

# BEHAVIORAL CONVERGENCE AND ADAPTIVE RADIATION: EFFECTS OF HABITAT USE ON TERRITORIAL BEHAVIOR IN *ANOLIS* LIZARDS

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Received August 13, 2009

Accepted September 30, 2009

Most studies of adaptive radiations focus on morphological aspects of differentiation, yet behavior is also an important component of evolutionary diversification, often mediating the relationship between animal ecology and morphology. In species within radiations that are convergent in ecology and morphology, we then also expect convergence in behavior. Here, we examined 13 *Anolis* lizard species to determine whether territorial strategies have evolved convergently with morphology and habitat use. We evaluated two aspects of territoriality: behavioral defense of space via territorial displays, and territory overlap within and between sexes. Controlling for the phylogenetic relationships of the taxa in our study, we found that species similar in perch height and diameter convergently evolved patterns of territory overlap, whereas species similar in habitat visibility (the proportion of space that can be seen from a perch) convergently evolved display behavior. We also found that species with greater display time have more extensive male–male territory overlap. This study provides strong evidence for the role of habitat in the evolution of territoriality and suggests that the social structure of a species ultimately evolves in concert with habitat use and morphology.

**KEY WORDS:** Comparative method, display rate, ecomorph, social organization, territory overlap, visibility.

The phenomenon of replicated adaptive radiations—the observation that related clades diversifying in different geographic areas, but over the same range of habitats, produce very similar sets of descendant species—has received increasing attention in recent years. Such replicated radiations have been found, for example, in temperate northern lake fishes, East African cichlids, Pacific Island land snails, and Caribbean *Anolis* lizards (Schluter 2000; Losos 2009). Almost all comparative studies of these groups have

focused primarily on morphological aspects of differentiation. However, behavior is a key link between ecology and morphology in animals; if radiations are truly replicated, then we should expect to see convergent patterns of behavioral evolution that are correlated with convergence in morphology and ecology. Nonetheless, to date this hypothesis has been little tested (Blackledge and Gillespie 2004; Stoks et al. 2005).

Caribbean lizards in the genus *Anolis* (anoles) provide an example of a radiation whose morphology and ecology has been extensively studied, but few analyses of their behavioral evolution exist. In this group, on each island of the Greater Antilles (Cuba, Hispaniola, Jamaica, and Puerto Rico), the same set of habitat specialists, called ecomorphs, has repeatedly evolved adaptations

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to use different parts of the structural habitat (as measured by perch height and diameter; Williams 1983; Losos 1990a; Losos et al. 1998). Six ecomorph types, named for the structural habitat they most frequently use (grass–bush, trunk–ground, trunk–crown, twig, and crown giant), have evolved multiple times across these islands; distantly related species within each ecomorph category have convergently evolved complex suites of morphological and behavioral traits.

One striking example of the association between behavioral and morphological convergence in this group comes from the relationship between locomotor performance and limb length: species with short limbs exist on narrow perches (e.g., small branches or grass) and move slowly but adeptly in their habitat, whereas species with long limbs exist on broad perches (e.g., tree trunks) and run and jump frequently (Moermond 1979a,b; Losos 1990a; Irschick and Losos 1998, 1999; Irschick 2000; reviewed in Losos 2009).

Anoles, however, vary in a wide range of behaviors that are not obviously related to locomotor adaptations, and little work has investigated whether these behavioral traits also exhibit patterns of convergence related to habitat use. One especially prominent trait is territoriality, the behavioral defense of space, which exhibits substantial variation among anole species (e.g., Rand 1967; Hicks and Trivers 1983; Losos 1990b; reviewed in Losos 2009). Although many studies have categorized some species as territorial and others as nonterritorial, territoriality is actually just one end of a continuum of spacing patterns (Jarman 1974; Stamps 1994; Maher and Lott 1995, 2000). In addition to the traditional definition of defense of exclusive space, territorial strategies may also include individuals defending space but still experiencing high home range overlap, or individuals maintaining exclusive space without appearing to defend it (Stamps and Krishnan 1998). We therefore consider variation in both behavioral defense and space use patterns in anoles. In this study, we test the hypothesis that species in the same ecomorph class—that is, species convergent in habitat use (in terms of perch height and diameter) and morphology (in terms of limb dimensions)—are also convergent in territorial strategy (Hypothesis 1).

