Communication Signal Rates Predict Interaction Outcome in the Brown Anole Lizard, *Anolis sagrei*

Valerie B. Simon[1]

Communication signals often function in multiple contexts such as territory defense, mate attraction, and predator deterrence. If signals indicate the quality of the signaler, then high rates of signal use may be associated with successful outcomes across multiple contexts. Here, I examined the relationship between signal use and interaction outcome during territorial defense and courtship bouts in field populations of the Brown Anole lizard, *Anolis sagrei*, in the middle of their breeding season. High bobbing rates, which are associated with high endurance in males of other lizard species, predicted both successful territorial defense and courtship bouts that resulted in copulation, while high rates of nodding, a signal typically associated with subordinate behavior during agonistic encounters, predicted unsuccessful outcomes in both contexts. Males performed dewlap extensions to females at a higher rate than to other males, independently of interaction outcome. In interactions with females, dewlap extension rates by males were higher during courtship bouts that did not result in copulations than during interactions preceding copulations. Assuming that increasing the rate of dewlap extensions benefits the signaler, this finding suggests that the use of the dewlap may play a larger role in stimulating or accelerating receptivity in an unreceptive female than in attracting an already-receptive female.

THE use of communication signals is associated with benefits to the signaler. During agonistic encounters, signals can prevent costly escalated combat by revealing asymmetries in motivation or fighting ability between opponents (Maynard Smith and Harper, 2003). During courtship, signal use by males can also facilitate mate attraction by increasing the conspicuousness of the signaler to potential mates, encoding species identity, advertising receptivity, or advertising the quality of the male. If signals are associated with male quality, such as handicap signals that are costly to produce (Zahavi, 1975), males able to sustain a high rate of those signals may be more likely to have interactions that end successfully across different contexts; thus, signal rate may predict interaction outcome.

Anoline lizards communicate with an array of visual displays during mate attraction (Greenberg and Noble, 1944), territory defense (Greenberg and Noble, 1944), and predator deterrence (Leal, 1999). Despite the attention focused on anoline lizards, there is still considerable uncertainty about the relationship between signal use by males and interaction outcome. While there is evidence that male lizards of other genera do not escalate contests when rivals signal at high rates (Ord et al., 2002; Ord and Evans, 2003), in some anoline lizards, smaller males with a low probability of winning contests match signals of their larger opponents, and frequently escalate interactions to the point of physical combat (Jenssen et al., 2005). The relationship between signal use and mate attraction is similarly ambivalent, since female anoline lizards do not exhibit mate choice (reviewed by Tokarz, 1995; Lailvaux and Irschick, 2006), yet males signal to females at relatively high rates.

Few studies of anoline lizards have compared the relationship between signal rates and interaction outcomes within and across both mating and agonistic contexts. In particular, little attention has been devoted to comparing male signals used in courtship immediately preceding mating with those not immediately preceding mating. This approach can elucidate the specific contexts under which high rates of certain signals may be favored. Many studies of anoline lizards have focused on interactions during the period of territory establishment, using paired subjects that are unfamiliar with one another. Males of *Anolis* exhibit neighbor recognition (Paterson and McMann, 2004), and respond to unfamiliar males with greater signal intensity and aggression during territory defense (Paterson and McMann, 2004), consistent with the "dear enemy" phenomenon (Fisher, 1954). Additionally, males respond to unfamiliar females with greater signal intensity during courtship (Tokarz, 1992; Orell and Jenssen, 2002). Thus, the conclusions of studies examining encounters between unfamiliar subjects may not be as applicable to understanding encounters that occur during the greater part of the breeding season following territory establishment. In this study, I examined the relationship between communication signal use and interaction outcome in *Anolis sagrei* in the field during the latter half of the species' breeding season, after territories have been established. I predicted that if the outcome of conspecific encounters varies as a function of signal rates, then lizards may be assessing each other based on signal use. Alternately, if signal rates do not mediate contests, there should be no relationship between signal rates and interaction outcome.

Anolis sagrei is a territorial, polygynous species whose range includes the southeastern United States, the Bahamas Islands, and the Caribbean. Its repertoire of displays consists of three major signals: nods, continuous up and down motions of the head and/or fore-body (also referred to as rhythmic quick bobs in Scott [1984], and nodding displays in McMann [2000]); bobs, up and down motions of the body that often feature characteristic inter-bob pauses; and extensions of the dewlap, an expandable throatfan which, in this species, ranges from yellow to red. All three signals can appear during courtship and territory defense (Scott, 1984). Most anoline lizards perform bobbing movements in sequences that are unique to the species, in which dewlap extensions and postures such as crest erection are used as modifiers of the central bobbing pattern (Jenssen, 1977). Dewlap extensions can also appear independently of bobbing displays (Scott, 1984). The central bobbing patterns

