

Notes and Comments

Species Identity Cues in Animal Communication

Terry J. Ord^{1,2,*} and Judy A. Stamps²

1. Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138; 2. Department of Evolution and Ecology, University of California, Davis, California 95616

Submitted October 19, 2008; Accepted April 22, 2009; Electronically published August 19, 2009

Online enhancement: appendix.

ABSTRACT: Researchers have suggested that animals should respond more strongly to conspecific than to heterospecific communication signals used in territorial or courtship contexts. We tested this prediction by reviewing studies that appeared in six prominent journals over the past 10 years. A meta-analysis based on these empirical studies revealed that overall support for this hypothesis was weaker than anticipated. To help clarify the extent to which experimental design might contribute to equivocal findings, we performed playback experiments in the field, using robotic lizards. We examined whether male tropical lizards, *Anolis gundlachi*, responded more strongly to robots producing conspecific territorial advertisement displays than to robots producing equivalent displays of a novel heterospecific. Although this experiment was conducted under natural conditions in the field, at signaler-receiver distances typical for animals at this locality, and with high statistical power, we found that lizards responded just as aggressively to a simulated rival performing a display they had never seen before as to the same rival performing a conspecific display. Our findings suggest that predicting how animals will respond to conspecific versus heterospecific signals is more complicated than has generally been anticipated.

Keywords: *Anolis*, courtship, meta-analysis, robot playback, species recognition, territoriality.

Introduction

The tremendous diversity in animal signals across closely related species can be explained by a number of interacting factors. Variation in the intensity of sexual selection can encourage the evolution of species differences in display elaboration and complexity (e.g., female mate choice [Spaulding 2007] and male-male competition [Ord et al. 2001]). Signal differentiation can also reflect variation among environments if different signal characteristics are best suited to different types of habitats (Patten et al. 2004; Doucet et al. 2007). Yet even when closely related species experience

similar social and ecological selective pressures, they typically differ with respect to some components of their communication signals. In this situation, the evolution of species-specific components of animal signals is assumed to reflect a basic need for accurate species identification (Andersson 1994; Bradbury and Vehrencamp 1998; Gröning and Hochkirch 2008).

Intuition suggests that the differential responses to species-specific signals should be especially important in the contexts of courtship and territorial defense. To produce viable offspring, mates must first recognize each other as appropriate partners of the same species. Mistakes in mate choice come at a cost for both sexes in terms of time diverted from other activities such as foraging and viable mating opportunities, energy expenditure, and wasted reproductive investment (sperm and eggs; reviewed in Gröning and Hochkirch 2008). Acquiring and maintaining a territory also involves costs, including energetic expenses (e.g., Brandt 2003), time taken from other activities (e.g., Radesäter et al. 1987), and increased risk of injury (e.g., Lappin and Husak 2005). Given the potential costs of responding to inappropriate mates or opponents, researchers have suggested not only that animals use species-specific signals to discriminate conspecifics from nonconspecifics but that they should also respond more strongly to the signals of the former (e.g., reviewed in Andersson 1994 and recently for birds in Price 2008). However, we can also imagine situations in which free-living animals are able to discriminate conspecific signals from heterospecific signals but respond similarly to both—for example, when individuals defend their territories against the members of another species (cf. Mikami and Kawata 2004) or when the costs of mistakenly ignoring a conspecific signal outweigh the costs of mistakenly responding to a nonconspecific signal (see “Discussion”).

In this note, we use a meta-analysis of published species recognition studies to evaluate the evidence that animals respond more strongly to conspecific than to nonconspecific signals. Our survey indicated that small sample sizes

* Corresponding author; e-mail: tord@oeb.harvard.edu.

and variation in venue (laboratory vs. field) might have contributed to variation in the results across species. To evaluate the extent to which experimental design influences findings, we conducted a field experiment using robotic lizards to perform “playbacks” of alternative territorial advertisement displays from conspecifics of and an allopatric heterospecific to free-living yellow-chinned anoles, *Anolis gundlachi*, on the island of Puerto Rico.