Aspects of habitat use not known to be convergent among the *Anolis* ecomorphs also exist and may influence the evolution of territoriality in this group. In particular, visibility, which varies as a function of the structural complexity of the habitat, is often cited as an important factor in territorial behavior in lizards (e.g., Stamps 1977), birds (e.g., Eason and Stamps 2001), and fish (e.g., Basquill and Grant 1998) by affecting the size and shape of territories and the behaviors used to defend them. Researchers have long argued that habitat complexity may determine the territorial strategies that are most successful in that habitat. Jarman (1974) first put forth this hypothesis in his classic work on African antelopes, in which he found that territorial defense was econom-

ically feasible in some habitats but not others. In particular, in species found in areas with clumped vegetation, individuals had stable, defended territories, whereas for species found in habitats with evenly spaced vegetation, the home ranges of both sexes were large and undefended. He concluded that the social structure of a species (i.e., the patterns describing how individuals interact with one another) depended on the complexity of the habitat in which it occurred.

Although this work was highly influential, no comparable comparative study in any other group has been conducted. Consequently, the generality of this ecology–social structure relationship cannot yet be assessed. Further, although visibility has been proposed as an important factor in the evolution of *Anolis* display behavior (i.e., Butler et al. 2000), it has not yet been quantitatively measured in a comparative study of this group. Here, we test the hypothesis that increased visibility is associated with the evolution of increased territoriality in anoles, as measured by higher territorial display rates and decreased territory overlap within males (Hypothesis 2). Because visibility is not a trait known to be convergent within ecomorphs, this prediction differs from Hypothesis 1, in which we investigate behavioral convergence as a function of ecomorph category.

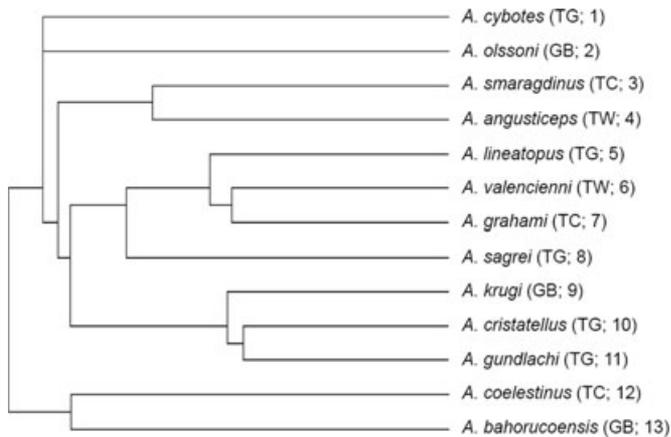
## Methods

### FOCAL SPECIES AND STUDY SITES

We examined the behavior of 13 *Anolis* species in four ecomorph classes during late spring and summer in 2004–2006. We studied *A. gundlachi* and *A. krugi* at El Verde Field Station near Río Grande, Puerto Rico (18°19.22'N, 65°49.13'W), and *A. cristatellus* near El Verde's Stream House (18°20.51'N, 65°49.49'W). We studied *A. grahami*, *A. lineatopus*, and *A. valencienni* on the grounds of Discovery Bay Marine Laboratory in Discovery Bay, Jamaica (18°28.14'N, 77°24.90'W). *Anolis angusticeps*, *A. sagrei*, and *A. smaragdinus* were studied on South Bimini, Bahamas (25°42.13'N, 79°18.11'W, and 29°42.25'N, 79°17.87'W). We studied *A. coelestinus*, *A. cybotes*, and *A. olssoni* on the grounds of Coralsol Beach Resort near Bauruco, Dominican Republic (18°03.45'N, 71°06.75'W), and *A. bahorucoensis* near the montane town of Polo, Dominican Republic (18°07.59'N, 71°16.12'W). Phylogenetic relationships among these species (Nicholson et al. 2005), along with ecomorph assignments, are shown in Figure 1.