are often given functional labels that describe the context in which they are performed, and can be differentiated on the basis of the modifiers that appear with them (e.g., the non-directed ''assertion'' display is given by patrolling territorial males; the ''challenge'' display is given by contesting males; Crews, 1975a; Jenssen, 1977). There is considerable intra- and inter-individual variation in modifier use during the displays and the total number of bobs performed in a display (Crews, 1975a; Jenssen, 1977; Scott, 1984). Because different signal types can convey different information about signal-ers (Meyers et al., 2006) and since receivers may be sensitive to the rates of individual signal types, I examined signaling behavior at the level of individual signal types (i.e., nods, bobs, dewlap extensions) instead of measuring rates of various display types (i.e., assertion, challenge).

Agonistic interactions in anoline lizards appear to be mediated primarily by the relative body size of the opponents (Tokarz, 1985) and prior residency (McMann, 1993, 2000; Leuck, 1995), but performance-based factors such as endurance (Perry et al., 2004) and bite force (Lailvaux et al., 2004; Lailvaux and Irschick, 2007) also contribute to dominance. Signals may function as honest indicators of performance-based characteristics. The pushup may be an honest signal of endurance in some anoline lizards (Leal, 1999), particularly if it is performed with lateral compression of the body, which handicaps the signaler's endurance to a greater extent in other lizard genera (Brandt, 2003) and is often a feature of male–male contests. Therefore, a dominant male may signal with pushups or bobbing displays more often than subordinates. In labora-tory studies pairing males of *A. sagrei*, smaller males who lost contests performed a higher frequency of nods, while larger males performed more bobbing challenge displays (Scott, 1984; Tokarz, 1985). Resident males of *A. sagrei* also exhibited a higher frequency of bobbing displays relative to nodding displays, compared to intruders (McMann, 2000). Based on this research, I predicted that higher bobbing rates and lower nodding rates would also charac-terize males that are successful in agonistic interactions in the field.

The role of the dewlap in anoline courtship generally, and *A. sagrei* specifically, is equivocal. In some anoline lizards, dewlap size is an honest signal of bite force (Vanhooydonck et al., 2005a; Lailvaux and Irschick, 2007) or jumping ability (Vanhooydonck et al., 2005b). Although absolute dewlap size is positively correlated with bite force in *A. sagrei*, the dewlap in this species is not an honest signal of bite force after correcting for body size (Lailvaux and Irschick, 2007). Males of *A. sagrei* with inoperative dewlaps mated at the same rate as normal males (Tokarz, 2002; Tokarz et al., 2005), suggesting that an operational dewlap is not necessary for attracting resident females. However, females of *A. carolinensis* were more receptive to males with intact dewlaps than males with inoperative dewlaps (Crews, 1975b). In addition, ovarian recrudescence of females of *A. carolinensis* occurred more rapidly when in the presence of males with operational dewlaps (Crews, 1975b). The dewlap may also function to attract females at a distance (Sigmund, 1983) or play a role in species recognition (Rand and Williams, 1970; Williams and Rand, 1977; Losos, 1985). In staged pairings of *A. sagrei*, males did not signal with the dewlap extension more often in courtship than in agonistic encounters (Scott, 1984). However, signal use was only examined during courtship bouts immediately preceding

mating. I predicted that if the dewlap primarily functions to signal an aspect of the male's fighting ability, it may be used more frequently in agonistic interactions, particularly among males that win contests. If the dewlap primarily functions to facilitate female receptivity, it may be used to a greater extent in female interactions.

MATERIALS AND METHODS

Adult males of *Anolis sagrei* were observed in four sites in Florida and four sites in the Bahamas, June–August 1998– 2001, which corresponds to the latter half of the breeding season (Licht and Gorman, 1970). The sites in the Bahamas included two sites on Andros Island (6000 km^2; 24°50′N, 77°53.3′W); one site on Calabash Cay (24°53′N, 77°55′W), a small (0.085 km^2) island approximately 2.5 km from Andros Island; and one site on Gun Cay (25°35′N, 79°18′W), another small (0.028 km^2) island 80 km from mainland Florida. All sites in the Bahamas were forested, except one site on Andros was an open area with short vegetation less than 1.5 m in height. The sites in Florida included the Pahokee Campground (26°49.5′N, 80°40′W), which consist-ed of strands of Australian Pine (*Casuarina equisetifolia*) interspersed with man-made structures, and the adjacent rocky shoreline of Lake Okeechobee. Three other Florida sites were in Key Largo in the Florida Keys. One site was an orchard with various species of fruit trees within John Pennekamp State Park (27°07.4′N, 80°24′W). Another site in Pennekamp was comprised of a screened greenhouse bordered by several large trees. The third site was a residential area in north Key Largo (25°17.6′N, 80°17.4′W) consisting of a house and surrounding forest. *Anolis sagrei* were abundant in each site. I observed subjects at Calabash Cay in 1998 and 2000, and at one site in Key Largo in 1999 and 2000. None of the males observed in the later year were the same as those from the previous year, as evidenced by the lack of clipped digits.