Material and Methods

Meta-analysis

We searched the contents of the *American Naturalist*, *Animal Behaviour*, *Behavioral Ecology*, *Behavioral Ecology and Sociobiology*, *Evolution*, and the *Journal of Evolutionary Biology* from 1997 to 2008, using the ISI Web of Science database and the search terms “conspecific discriminat*” and “conspecific AND heterospecific” (searches were conducted on April 4, 2008). Of the 197 articles found, we examined in detail those that compared the responses of focal animals to conspecific versus heterospecific signals and those that compared responses to conspecific versus biologically relevant artificial signals ($N = 53$). These studies included acoustic/vibration playbacks, presentations of olfactory cues or live animals as stimuli, or a combination of these stimuli.

A number of different effect size indices can be calculated, depending on the type of data reported by a study (e.g., Cohen’s d statistic, binomial proportion, odds ratio), but direct comparisons across different indices are difficult. To circumvent this problem, we selected those studies for which we could calculate a single standardized effect size and that would also make up the majority of studies published on this topic. Most studies (68%) reported some type of quantitative response measure (e.g., average time spent displaying or near stimuli, average latency to respond to stimuli). We focused on these studies and a modification of Cohen’s d statistic for our meta-analysis. This resulted in the omission of 17 studies, most involving mate choice in amphibians that provided focal animals with a choice of one or two signals and measured the proportion of responding animals (in this situation, the effect size index would be a binomial proportion or an odds ratio).

To evaluate the accuracy of the effect size estimates for each study, we computed the width of the effect size confidence intervals (CIs), an index that is proportional to the ability of an investigator to detect a treatment effect, should it exist (Colegrave and Ruxton 2003; Nakagawa and Cuthill 2007). Although some biologists believe that post hoc calculations of statistical power are adequate for this purpose, statisticians have emphasized that the practice of post hoc calculation of power is fundamentally

flawed (e.g., Hoenig and Heisey 2001). Hence, in this note we present estimates of effect sizes and their 95% CIs for each empirical study.

Of the 36 qualifying studies, we obtained the means, standard deviations, and sample sizes of test groups for all of the response measures reported by the authors from the text, tables, or figures (in the latter instance, means and error bars were digitally measured from plots with the use of Adobe Illustrator CS3, 13.0.0, Adobe Systems). The data for each response variable, i , were then converted into an effect size index, d_i , using a refinement to Cohen’s d statistic (Cohen 1969) developed by Hedges and Olkin (1985) that corrects for bias resulting from small sample size:

$$d_i = \frac{\bar{X}_c - \bar{X}_h}{\sqrt{[(N_c - 1)(SD_c)^2 + (N_h - 1)(SD_h)^2] / (N_c + N_h - 2)}} \times \left[1 - \frac{3}{4(N_c + N_h - 2) - 1} \right],$$

where \bar{X} is the mean value, SD is the standard deviation around the mean, and N is the number of focal animals tested for conspecific (c) and heterospecific (h) stimuli. The variance of the effect size, v_i , is then computed as

$$v_i = \frac{N_c + N_h}{N_c N_h} + \frac{d_i^2}{2(N_c + N_h - 2)}.$$

Finally, a 95% CI for d_i can be calculated by $d_i \pm 1.96v_i^{1/2}$. In many studies, the authors measured more than one response variable. We therefore computed two effect sizes: an “overall” effect size based on all the response variables that were measured by a study and a “maximum” effect size based on the response variable that showed the greatest difference between conspecific and nonconspecific stimuli reported by a study. In the latter instance, effect sizes (d_i) for all response variables were calculated for a study by using the formulas outlined above, and the variable with the largest value was selected to represent the maximum effect size for that study. To calculate an overall effect size, we combined the estimates for the different response variables reported by authors, using the approach outlined by Gurevitch and Hedges (1993). Here, effect sizes are weighted on the basis of the inverse of their associated variance, $1/v_i$; this weight value is notated by w_i . The overall effect size, d_+ , is subsequently calculated as

$$d_+ = \frac{\sum w_i d_i}{\sum w_i},$$

with a 95% CI for d_+ calculated by

$$d_+ \pm 1.96 \sqrt{\frac{1}{\sum w_i}}.$$

These formulas were also used in turn to combine the d_+ estimates for individual studies to calculate a “global” effect size estimate across all studies, notated by d_{++} .