### BEHAVIORAL OBSERVATIONS

For each species, we established one or two approximately 500 m<sup>2</sup> (20 m × 25 m) plots. When possible, we studied multiple species in the same plot. We attempted to choose all study plots for a given species such that they possessed similar macrohabitat characteristics (e.g., canopy cover, perch availability). Within



**Figure 1.** Phylogenetic relationships among species. Ultrametric tree pruned from the phylogeny in Nicholson et al. (2005) to include only the species in this study. Acronym indicates ecomorph category. GB, grass-bush; TC, trunk-crown; TG, trunk-ground; TW, twig. Numbers are assigned to identify each species in Figure 3.

each plot, we captured all detected adult lizards of the study species by noose or hand, and we sexed and measured the snout-vent length (SVL) of each individual. To perform undisturbed observations of lizards subsequent to capture, we marked each lizard either by sewing distinct combinations of beads into the most proximal region of the tail (Fisher and Muth 1989) or by attaching queen bee marking tags in unique locations on the dorsum (Johnson 2005). For a separate genetic study, we removed minimal tissue samples (~10% of tail) for molecular analyses and then released each lizard at the site of capture.

Over a period of 2–3 weeks for each plot, we conducted focal observations on marked lizards for an average of 65 observation hours per species. For most species, we performed 20 min observations, but for the more cryptic species, and those occurring at lower densities (*A. angusticeps*, *A. bahorucoensis*, *A. smaragdinus*, and *A. valencienni*), observation periods lasted up to 180 min. We typically located lizards for observation by walking slowly through the habitat until finding an apparently undisturbed subject. For the cryptic species, we also located lizards in their sleeping sites before sunrise and observed them upon waking. We found no evidence that animals observed from daybreak are consistently different in display rates from animals observed at other times of day. During observations, we recorded all behaviors performed by the individual, including territorial displays such as extensions of the dewlap (i.e., throat fan), pushups, and headbobs. To prevent observer bias in distinguishing between headbobs and pushups among different species, we grouped these two similar motions into one category for analyses. We also measured the total proportion of time a lizard spent performing all displays during the observation period. We observed each lizard for no more

than five periods (or, for species observed longer than 20 min at a time, no more than 5 h total), and averaged behavioral rates across observations for each individual. We did not conduct observations before 0600 h or after 1900 h, or during inclement weather, as lizards often take refuge during these periods (Hertz et al. 1993).

#### HABITAT AND TERRITORY MEASUREMENTS

We estimated visibility at the location where each lizard was first sighted on each half-day of observation (i.e., once before 1200 h and once after 1300 h). To this end, we measured the diameter of each object within a 0.5 m radius around the perch in two planes (horizontal and vertical) and the distance of that object from the perch. We then used these measures to estimate the proportion of a lizard's habitat that can be seen from the perch (Johnson et al. 2006). We averaged these measurements for each lizard, and then computed an average for each sex of each species for statistical analyses.

We also determined the lizard's location within the plot by measuring the distance and compass angle from the perch to predetermined reference points located throughout the plot. For each location, we also measured perch height to determine whether territories were vertically “stacked” in the same two-dimensional area (e.g., Jenssen and Nunez 1998). After ensuring that this was not the case for any of the species in this study, we analyzed the two-dimensional data only. We used these location data to estimate territory boundaries for every adult lizard for which we obtained three or more sightings. Although three sightings per individual are likely to underestimate the size of an animal's territory, we felt that the advantages of including these individuals in territory overlap analyses outweighed the disadvantages of excluding them, which include underestimating the proportion of territory overlap and the number of overlapping individuals within the population. Furthermore, in our dataset the average number of individual sightings per species is not correlated with any measures of territory size or overlap (results not shown). However, because three points are not adequate to estimate territory size, we do not analyze that variable in this study.

We determined the 95% minimum convex polygon (MCP; Rose 1982) describing the territories of each of these lizards using the program CALHOME (Kie et al. 1996). For each individual, we calculated an overlap index (following Morrison et al. (2002), who called this “overlap pressure”) as follows. Using ArcGIS 9, we determined the area of overlap between a lizard and every other individual of the same sex that overlapped that lizard's territory. We then summed these areas and divided the sum by the area of the focal individual's territory to give the overlap index for an individual. We also determined the number of males and females that overlapped a male's territory.

## STATISTICAL ANALYSES

To determine the relationship between habitat use and behavioral measures of territoriality, we performed phylogenetic multivariate analyses of variance (phylogenetic MANOVA) using data for males of each species in which ecomorph was the fixed factor and behavioral traits were independent variables, and we performed regression analyses using independent contrasts of behavioral traits and visibility. We conducted all of our phylogenetic analyses using the anole phylogeny of Nicholson et al. (2005) pruned to include only the taxa of our study, and with branch lengths rendered proportional to time using the program r8s (Sanderson 2003).