At each site, I captured and toe-clipped 4–12 adult males. Snout–vent length was measured to the nearest mm. To facilitate recognition of individuals in the field, I applied dots of correction fluid (Liquid Paper, Sanford) to the dorsum of each captured lizard. A minimum of 24 h separated capture and start of behavioral observations to allow lizards to acclimate to the toe clipping and paint markings.

Observations took place on warm (>27°C) days when lizards at the study site were active. I observed each subject for 30–60 min per day for 2–4 days. The SVL of males that I observed ranged from 43–59 mm, which is above the threshold size of 39 mm at which sexual maturation occurs (Licht and Gorman, 1970). I remained at least 5 m from the subject and observed with binoculars at longer distances. I recorded my observations with a microcassette recorder to permit continual observation of the subjects, and recorded the time with a stopwatch at intervals of 30–90 s to determine the duration of social encounters. During the observation periods, I recorded the behavior of the subject, including use of each of the three major signals: bob, nod, extension of dewlap. Scott (1984) described an additional display, the jiggling display, consisting of rapid, shallow bobs performed by males during courtship, just prior to mating. I did not record instances of this display. When the subject signaled to conspecifics, I recorded the sex of the receiver and its approximate distance from the subject. Classification of a sequence of behaviors as an interaction

was based upon (1) the subject's movement towards the individual (occasionally resulting in a mating with a female and conflicts with males), (2) modifiers used during male–male interactions such as the erection of crests on the back and tail, and (3) behaviors exhibited by the receiver in response to the subject. Receiver responses included: for subordinate males, a retreat from an approaching male; for challenging males, an approach towards the subject and/or the performance of reciprocal displays; for females, a retreat from, or approach to, an approaching male, signaling displays, or a neck-bending display indicating receptivity (Greenberg and Noble, 1944). All interactions were close range, with a distance of 1.5 m or less separating individuals. At distances greater than 1.5 m, identifying the receiver of a focal male's signals became ambiguous.

Occasionally, subjects moved to positions out of view. If the focal lizard was out of view for longer than one minute, the interaction was omitted from subsequent analyses. In addition, interactions shorter than 2.5 min were not analyzed, since uncertainty in signal rates would be considerable based on the intervals in which I recorded the time. If subjects were out of view for less than one minute, I subtracted this time interval from the interaction duration to maintain accurate signal rates.

One difficulty in observing heterosexual interactions was that for six of 11 interactions that involved copulations, I did not locate the female until just prior to the copulation. Receptive females tended to be less conspicuous than unreceptive females. In the present study, receptive females often remained stationary and/or performed a neck bending display similar to those performed by females of *A. carolinensis* (Greenberg and Noble, 1944; Orrell and Jenssen, 2002) whereas unreceptive females often fled from or performed signaling displays to an advancing male, as described by Orrell and Jenssen (2002). For interactions in which I did not observe the female at least 2.5 min prior to copulation, I analyzed the five-minute interval prior to the mating. This duration was less than one standard deviation of the duration of interactions in which I had spotted the females beforehand (mean = 4.2 min, SD = 2.2, n = 5).

Interactions were classified into four categories: "copulation" was defined as a courtship bout that concluded in a mating; "no copulation" was a courtship that did not result in a mating; "opponent retreat" was a male contest in which the opponent retreated from the focal male; and finally, "focal male retreat" was a male contest that concluded with the focal male's retreat from the opponent.

Since each male could engage in multiple interactions falling into different categories, I used a logistic regression model with subjects as a random effect in order to account for the non-independence of repeated observations of the same subject. Analyses were performed using the logistic generalized estimating equation (GEE) method (Liang and Zeger, 1986) with the geeglm function of the statistical software package R, version 2.5.1 (R Foundation for Statistical Computing, Vienna, Austria). Subjects were treated as repeated measures, and I assumed an independence working correlation structure, which is recommended when there is no prior information about the correlation between measurements of the same individual (Pan, 2002). I used the model-building procedures outlined in Hosmer and Lemeshow (1989) to test the contribution of several factors to contest outcome: rates of nodding (NOD), bobbing (BOB), and dewlap extension (DE); sex of the receiver (SEX); and the interaction of receiver sex and signal rate for each signal type. Parameter estimates are logit estimates since a binomial function was used to model contest outcome. Distributions of continuous independent variables were assessed for normality with Shapiro-Wilk tests, and transformed, if necessary, prior to further analyses.