To provide a familiar and bounded (−1 to 1) effect size metric, we converted effect sizes and their 95% CIs into r values, using the equation of Rosenthal (1994):

$$r_x = \sqrt{\frac{d_x^2 \bar{N}_c \bar{N}_h}{d_x^2 \bar{N}_c \bar{N}_h + (\bar{N}_c + \bar{N}_h)(\bar{N}_c + \bar{N}_h - 2)}}.$$

With this equation, maximum effect size estimates were converted into r values by replacing d_x with the largest value of d_i for a study, and \bar{N} is the number of focal animals assayed for that response variable to each stimulus type (c = conspecific signals; h = nonconspecific signals). Overall effect size estimates were converted to r values by replacing d_x with d_+ , and \bar{N} is the average number of focal animals used across all response variables measured by a study to a particular stimulus type. To convert global effect size estimates across studies, d_x is replaced by d_{++} , and \bar{N} becomes the average number of focal animals for each study (as above) averaged again across all studies. Thus, the maximum effect size of a study becomes r_p , the overall effect size for all response variables measured by a study becomes r_+ , and the global effect size across all studies becomes r_{++} .

Playback Study

Subjects. Playback experiments were conducted on a population of free-living *Anolis gundlachi* living in the montane shade forest of the Luquillo Mountains on Puerto Rico. Male anoles compete for territories that during the breeding season overlap the smaller home ranges of females, and the defense of mates is assumed to be a major function of male territorial defense (Ord 2008; Losos 2009). Males discourage territorial intrusions by conspecific neighbors and intruders by using broadcast displays that consist of an elaborate species-specific pattern of headbobs, which may also be accompanied by full extension of the dewlap. Playbacks of territorial displays were conducted in 2007, from June 16 to July 30, during the peak activity season for this species; all focal lizards were

adult males. We did not observe interspecific territorial defense by *A. gundlachi* during this study, but the extent to which males at this locality interact socially with sympatric congeners at other times of the year is unknown.

Robots. Three robotic lizards that could be programmed to perform virtually any display, natural or contrived, were used to perform field playbacks. Details on the construction (fig. A1 in the online edition of the *American Naturalist*) and programming of the robots are given in the appendix in the online edition of the *American Naturalist*. Special attention was given to matching the display movements and the dewlap color of robots to those of live animals, by use of motion analysis and spectroradiometry (fig. A2 in the online edition).

Playback Protocol. Playbacks were conducted in the forest surrounding the El Verde Field Station and areas accessed by foot from Route 186 and the El Toro Trail. We located adult male territorial holders by quietly walking through the forest. Once a focal male was found, we placed the robot on a tripod behind a tree such that the model appeared to be sitting perpendicular and level to the focal lizard in the typical “survey” posture of anole lizards. Trials began with the robot remaining stationary for 7 min, followed by a period of 10 min during which the robot displayed six times, a frequency that is typical for broadcast displays in *A. gundlachi* (see the appendix). We recorded focal lizard responses with a digital camcorder for later analysis.

We conducted two sets of playbacks. In the first, we measured the response of focal lizards to one of three stimuli: (1) the robot performing the conspecific headbob and dewlap display, (2) the robot performing a novel headbob and dewlap display, or (3) a control stimulus (a small bunch of plastic leaves attached to an empty robot box in lieu of the robot model). To study whether lizards attend to differences in headbob patterns in the absence of the dewlap extension, we conducted a second set of playbacks in which focal lizards were presented with a robot that kept the dewlap retracted and performed either (4) the conspecific headbob display, (5) the novel headbob display, or (6) no movement (the robot remained stationary throughout the playback period).

Recent studies of other taxa indicate that learning has a strong effect on the responses that individuals give to the signals of conspecifics versus heterospecifics (Magurran and Ramnarine 2004; Sedlacek et al. 2006; Dukas 2008). Hence, we used a novel display from an allopatric congener for the heterospecific signal in our study, to control for any possible effects of prior experiences the focal animals might have had with either the heterospecific signal or the animals that produce it. The Jamaican lizard

Anolis grahami was chosen to provide the novel display because its display sequence is quite distinct not only from those of *A. gundlachi* but also from those of other anoles sympatric with *A. gundlachi* on Puerto Rico. We predicted that lizards would respond aggressively to a simulated rival performing a conspecific display and less so (if at all) to one performing a functionally equivalent display unlike any they had seen before.