To determine whether territorial behavior has evolved convergently in the same manner as habitat use and morphology in these lizards (i.e., to determine if ecomorphs differ in territorial strategies) while controlling for the phylogenetic relationships among taxa in our study, we used phylogenetic MANOVA (using a program written by LJR) and post hoc phylogenetic analyses of variance (ANOVAs) (for detailed description, see Johnson et al. 2008) to compare the ecomorphs in display and overlap traits. In the phylogenetic MANOVA or ANOVA, *F*-statistics are calculated as per a typical ANOVA (e.g., Rencher 2002), but the null distribution of the test statistic is obtained via Brownian motion (BM) simulations on the phylogenetic tree for the included taxa (Garland et al. 1993). Thus, to obtain *P*-values for our MANOVA and post hoc ANOVAs, we performed 999 multivariate BM simulations using the covariance structure of the independent contrasts for the dependent variables as the generating matrix for BM (Felsenstein 1985; Revell et al. 2007). We then calculated the *P*-value of a given test by counting the fraction of datasets (1000, including the original data) in which the *F*-statistic was equal to or greater than that calculated from the observed data. For each univariate ANOVA, we also conducted post hoc phylogenetic *t*-tests between all groups according to the same procedure, while using the Bonferroni procedure to correct for multiple tests. Because each of the ecomorph classes is composed of two to four independently derived lineages, significant behavioral differences among the ecomorphs would have to be the result of convergent evolution.

To visually illustrate the extent of behavioral convergence within ecomorphs, we plotted territory overlap against display behavior. Because our behavioral measures are correlated, we first used principal components analyses (PCAs) to obtain a reduced number of uncorrelated independent variables. For the territory overlap data, we performed a PCA on the correlation matrix for male–male overlap index, number of males overlapping, and number of females overlapping. For the display behavior data, we performed a PCA on the correlation matrix for proportion of time spent displaying and total display rate (the sum of all dewlap extensions, headbobs, and pushups).

To determine the effect of visibility on territorial overlap and display, we conducted a series of regression analyses using independent contrasts (Felsenstein 1985) calculated using the program IDC (Revell 2006). Most contrasts were adequately standardized following Garland et al. (1992), but contrasts for display time were correlated with contrast length (the sum of the corrected branch lengths subtending the contrasted nodes; Felsenstein 1985). We standardized this measure by recalculating the contrasts for this variable after logarithmically transforming branch lengths (plus a value of one). We then regressed contrasts of individual measures of territory overlap and contrasts of individual measures of display behavior against visibility contrasts.

Further, to explore the relationship between territory overlap and social display, we calculated uncentered correlations (i.e., vector correlations) on independent contrasts of a subset of these traits. We determined the significance levels for these correlations using *P*-values obtained by regression analysis (Garland et al. 1992).

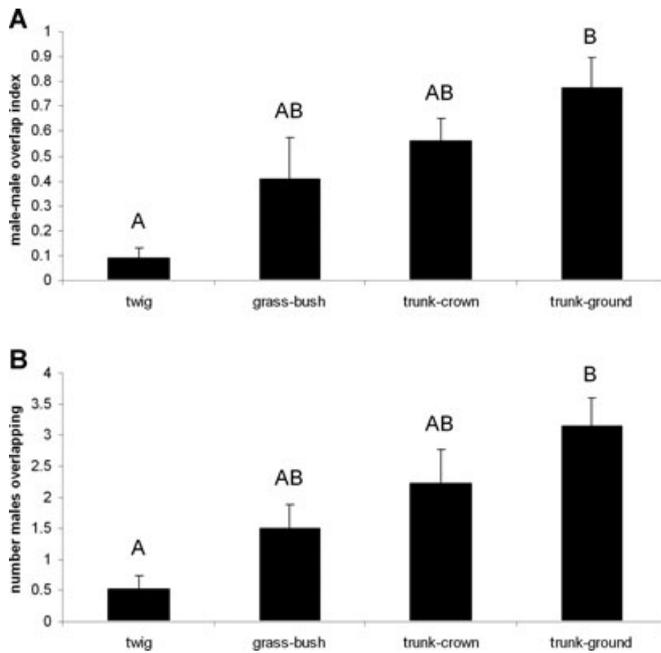
## Results

In approximately 850 h of behavioral observation on the 13 species in this study, we collected behavioral, territory overlap, and habitat use data on an average of 26 males (range 15–50) per species.