To determine whether signal rates of males varied according to the sex of the receiver, I also examined the rate of each signal type in relation to receiver sex after factoring out the variance due to interaction outcome. Additionally, since other studies have found that rate of DE varies as a function of receiver distance, I examined signal rates in relation to the closest approach distance for each subject (DIST), which was square-root-transformed to normalize the distribution. I examined these relationships with the geeglm function using a Gaussian (normal) distribution. Signal type was the dependent variable, and SEX, DIST, and interaction outcome were the independent variables. Since I was only interested in the independent variables SEX and DIST for this analysis, only these factors are reported in the results section. *P*-values of this analysis were Bonferroni-corrected to account for the multiple tests, with P_{crit} = 0.017.

The size asymmetry of contestants in a dyad is known to be a factor that determines the outcome of male conflicts. Thus, I determined whether winners of male contests were larger than losers with a binomial test with P_{crit} = 0.05. Additionally, I tested for the influence of a potentially confounding variable: population-level differences in signaling intensity. Signaling behavior of the same populations had been examined previously (Simon, 2002). For the current study, I analyzed data from the earlier study (Simon, 2002) with an ANOVA, which revealed differences in NOD, DE, and BOB frequencies among populations (NOD: $F_{8,61}$ = 2.59, P = 0.017; DE: $F_{8,61}$ = 5.39, P < 0.001; BOB: $F_{8,61}$ = 2.67, P = 0.014). For each signal type, I divided the eight populations into a "high signal rate" group of four populations with the higher mean rates and a "low signal rate" group of four populations with the lower mean rates, and counted the number of individuals in win versus loss categories. Fisher's exact tests with P_{crit} = 0.05 were used to determine if the ratios of subjects in each group differed across outcome categories for male interactions, female interactions, and all interactions combined.

RESULTS

A total of 50 social interactions were analyzed for 33 subjects. Fifteen males engaged in multiple interactions, and ten of these interactions encompassed different interaction categories. There were five focal male retreats, 13 opponent retreats, 21 no copulations, and 11 copulations. Of the 18 male contests, only two involved physical combat (11%). Five male interactions occurred between males with SVLs I had measured, and the body size of the winner was equal to (n = 1) or greater than (n = 4) the SVL of the retreating male in all cases, which approached significance (binomial test, P = 0.0625). All agonistic interactions analyzed involved adult males, except for one interaction between an adult and a juvenile male.

Population-level differences in signaling intensity are not likely to be confounding the relationship between signaling intensity and win/loss outcome categories. The *P*-values of all Fisher's exact tests were greater than 0.05 (range of *P*-values: 0.139–1.000), suggesting that the ratios of subjects
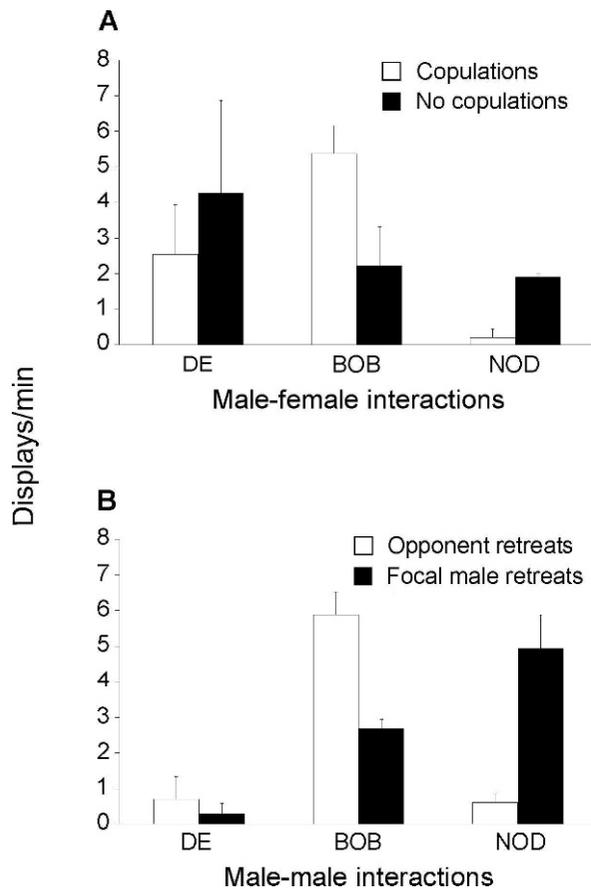
Fig. 1. Relationship between signal rates (displays/min) and interaction outcome across (A) courtship (male–female) and (B) agonistic (male–male) contexts. Means + SD shown. DE is dewlap extension rate, BOB is bobbing rate, and NOD is nodding rate.

from the two groups did not differ significantly between outcome categories.