Analyses. We first confirmed that lizards responded appropriately to the robot as a biologically relevant social stimulus, by comparing responses to the displaying robot with response to the controls (leaf control, still robot). For lizards that viewed the displaying robot, we measured several response variables to determine whether lizards responded more strongly to the conspecific territorial display than to the novel display (see the appendix for details). For illustration purposes, we focus here on one of the response variables, total time spent head-bobbing by focal lizards; the effect sizes were comparable for the other response variables in our analysis (see the appendix). In the meta-analysis, however, to be consistent with calculations for other studies, we present an overall effect size based on all the response variables we measured and results based on the response variable with the maximum effect size in our study. False discovery rate (FDR) thresholds (Benjamini and Hochberg 1995) based on an initial α of 0.05 and a total of six comparisons were calculated (i.e., for all tests conducted, including those presented in the appendix).

Results

Meta-analyses

From the 36 studies meeting our criteria, we compiled data for 47 species that included amphibians, birds, fishes, invertebrates, mammals, and reptiles (fig. 1). The studies examined a variety of signals and cues: nine focused on acoustic signals, six on olfactory, and eight on visual, and 13 examined signals across two or all of these sensory modalities. The majority of studies examined the responses of animals to territorial or mating signals. Other articles examined the responses to conspecific signals by worker bees (Nunes et al. 2008), colony-living shrimp (Duffy et

al. 2002), and juvenile birds (Braaten and Reynolds 1999); the responses of adult birds to the conspecific begging calls of juveniles (Nakagawa et al. 2001); and the orienting responses to adult conspecific calls in birds (Rollo and Higgs 2008) and primates (Teufel et al. 2007).

The global effect sizes, r_{++} , were all positive, with CIs that did not overlap 0. This indicates that, generally speaking, animals did respond more strongly to the signals of conspecifics than to the signals of nonconspecifics (see table 1 and fig. 1 for results based on all of the response variables for each species and table 1 and fig. A4 in the online edition of the *American Naturalist* for results based on the maximum effect size for each species). Three studies presented both familiar (from sympatric congeners) and novel nonconspecific signals to focal animals, and effect sizes for these tests are provided separately.

However, the global effect sizes were also relatively small (r values around 0.3), reflecting the considerable variation across studies and species in the strength of their effect sizes and the width of their CIs. Indeed, over a third of the species surveyed (18 of 48 species, including our study of *Anolis gundlachi*, discussed below) had CIs that either overlapped 0 or actually responded more strongly to the signals of nonconspecifics. The same pattern emerged when we focused on the maximum effect sizes (fig. A4). Hence, despite an overall tendency for animals to respond more strongly to conspecific than to nonconspecific signals, more than a third of the species in the survey failed to show this relationship.

Playback Experiments

The focal lizards responded just as aggressively to a novel territorial display as they did to a conspecific territorial display, despite the extensive differences in the headbob patterns of the two displays (table 2; fig. A3 in the online edition of the *American Naturalist*). It was also clear, however, that the focal lizards responded to the “behavior” of the robot because more lizards responded to the displaying robot than to the still robot and because the lizards responded more to displays with dewlap extension than to displays without it, as evidenced by both the proportion of lizards responding and the latency of those that responded (see the appendix).

It is unlikely that our failure to detect a significant dif-

Figure 1: Effect size and 95% CIs calculated for studies published in six international journals over the past decade. Estimates are the overall effect size for all of the response variables reported by authors combined. Positive values represent a greater response to a conspecific stimulus, while negative values represent a greater response to a nonconspecific stimulus. The dashed vertical line is equivalent to animals responding equally to both conspecific and nonconspecific signals; “F” corresponds to nonconspecific stimuli that might have been familiar to focal animals (i.e., from a sympatric congener), while “N” indicates stimuli that were unfamiliar to focal animals (i.e., either biologically relevant artificial signals or signals from an allopatric congener). “Multimodal” (*diamonds*) refers to those studies that presented more than one class of signal.

