-time scales

during the breeding season (approx. 2 wk) (Calsbeek & Sinervo 2002).

Here we present evidence that individual male *A. sagrei* defend territories with varying degrees of aggression depending on the location of invasion within territory boundaries. This is a salient result of our study, because it suggests that individual male lizards can differentiate between sites of greater and lesser value in their territories. Although we do not provide quantitative estimates of territory quality, it appears that sites on the ground and on elevated perches are both important to anoles, but in different ways. McMann & Paterson (2003b) also working with *A. sagrei* and Baird & Sloan (2003) working with collared lizards, *Crotaphytus*, both also report variation in display patterns at different locations within territories, though their studies did not focus on displays in response to territory invasion. Territorial behavior of male anoles is likely to serve several important functions. Numerous studies of *A. sagrei* have demonstrated the importance of territoriality for mate acquisition. Defending territories allows males to increase their exclusive access to females (Tokarz 1998; Paterson 2002), which may be important since females mate with multiple males and may promote sperm competition in this species (Tokarz 1998). Territories also provide food resources (Paterson 2002) and retreat sites from predators (Baird & Sloan 2003) (see below).

Although most of our initial observations were of males on elevated perching sites, territory space on the ground is still important in foraging bouts (Losos 1990), indicating that differences in defense are not the trivial result of under utilized space on the ground. Indeed, Baird & Sloan (2003) also report increased use of elevated perching sites by female collared lizards, *Crotaphytus collaris*, and suggest that these sites may serve as vantage points for scanning valuable areas of territory located on the ground. Territory residents in our study signaled significantly more using push-ups and dewlap displays, performed more arched back displays, and repeatedly approached intruders on the ground, but attacked intruders significantly earlier when on elevated perches. Although the patterns are not perfectly consistent, greater numbers of displays and approaching behaviors suggest that males may place high value on sites located on the ground. The one result not consistent with this interpretation is that males attacked intruders more quickly when territory invasion took place on elevated perches. However, this may be the result of the male's need to maintain his position on an elevated perch to scan the rest of his

territory. Overall, our data support the hypothesis that, in a species that values some parts of the territory over others, males will defend the preferred sites more vigorously.

We have also shown that the behaviors exhibited in response to territory invasion at different locations within territory boundaries can be summarized by two distinct principal components. Variation in head-bob, approach, and arched back displays, was strongly correlated (PC1) and variation along this axis allowed us to distinguish interactions with intruders on the ground from those on elevated perches. Similarly, variation in dewlap displays was correlated, although PC2 did not differ between the two sites of territory invasion.

One possible explanation for differential use of sites on the ground vs. elevated perches in our study population is the presence of the terrestrial lizard *Ameiva* that occasionally preys on *A. sagrei* (R. Calsbeek, personal observation). In our study, nearly 97% of all lizard sightings were of residents perched on tree branches or trunks. Anoles on other islands increase their use of elevated perches in the presence of terrestrial lizard predators (Losos et al. 2004) and excursions onto the ground may be dangerous. This suggests that territory residents may be less vulnerable to predators on elevated perches, and could be under increased pressure to defend those sites against intruders.

Nevertheless, our data suggest that males guard sites on the ground more vigorously compared with elevated perching sites. Selection may also act to prevent territory defense at risky sites, which would explain why males are less likely to directly attack intruders on the ground. Finally, a resident male's perception of threat has also been shown to influence signaling behavior (McMann 2000) and may explain some of the variation in displays in different parts of the territory. Future research directions could resolve the role of predators in this result by testing elements of territory defense while experimentally manipulating the presence or absence of lizard predators.

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