The probability of a contest success (either a copulation or opponent retreat) was examined in relation to NOD, BOB, DE, SEX, and the interactions NOD*SEX, DE*SEX, and BOB*SEX. NOD and BOB were cube-root and square-root transformed, respectively. The initial model was significant (Wald$_7$ = 25.00, $P < 0.001$), suggesting that at least one explanatory variable explained variance in interaction outcome. The interaction NOD*SEX was not significant (Wald$_1$ = 0.48, $P = 0.49$), nor was BOB*SEX (Wald$_1$ = 0.50, $P = 0.48$), so both terms were sequentially removed from the model. SEX alone was not significant (Wald$_1$ = 0.65, $P = 0.42$), but the interaction DE*SEX was significant (Wald$_1$ = 7.03, $P = 0.0080$; Fig. 1) and was therefore retained in the model. DE was negatively associated with copulations when the receiver was female ($\beta = -0.0086$, SE = 0.0036, $P = 0.017$; Fig. 1A), and positively associated with contest outcome when the receiver was male ($\beta = 0.072$, SE = 0.027, $P = 0.0080$; Fig. 1B). BOB was a significant main effect, and positively associated with winning interactions (Wald$_1$ = 5.52, $P = 0.019$, $\beta = 0.188$, SE = 0.080; Fig. 1). NOD was also a significant main effect, and negatively associated with winning interactions (Wald$_1$ = 7.60, $P = 0.0058$, $\beta = -0.47$, SE = 0.17; Fig. 1). The final model included NOD, BOB, DE, SEX, and DE*SEX. A Pearson Chi-square goodness of fit test evaluated for GEE models (Pan, 2002; Evans and Li, 2005) indicated good fit of this model ($U = 5.83$, mean = 5.74, variance = 1.14, $P = 0.42$).

Males varied their signal frequency according to the sex of the receiver, independently of contest outcome, only for the dewlap extension. Males performed fewer dewlap extensions to other males than to females (Wald$_1$ = 29.8, $\beta = -175.15$, SE = 34.44, $P < 0.001$; Fig. 1). DIST was not significant (Wald$_1$ = 0.95, $P = 0.33$). Bobbing rates did not vary significantly by SEX (Wald$_1$ = 0.16, $P = 0.69$) or DIST (Wald$_1$ = 0.38, $P = 0.85$). Nodding frequency did not vary by SEX (Wald$_1$ = 1.22, $P = 0.27$) or DIST (Wald$_1$ = 0.76, $P = 0.38$).

DISCUSSION

Overall, these results support the hypothesis that patterns of signal use in males of *A. sagrei* were associated with interaction outcome. High rates of bobbing are associated with both successful territorial defense and mating encounters. In the context of territorial defense, the bobbing signal may be an honest signal of endurance. In *Anolis cristatellus*, there is a positive association among endurance, rates of assertion displays, and winning contests with size-matched male opponents (Perry et al., 2004). In a different context, predator avoidance, the number of pushup displays (four-legged bobbing displays) that males of *A. cristatellus* perform to predators was correlated with endurance (Leal, 1999). Thus, males may be able to assess endurance of rivals with this signal.

In contrast to bobbing rates, high rates of nodding were associated with males that retreated from their opponents. During aggressive encounters with other males, nodding is more frequently performed by subordinates in many anoline species (Greenberg and Noble, 1944; Stamps and Barlow, 1973; Crews, 1975a; Scott, 1984), so it most likely functions to de-escalate agonistic encounters and reduce the likelihood of physical injury to males less likely to win contests. The pattern of bobbing and nodding rates found in retreating and non-retreating males in the present study are consistent with those of subordinate and dominant males in staged agonistic encounters of *A. sagrei* (Scott, 1984; Tokarz, 1995), and of new arrivals and residents, who won all contests against new arrivals, in short-distance contests (McMann, 2000). Although unchallenged territorial males most frequently perform nods in an advertising context (McMann, 2000; McMann and Paterson, 2003) in which nods would not be considered a subordinate signal, this context differs from the agonistic context examined here. In addition, unchallenged males of *A. sagrei* perform a greater proportion of bobbing versus nodding displays at the periphery than at the core of their territories (McMann and Paterson, 2003). This pattern may be related to their closer proximity to potential rival males or neighboring females at territory boundaries. The results of the current study may provide insight into this phenomenon. Since high bobbing rates are associated with the retreat of rivals in the present study, it is possible that bobs also function over greater distances to prevent rivals from intruding.