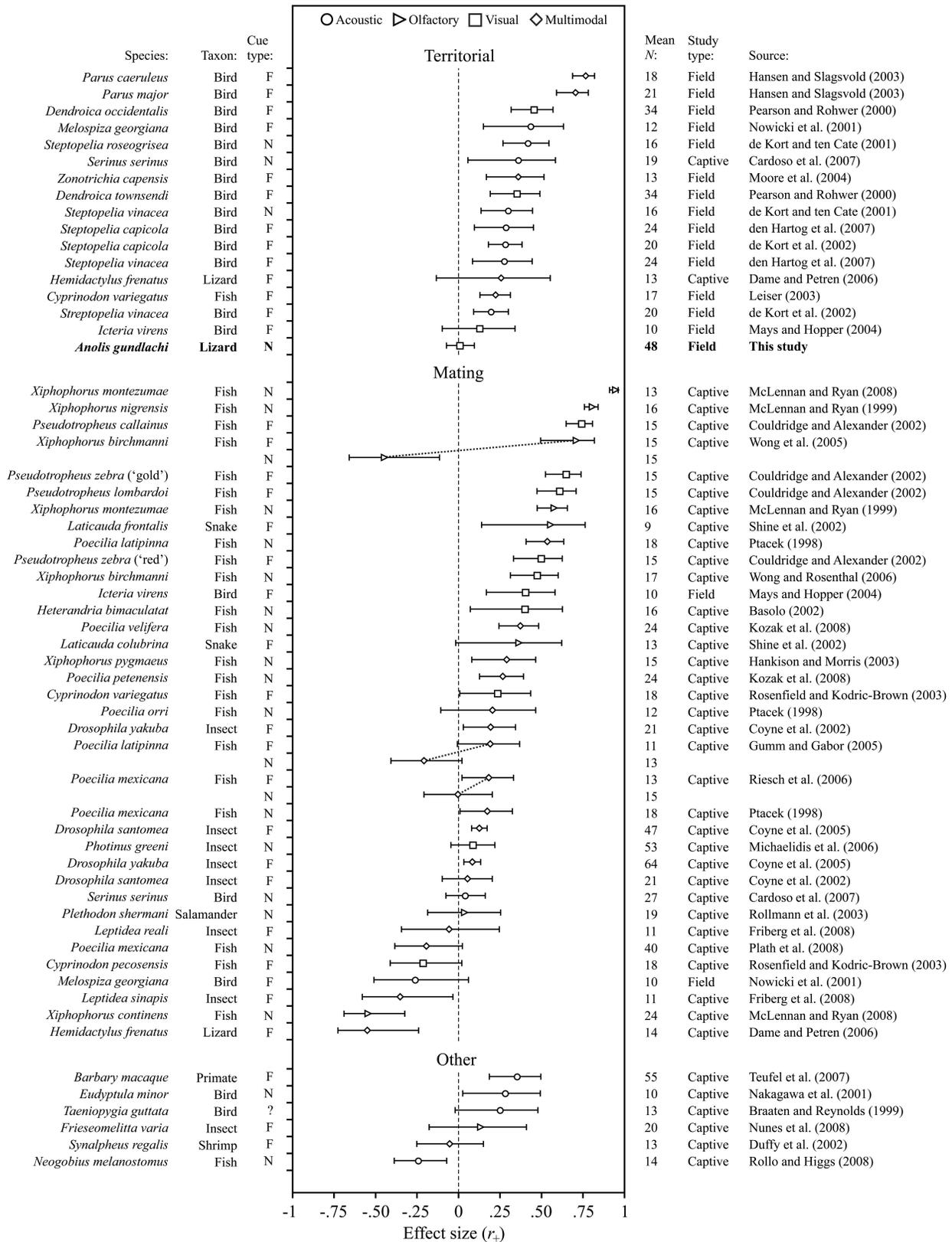


Table 1: Meta-analyses of evidence that animals respond differently to conspecific and nonconspecific signals

	Global effect size		N_{species}
	r_{++}	95% CI	
Overall: ^a			
All cues/signal types	.25	.21–.29	48
Novel cues/signals only	.23	.16–.29	24
Familiar cues/signals only	.28	.22–.34	27
Maximum: ^b			
All cues/signal types	.37	.32–.41	48
Novel cues/signals only	.35	.29–.41	24
Familiar cues/signals only	.40	.34–.46	27

Note: Results from the robot playbacks with *Anolis gundlachi* were included in the meta-analyses, along with the information from 47 species compiled from the literature. See text for details on how estimates were calculated and figure 1 for species and study lists.