Ecomorphs differed significantly in their overall territorial strategies (phylogenetic MANOVA: Table 1A), and post hoc analyses showed that ecomorphs differed in territory overlap, but not display behavior (phylogenetic ANOVA: Table 1B,C). Investigation of individual measures of overlap revealed that the ecomorphs

**Table 1. Results from phylogenetic MANOVA and post hoc phylogenetic ANOVA comparing ecomorphs in measures of territoriality. Significant *P*-values, where significance was obtained by multivariate BM simulations on the phylogeny, are indicated in bold type.**

| (A) MANOVA results                                    |       |                  |              |
|---|-------|------------------|--------------|
|   | df    | Wilks' $\lambda$ | <i>P</i>     |
| Ecomorph  | 6, 16 | 0.19             | <b>0.015</b> |
| (B) ANOVA results for components of territory overlap |       |                  |              |
|   | df    | <i>F</i>         | <i>P</i>     |
| Male–male overlap index                               | 3, 9  | 4.14             | <b>0.036</b> |
| Number of males overlapping                           | 3, 9  | 5.10             | <b>0.021</b> |
| Number of females overlapping                         | 3, 9  | 1.52             | 0.269        |
| (C) ANOVA results for components of display behavior  |       |                  |              |
|   | df    | <i>F</i>         | <i>P</i>     |
| Proportion of time displaying                         | 3, 9  | 2.09             | 0.180        |
| Total display rate                                    | 3, 9  | 2.43             | 0.113        |

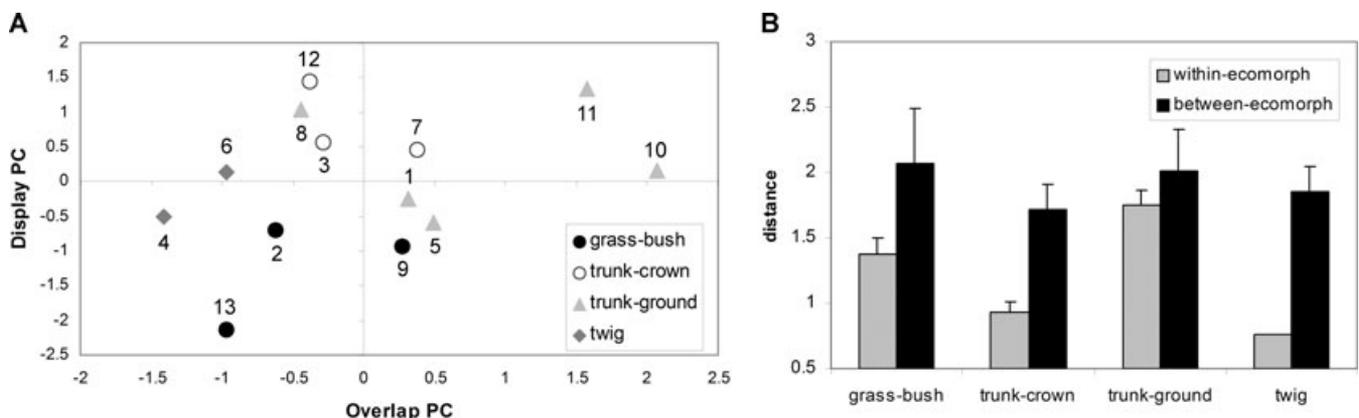


**Figure 2.** Average male overlap measures (+1 SE) by ecomorph categories. Ecomorphs with different uppercase letters were significantly different using pairwise *t*-tests, corrected for multiple comparisons. (A) Male–male overlap index (see text for details). (B) Number of males overlapping male territory.

differed in their male–male overlap index and number of males overlapping male territories, but not in the number of females overlapping male territories (phylogenetic ANOVA: Table 1B and Fig. 2). In particular, twig anole species showed low male overlap, trunk–ground species exhibited high overlap, and grass–bush and trunk–crown species did not differ from any other ecomorph. Results from standard ANOVA and Tukey’s HSD post hoc tests were consistent with phylogenetic ANOVA results, but are not shown here.