During agonistic encounters, dewlap extension rates were positively associated with winning contests, but in contrast to Scott (1984), I found that dewlap rates were lower during agonistic encounters than during courtship. Other studies have found reduced dewlap use when males are within close range (McMann, 1993; DeCourcy and Jenssen, 1994). It is possible that dewlap size in *A. sagrei* is correlated with body size as in other *Anolis* species (Lailvaux et al., 2004). If so, large males may benefit from advertising their size by pulsing the dewlap. Since body size is a trait that remains

static over the course of the interaction, unlike a dynamic trait such as endurance, performing repeated displays after initial assessment by the opponent may be redundant and energetically costly. Additionally, dewlaps in *Anolis* contrast against the background vegetation of their habitats (Persons et al., 1999; Leal and Fleishman, 2004), and this conspicuousness may also serve to elicit the attention of the receiver, particularly at the beginning of the interaction when larger distances separate opponents. However, it may also be conspicuous to potential predators, and thus may be particularly costly during periods of reduced vigilance as males assess one another. If dewlap use is risky, males that display the dewlap at higher rates may be more able to bear the potential predation costs associated with its use. Dewlap use may also be reduced during male–male interactions because the dewlap may also be vulnerable to damage during physical combat, as suggested by other researchers (DeCourcy and Jenssen, 1994). Although higher rates of dewlap extensions characterized winners of contests, dewlap extensions may not be as crucial to territory defense as bobbing, since males of *A. sagrei* with inoperative dewlaps did not differ from control lizards in their ability to defend territories (Tokarz et al., 2003).

The results of this study suggest that in the middle of the breeding season, signal use, and not physical aggression, typically mediates interactions between males of *A. sagrei*. Other field studies have also documented low levels of physical aggression in established neighborhoods of *A. carolinensis* (Jenssen et al., 1995). Dominance relationships established early in the breeding season remain stable in other anoline lizards (Stamps and Krishnan, 1994). Moreover, initial escalated fights may discourage future escalated encounters (Stamps and Krishnan, 1994), suggesting that physical fighting decreases after territory establishment. According to game theoretical models of opponent assessment, such as the asymmetric war of attrition, role mistakes in which a probable loser mistakenly assumes the role of probable winner are less common when neighbors are familiar with one another, thus reducing the frequency of escalated encounters (Ydenberg et al., 1998). The familiarity level among individuals was not explicitly examined in this study, but it is likely that most individuals were familiar with neighbors by the midpoint of the breeding season. However, territorial displacements, possibly by unfamiliar intruders, do occasionally occur in the middle of the breeding season of *A. sagrei* (Tokarz, 1998). When territorial displacements are common, longer and more intense interactions may be more prevalent (Ruibal and Philibosian, 1974).

An alternate explanation for these results is that species or populations differ in their reliance on signals to mediate contests, regardless of their level of familiarity with opponents. Nine species of anoline lizards exhibited wide variations in signal use and biting in staged agonistic interactions (Lailvaux and Irschick, 2007). Compared to other species such as *A. carolinensis*, *A. sagrei* may be more likely to settle disputes with communication signals rather than physical combat. Among dyads of strangers of *A. sagrei*, larger males won more interactions and performed a greater number of challenge displays than their opponents, while physical combat occurred in only 24% of contests (Tokarz, 1985). Similarly, in dyads of male neighbors or strangers of *A. sagrei* tested in the middle of the breeding season, physical combat was not observed in either group (Paterson

and McMann, 2004). Conversely, all contests among unfamiliar males of *A. carolinensis* involved signal-matching and physical combat, even in dyads with size asymmetries (Jenssen et al., 2005). However, in *A. sagrei*, when asymmetries in size or residency status are not present between strangers, interactions can be intense, with frequent biting attacks (Lailvaux and Irschick, 2007). One drawback of the present study is that opponent body size and residency status were not known in all pairings, which would have aided interpretation of the current findings.