^a Effect size estimates calculated using all response measures reported by a study.

^b Effect size estimates calculated using only the response measure with the greatest difference between conspecific and nonconspecific stimuli reported by each study.

ference between conspecific and novel territorial displays was due to deficiencies in experimental design. Based on the width of the CIs associated with effect sizes in figure 1, the power of our study was among the highest of all the studies in our meta-analyses, ranking second behind a mating study on *Drosophila* (Coyne et al. 2005), and our study had one of the largest sample sizes in the meta-analysis (fig. 1). Our ability to detect an effect was therefore much higher than most of the studies that have reported statistically significant differences in responses.

Discussion

Our meta-analyses provide general support for the hypothesis that animals respond more strongly to conspecific signals; when the results of all studies were combined, the global effect sizes were all positive and significantly different from 0 (table 1). However, the global effect sizes were small, and more than a third of the studies either did not detect any difference in response or detected a stronger response to the nonconspecific signal. Particularly surprising were the mixed results of many mating studies (figs. 1, A4), since we would expect selection for higher responsiveness to conspecific signals to be strong for mate choice, especially when the signals in question are produced by sympatric congeners. Unfortunately, we were unable to compare the results of studies conducted in territorial versus mating contexts because, thus far, researchers have focused on different taxa and modalities when studying territorial and mating signals (i.e., most territorial studies were conducted in the field and focused

on acoustic signals in birds, while most mating studies were done in the laboratory and focused on visual signals in fish; fig. 1).

The results of our empirical study of *Anolis gundlachi* indicate that robustly negative results can be obtained even in an experiment specifically designed to control for factors that may have affected the results of previous studies. The lack of any discernible difference between the lizards' aggressive responses to conspecific displays and those to novel heterospecific displays was particularly notable, given other results demonstrating that lizards did attend to other aspects of the displays, responding more to moving robots than to stationary ones and responding more to displays (either conspecific or heterospecific) accompanied by dewlap extension than to displays that lacked dewlap extension (see the appendix).

There are several nonexclusive hypotheses that might explain why some animals “fail” to respond differently to conspecific and nonconspecific signals. First, they may fail to discriminate conspecific from nonconspecific signals. Studies of signal perception that use operant or other techniques (e.g., see Shettleworth 1998; Rowe and Skelhorn 2004) suggest that lack of discrimination is most likely when the signals of heterospecifics are both novel and similar to the signals of conspecifics. By this view, it seems unlikely that *A. gundlachi* was unable to distinguish the heterospecific display from its own, given the pronounced

Table 2: Total time spent by *Anolis gundlachi* performing aggressive displays during robot playbacks of conspecific and novel displays

	df	F	P
Overall model ^a	6, 193	.39	.88
Independent variable:			
Intercept	1	.14	.71
Display type (F): conspecific vs.			
novel	1	.18	.67
Dewlap (F): present vs. absent	1	2.03	.16
Display type × dewlap	1	.07	.90
Robot distance from focal (C)	1	.05	.83
Habitat light (C)	1	.01	.93
Number of male neighbors (C)	1	.14	.71

Note: Factors (F) and covariates (C) were analyzed in a univariate general linear model (ANCOVA). All covariate interactions with factors for display type and dewlap were considered but failed to contribute significantly to the model ($P > .10$) and were removed. Four playback displays were presented: conspecific headbob and dewlap display ($N = 49$), novel headbob and dewlap display ($N = 45$), conspecific headbob display only ($N = 59$), and novel headbob display only ($N = 47$). Analyses of other response variables presented in the appendix were qualitatively similar, the only exception being that a greater proportion of lizards responded, and with quicker response latencies, to a robot that extended the dewlap (irrespective of display type).