In the PCA using territory overlap measures, only one PC (Overlap PC) had an eigenvalue greater than one ( $\lambda = 2.60$ , percent variance explained = 86.7%), on which all three variables loaded highly (loadings: male–male overlap index = 0.945, number of males overlapping = 0.948, number of females overlapping = 0.889). In the PCA with display measures, again one PC (Display PC) was extracted ( $\lambda = 1.28$ , percent variance explained = 63.9%), on which both variables loaded highly (loadings: proportion of time displaying = 0.799, total display rate = 0.799). Plotting species’ data for the Overlap PC and Display PC revealed that members of the same ecomorph class tended to lie near each other in a multivariate behavioral space even though they are not closely related (Fig. 3). These results indicate that behavioral similarity among members of the same ecomorph class is generally convergent, although it is possible that one of the ecomorph classes retains the ancestral character state and thus does not display convergence; even in this scenario, however, similarity among the other three ecomorph classes would be convergent. Thus, together with the qualitative observations that ecomorph species are not closely related (Nicholson et al. 2005) and do not cluster in behavioral space (Fig. 3), we infer that the significant phylogenetic MANOVA and ANOVAs in this study are in general the result of evolutionary convergence.

Although ecomorph species occupy statistically different portions of multivariate space and, normally, species are closer to other members of their own ecomorph class than they are to most or all members of other classes (Fig. 3B), there are some exceptions. In particular, there appear to be two discrete clusters of trunk–ground species, as three of these species (*A. cybotes*, *A. lineatopus*, and *A. sagrei*) form one cluster, and the two Puerto Rican trunk–ground species (*A. gundlachi* and *A. cristatellus*) form another. Why this occurs is not obvious, although the same phenomenon is seen, to a lesser extent, in morphological



**Figure 3.** (A) Species in the same ecomorph tend to occur near each other in the behavioral space defined by territory overlap and display behavior even though they are not closely related. Numbers correspond to species in the phylogeny (Fig. 1). (B) Using the data in panel a, for each ecomorph, the average phenotypic distance between species in the same ecomorph is smaller than the average distance between species in different ecomorphs.

**Table 2.** Results from regression analyses using independent contrasts, with visibility as the independent variable and measures of territoriality as dependent variables. Significant *P*-values are indicated in bold type.

| Variable   | <i>R</i> <sup>2</sup> | df    | <i>F</i> | <i>P</i>     |
|--|-----------------------|-------|----------|--------------|
| (A) Regression analyses with visibility and territory overlap measures |                       |       |          |              |
| Male–male overlap index  | 0.13                  | 1, 10 | 1.47     | 0.253        |
| Number of males overlapping  | 0.15                  | 1, 10 | 1.71     | 0.220        |
| Number of females overlapping  | 0.25                  | 1, 10 | 3.31     | 0.099        |
| (B) Regression analyses with visibility and display measures           |                       |       |          |              |
| Display time   | 0.51                  | 1, 10 | 10.6     | <b>0.009</b> |
| Total display rate   | 0.40                  | 1, 10 | 6.72     | <b>0.027</b> |
| Dewlap extension   | 0.10                  | 1, 10 | 1.08     | 0.323        |
| Headbobs+pushups   | 0.33                  | 1, 10 | 4.81     | 0.053        |

data (see discussion of ecomorph clustering in Losos 2009, pp. 40–49).

Visibility, an aspect of habitat that is not known to differ among ecomorph classes, was significantly associated with display behavior, but not territory overlap (Table 2A,B). The relationship between visibility and display was affected by both components of display (proportion of time spent displaying and total display rate; Table 2B). Further post hoc analyses showed that the composition of displays were only somewhat associated with visibility, as dewlap extension rate had no relationship with visibility, and combined headbob and pushup rate was marginally significantly associated with visibility (Table 2B).

Uncentered correlations among contrasts of overlap and display traits revealed that although the Overlap PC and Display PC were not statistically related ( $r = 0.33$ ,  $P = 0.27$ ), associations did exist among some aspects of these two components of territoriality. In particular, as male–male overlap increased, so did the proportion of time spent displaying ( $r = 0.67$ ,  $P < 0.0001$ ), although male–male overlap and overall display rate were unrelated ( $r = 0.08$ ,  $P = 0.78$ ).

Taken together, these results indicate that ecomorphs show convergence in territorial overlap, that visibility is an important predictor of general display behavior, and that aspects of territory overlap and display behavior are positively associated.