These results contrast with a study of *Anolis aeneus* in which territorial males typically interacted symmetrically and matched signals with their neighbors (Stamps and Krishnan, 1998). Even during contests characterized by signal matching, in which display rates do not differentiate the winner from the loser, subtle behavioral differences in *A. carolinensis* may determine contest outcome (McMann, 1993). Although the territorial status of all interacting males was not recorded in the present study, at least four of the interactions involved territory-holding males (unpubl.). It is possible that there are between-species or between-population differences in factors influencing the payoff of escalated encounters, such as the value of territories (which may be higher if they are scarce), or the degree to which signals are handicapping versus conventional, that would make it worthwhile for smaller males to escalate during contests. In addition, the physical condition of males may vary over the course of a breeding season in some species or populations more than others (for example, due to malaria), such that relying on prior information to assess opponents may not be reliable. One potentially important characteristic of *A. sagrei* is that populations can occur in high densities (Schoener and Schoener, 1980), which typically results in higher interaction rates (Stamps and Krishnan, 1998). It may be prohibitively costly to escalate contests when they occur at high rates, unless asymmetries between opponents are slight. *Anolis sagrei* may therefore be more sensitive to such asymmetries such as body size and residency status. Strategies during agonistic interactions have been found to differ as a function of population density even within a species (Stamps and Krishan, 1998), supporting this idea.

Large body size is strongly associated with dominance in lizards (Stamps, 1983), so this trait is one of importance as males assess one another. However, performance capacities can outweigh the importance of body size in some cases. In the Jacky dragon, *Amphibolurus muricatus*, videos of a smaller male performing displays at a high rate elicited submissive signals from larger male opponents, and more often than a large male performing displays at a slower rate (Ord et al., 2002), suggesting that endurance may outweigh body size. In other lizard taxa, bite force independent of body size was a stronger predictor of dominance than body size (Huyghe et al., 2005). Thus, assessing just the size of the opponent may not provide adequate information about the potential outcome of the contest, which would favor the evolution of signals that indicate multiple aspects of fighting ability, including performance.

In general, patterns of bobbing and nodding by males associated with successful matings were similar to that of successful agonistic encounters with the exception of the dewlap. It is unclear how high signal rates that are possibly associated with male quality during agonistic encounters would be advantageous during courtship, since females of *Anolis* are not choosy. Females settle on home ranges prior

to the emergence of males in some seasonal species, precluding females from choosing among reproductively active males early in the breeding season (Jenssen et al., 2001); tend not enter other males' territories (Tokarz, 1998); and generally do not advertise receptivity to neighboring males (Tokarz, 1998). Moreover, when territorial displacements occur, females mate with the new resident males (Tokarz, 1998). This observation, plus the evidence that females are able to store sperm for several months (Fox, 1963; Conner and Crews, 1980), suggests that sperm competition, rather than female mate choice, may be a mechanism through which females obtain good genes. It is possible that the performance of bobbing displays has a motivational component, as well as indicating the endurance of the signaler, such that its use would be higher among males more likely to mate.

Although females may not actively choose mates, male signals, particularly the dewlap, may play other roles such as stimulating female receptivity or signaling gender recognition. Males performed dewlap extensions to females more frequently than to males at close range, suggesting that high rates of the dewlap may have a specialized function during courtship. This pattern is consistent with studies suggesting that the dewlap extension may accelerate female receptivity at the beginning of the breeding season (Crews, 1975b), and continued exposure may be necessary for maintaining ovarian recrudescence after its onset (Crews, 1974). One unexpected finding was that that dewlap rates were higher during interactions with females that did not lead to copulation. It is possible that exposure to high rates of dewlap use also accelerates female receptivity between ovarian cycles, and that males increase dewlap rates when females are unreceptive. High rates of the dewlap may not be as necessary once the female has reached estrous, as other studies have shown that males with inoperative dewlaps copulate at the same rate as control males (Tokarz, 2002; Tokarz et al., 2005). Another possible explanation is that that there is no selective advantage to males performing high rates of the dewlap display when females are not receptive, and that it is the result of male inexperience. It is also possible that dewlap use is advantageous prior to copulation, but is balanced by predation costs if this signal attracts predators at a time when the ability of the male or female to escape an attack would soon be compromised. Males of *A. sagrei* marginally decrease use of the dewlap when predation risk is high (Simon, 2007).

A second explanation for male signaling patterns during courtship is that higher rates of the dewlap display may indicate to a female that a male has correctly identified her as a female and not a small male, thus reducing the risk of physical attack. Male anoles occasionally attack unfamiliar females, presumably mistakenly (Stamps, 1977), and females have been observed to flee from unfamiliar males more often than resident females (Orrell and Jenssen, 2002), suggesting that unfamiliar males may pose a threat. Additionally, the duration of male courtship necessary to induce a female to mate decreases with increasing time they have shared a home range (Stamps, 1977), suggesting that a female's familiarity with a male may be important to mating success, and familiar males may not have to expend as much courtship effort. In other taxa such as the Japanese quail, females avoid aggressive males to reduce the risk of physical harm during courtship or mating (Ophir et al., 2005). In a more general sense, male courtship displays may advertise

sexual receptivity to the female, and allow the male to gauge female receptivity in a manner that is less costly to both individuals than coercion. Since females tend to mate with territorial owners, aggressive male sexual tactics, which can reduce female fecundity or survival (Clutton-Brock and Parker, 1995; Le Galliard et al., 2005) may not be favored. In conclusion, high dewlap rates may be particularly important during courtship bouts involving unreceptive females, which merits further study.