^a FDR- $\alpha = .008$.

differences between their bob patterns, although further study would be required to test this assumption.

Even if animals are able to discriminate conspecific from heterospecific signals, they may not do so under natural conditions. One possible reason is that when animals rely on multiple sources of information to discriminate conspecifics from heterospecifics (Hankison and Morris 2003), they may not attend to one of those sources of information, at least when making an initial response. For instance, in our experiment the robot rival was the same size, shape, and color as *A. gundlachi*; had the same dewlap color as *A. gundlachi*; was perched in the same posture, at the same height, and on the same structures (tree trunks of a certain diameter) used by male *A. gundlachi*; and displayed at the same time of day and under the same set of environmental conditions as free-living *A. gundlachi*. All of our subjects would have had abundant opportunity to learn to associate these stimuli and contextual cues with conspecific rivals during the months to years since they began defending their own territory. If animals, including *A. gundlachi*, rely on multiple cues for species discrimination, it would not be surprising if they continued to react strongly to a stimulus animal if just one of those cues was out of place.

Signal detection theory provides another reason why animals might respond to nonconspecific signals. This model argues that responses to signals depend on the costs of making two types of mistakes: either incorrectly responding to the wrong signal or failing to respond to the right signal (Wiley 2006; e.g., see Leonard et al. 2005). That is, animals should be more likely to respond to nonconspecific signals when the costs of (incorrectly) responding to a nonconspecific signal are low and when the costs of (incorrectly) failing to respond to a conspecific signal are high (Bradbury and Vehrencamp 2000). Again with *A. gundlachi* as an example, the costs of giving a few headbob displays to a lizard that is not a conspecific rival are likely to be low relative to the costs of failing to respond to a challenge from a conspecific rival bent on taking over the territory. In this situation, we might expect territory owners to err on the side of caution and respond to displays that differ from their own, especially if other cues suggest that the signaler is probably a member of their species (see above). Along similar lines, high search costs associated with finding a mate in highly dispersed populations might encourage individuals to attend (at least initially) to potential mates that produce “odd” courtship displays rather than to be so selective that they mistakenly reject courting mates of their own species.

In conclusion, our study suggests that the role of communication signals in species recognition under natural conditions may be more complicated but also more interesting than is envisioned by the notion that species

differences in communication signals automatically lead to higher responses to the signals of conspecifics (see also Gerhardt 1982; Ryan and Rand 1993). Understanding species-specific responses to signals in nature is likely to require information about signal production and reception under difficult environmental conditions (Wollerman 1999; Ord and Stamps 2008), consideration of the potential costs and benefits of responding or failing to respond to particular signals (Bradbury and Vehrencamp 2000; Wiley 2006), and an appreciation of the wide range of proximate mechanisms that affect stimulus discrimination and relationships between stimuli and responses in animals (Shettleworth 1998; Rowe 1999; ten Cate and Rowe 2007; Bailey and Zuk 2008; Dukas 2008). With this information in hand, it should be easier to understand how animals avoid or minimize social interactions with members of other species under the challenging conditions in which these animals live and communicate with one another in nature.

Acknowledgments

We thank Z. Costa, A. Harrison, D. Hooper, S. Seil, and C. Steinberg for assistance in the field and N. Khan and the Harvard-MIT Data Center for statistical advice. K. Mabry advised on panty hose and suppliers for other materials used in the construction of the robots. Special thanks go to L. Fleishman for his help with the robot dewlap and for sharing data on dewlap spectra (see the appendix). The lizard robot was the original concept of J. Thompson and E. Martins. The University of Puerto Rico and A. Ramirez provided access to facilities at the El Verde Field Station. This work was supported by grants from the National Geographic Society and the National Science Foundation (IOB-0517041/0516998) to T.J.O., J.A.S. and J. B. Losos. The work described in this note is covered by Animal Use and Care Protocol 05-11652, initially approved on March 24, 2005, and reviewed most recently on March 22, 2007, by the Institutional Animal Care and Use Committee of the University of California, Davis. We are also indebted to D. Collar, A. Harrison, A. Herrel, C. Infante, J. Losos, L. Mahler, Y. Stuart, and two anonymous reviewers for comments on a previous version of this manuscript.

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