## Discussion

Many examples exist of species that are found in similar environments convergently evolving similar phenotypes. Morphological, physiological, and life-history traits are among those most often cited, but it may be just as likely that behavioral traits commonly converge as well. In fact, research continues to reveal that the evolution of complex behavior can be strikingly predictable. Studies of web architecture in Hawaiian *Tetragnatha* spiders have shown that the same types of web builders (called “ethotypes”) have evolved on different islands (Blackledge and Gillespie 2004). Also, in a comparative study of damselfly (*Enallagma*) larvae, Stoks et al. (2005) found that the same suites of behavior associated with predator avoidance (including foraging and locomotor behavior) have evolved in environments similar in predation risk. In Caribbean *Anolis* lizards, locomotor behavior (Losos 1990a; Irschick and Losos 1998, 1999; Irschick 2000), foraging mode (Johnson et al. 2008), and territorial strategies (Losos 1990b and this study) have evolved convergently with habitat use (reviewed in Losos 2009).

Territorial behavior is a major determinant of the evolution of a species' social structure, as it strongly influences how members of a species interact with one another, but has been rarely considered in studies of behavioral convergence. Here, we provide clear evidence for the convergent evolution of territoriality in a group of Caribbean *Anolis* lizards. An earlier study of *Anolis* (Losos 1990b) considered the effect of habitat on display rate; here we extend these findings considerably by examining display types and measures of territory overlap, as well as their relationship to visibility. As we predicted, the proportion of time a member of a species spends displaying and overall display rate are positively related with the visibility of its habitat, although the types of displays performed appear to be less influenced by habitat use. Unexpectedly, we also found that species that spend more time displaying have higher male–male territory overlap. We explore these results in more detail below.

## TERRITORY OVERLAP

Male–male territory overlap was strongly convergent within ecomorphs in the *Anolis* lizards in this study (Table 1 and Figs. 2 and 3). This provides convincing evidence that in addition to the complex suite of morphological, ecological, and behavioral traits previously shown to have evolved convergently within ecomorphs, the social structure of a species has also evolved in concert with its habitat use, and that adaptations to particular microhabitats are even more complex than previously appreciated.

One trait that has convergently evolved within ecomorphs and may provide further insight into the relationship between territory overlap and habitat use in this group is sexual size dimorphism (SSD), a trait that generally evolves when selection on body size differs between males and females (Shine 1989; Andersson 1994; Blanckenhorn 2005). SSD is convergent within ecomorphs, possibly because different habitats may offer different opportunities for sexual selection (Butler et al. 2000; Stuart-Fox and Moussalli 2007). SSD is also strongly linked with the territoriality and social organization of a species. If larger male body size evolves because territorial males compete for access to mating opportunities with

females, SSD and territorial strategies will coevolve. Evidence for this comes from several comparative studies; greater SSD is associated with increased home range overlap in ungulates (Jarman 1983) and male to female home range ratio is positively related to SSD in *Anolis* lizards (Stamps 1983; Cox et al. 2003).

In this study, we found that patterns of SSD among ecomorphs are paralleled in measures of territory overlap; the ecomorphs with low SSD (twig and grass–bush) also exhibit low territory overlap, and the ecomorphs with high SSD (trunk–ground and trunk–crown) exhibit high territory overlap; indeed the relationship between SSD and territory overlap is significant for species in this study (regression using contrasts;  $R^2 = 0.298$ ,  $F_{1,10} = 4.67$ , one-tailed  $P = 0.027$ ). If the varying habitats used by the different ecomorphs differ in the selective pressures they create, then habitat use may concurrently drive the evolution of both SSD and territory overlap.

### TERRITORIAL DISPLAY BEHAVIOR

In many species, social behavior is driven by the complexity of the habitat in which the species occur. In particular, a relationship between aggression and habitat complexity has been found in several fish species. Zebrafish (*Danio rerio*; Basquill and Grant 1998) and brown trout (*Salmo trutta*; Sundbaum and Näslund 1998) occurring in more complex habitats (i.e., with decreased visibility) are more visually isolated, which reduces the ability of dominant individuals to monopolize resources from subordinates. Höjesjö and colleagues (2004) suggested that complex habitats may select against aggressive strategies, as more resources are required to perform aggressive behavior than nonaggressive behavior, but aggressiveness was not as effective in lower visibility habitats. This hypothesis is consistent with the prediction that decreased visibility increases the cost of defense in territorial animals by increasing the effort required to detect and expel intruders (Schoener 1987; Eason and Stamps 1992).

In this study, we also found a strong relationship between visibility and social behavior. Among the species of *Anolis* lizards in this study, visibility and territorial display behavior are positively related, such that as visibility increases, members of a species perform more displays and spend more time performing displays. It is possible that increased visibility increases the encounter rate of lizards in a population, because lizards can see one another more easily in more open habitats. Alternatively, lizards in lower visibility (i.e., higher “noise”) habitats may perform shorter, quicker displays to maximize their contrast against the environmental background noise, as found previously for two species of *Anolis* lizards (Ord et al. 2007).

Although *Anolis* display behavior is strongly related to habitat visibility, the particular types of displays (dewlap extensions vs. pushups and headbobs) do not individually show a relationship with habitat. Furthermore, none of the individual display traits

measured is convergent within ecomorphs. Overall, it appears that although species have converged in display time, they have done so by different means. This situation is analogous to that described in Huey et al. (2000) in which populations of *Drosophila subobscura* evolved convergent wing size along a geographical gradient, but this overall pattern was achieved by size changes in different parts of the wing. These results thus indicate that, just as with morphology, convergent behaviors may evolve by divergent means.

### RELATIONSHIP BETWEEN DISPLAY BEHAVIOR AND TERRITORY OVERLAP

Territoriality is generally thought of as a strategy that involves both the behavioral defense of space and use of exclusive space (Kaufmann 1983; Stamps 1994; Maher and Lott 1995). In this study, we expected to find that animals who displayed frequently would have low territory overlap, as we presumed that display frequency would be symptomatic of territory defense. Instead, we found that species that spend more time displaying also have higher within-sex territory overlap. This is a correlative relationship, and although no causative direction can be inferred from our analyses, it seems likely that members of species that experience higher overlap would encounter one another more often, and therefore have more social interactions that result in displays.

This relationship between display behavior and overlap does not appear to be the result of differences in population density among the species (cf. Stamps and Krishnan 1998, on intraspecific patterns in *A. aeneus*), because no significant correlation exists between density and any of the overlap or display behavior variables in this study (for correlation between density and all other variables,  $P > 0.2$ ). Although density is an important factor in determining the social structure of a species, it is not statistically related to the variables measured here, perhaps because all species were studied in relatively high-density areas. Furthermore, we found no density differences among the ecomorphs (ANOVA  $F_{3,9} = 2.26$ ,  $P > 0.15$ ), suggesting that the ecomorph-level differences reported here are not confounded by population density.

### CONVERGENT BEHAVIORAL EVOLUTION

We present here a clear example of behavioral convergence in a replicated adaptive radiation. For Caribbean *Anolis* lizards, we suggest that the evolution of territorial strategies has occurred along two axes. The behavioral component of territoriality, that is, aggressive displays, has evolved primarily as a function of habitat visibility, such that species in more open habitats spend more time performing territorial displays. The spatial component of territoriality, however, has evolved as a function of perch height and diameter, the habitat characteristics that define *Anolis* ecomorphs. These relationships might well extend to many other animal taxa.

If habitat generally drives the evolution of social structure, the extent of sexual selection and the mating systems that result might ultimately be predictable as a function of habitat use.

#### ACKNOWLEDGMENTS

For their enthusiastic assistance during months in the field, we are much indebted to R. Kirby, A. Chen, C. Fresquez, J. Ladner, T. Ramsey, J. Shaw, S. Singhal, and S. Wang. We are grateful for the logistical support and friendship of the staffs of El Verde Field Station, Discovery Bay Marine Laboratory, and Coralsol Beach Resort. We also thank D. Irschick, J. Kolbe, and S. Singhal for their thoughtful comments on a previous version of this manuscript. Financial support for this study was provided by National Science Foundation (DEB 9982736 to JBL and a Graduate Research Fellowship to MAJ), and funds from the American Association of University Women, the Exploration Fund of the Explorer's Club, and the Educational Foundation of the Association for Women in Science (MAJ). Undergraduate assistants were funded through Washington University's Summer Undergraduate Research Fellowships (RK and JS), Israelow Fellowship (JL), Lennette Fellowship (to SS), International Activities Fund (to SS), and Hoopes Undergraduate Research Award (to SS). SS was also supported by a Sigma Xi GIAR. Finally, this study would not have been possible without the extensive support of Washington University's Division of Biology and Biomedical Sciences and the Department of Biology during MAJ's dissertation research.

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Associate Editor: A. Badyaev