LITERATURE CITED

Brandt, Y. 2003. Lizard threat display handicaps endurance. Proceedings of the Royal Society of London B: Biological Sciences 270:1061–1068.

Clutton-Brock, T. H., and G. A. Parker. 1995. Sexual coercion in animal societies. Animal Behaviour 49:1345–1365.

Conner, J., and D. Crews. 1980. Sperm transfer and storage in the lizard, *Anolis carolinensis*. Journal of Morphology 163:331–348.

Crews, D. 1974. Effects of group stability, male–male aggression and male courtship behavior on environmentally-induced ovarian recrudescence in the lizard, *Anolis carolinensis*. Journal of Zoology, London 172:419–441.

Crews, D. 1975a. Inter- and intraindividual variation in display patterns in the lizard, *Anolis carolinensis*. Herpetologica 31:37–47.

Crews, D. 1975b. Effects of different components of male courtship behaviour on environmentally induced ovarian recrudescence and mating preferences in the lizard, *Anolis carolinensis*. Animal Behaviour 23:349–356.

DeCourcy, K. R., and T. A. Jenssen. 1994. Structure and use of male territorial headbob signals by the lizard *Anolis carolinensis*. Animal Behaviour 47:251–262.

Evans, S., and L. Li. 2005. A comparison of goodness of fit tests for the logistic GEE model. Statistics in Medicine 24:1245–1261.

Fisher, J. B. 1954. Evolution and bird sociality, p. 71–83. *In*: Evolution as a Process. J. Huxley, A. C. Hardy, and E. B. Ford (eds.). Allen and Unwin, London.

Fox, W. 1963. Special tubules for sperm storage in female lizards. Nature 198:500–501.

Greenberg, G., and G. K. Noble. 1944. Social behavior of the American chameleon (*Anolis carolinensis* Voigt). Physiological Zoology 17:392–439.

Hosmer, D. W., and S. Lemeshow. 1989. Applied Logistic Regression. J. Wiley, New York.

Huyghe, K., B. Vanhooydonck, H. Scheers, M. Molina-Borja, and R. Van Damme. 2005. Morphology, performance and fighting capacity in male lizards, *Gallotia galloti.* Functional Ecology 19:800–807.

Jenssen, T. A. 1977. Evolution of anoline lizard display behavior. American Zoologist 17:203–215.

Jenssen, T. A., K. R. DeCourcy, and J. D. Congdon. 2005. Assessment in contests of male lizards (*Anolis carolinensis*):

How should smaller males respond when size matters? Animal Behaviour 69:1325–1336.

Jenssen, T. A., N. Greenberg, and K. A. Hovde. 1995. Behavioral profile of free-ranging male lizards, *Anolis carolinesis*, across breeding and post-breeding seasons. Herpetological Monographs 9:41–62.

Jenssen, T. A., M. B. Lovern, and J. D. Congdon. 2001. Field-testing the protandry-based mating system for the lizard, *Anolis carolinesis*: Does the model organism have the right model? Behavioral Ecology and Sociobiology 50:162–172.

Lailvaux, S., A. Herrel, B. Vanhooydonck, J. Meyers, and D. J. Irschick. 2004. Performance capacity, fighting tactics, and the evolution of life-stage morphs in the green anole lizard (*Anolis carolinensis*). Proceedings of the Royal Society of London B: Biological Sciences 271: 2501–2508.

Lailvaux, S. P., and D. J. Irschick. 2006. No evidence for female association with high-performance males in the green anole lizard, *Anolis carolinensis*. Ethology 112:707–715.

Lailvaux, S. P., and D. J. Irschick. 2007. The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. The American Naturalist 170:573–586.

Le Galliard, J.-F., P. S. Fitze, R. Ferriere, and J. Clobert. 2005. Sex ratio bias, male aggression, and population collapse in lizards. Proceedings of the National Academy of Sciences of the United States of America 102:18231–18236.

Leal, M. 1999. Honest signalling during predator–prey interactions in the lizard *Anolis cristatellus*. Animal Behaviour 58:521–526.

Leal, M., and L. J. Fleishman. 2004. Differences in visual signal design and detectability between allopatric populations of *Anolis* lizards. The American Naturalist 163:26–39.

Leuck, B. E. 1995. Territorial defense by male green anoles: an experimental test of the roles of residency and resource quality. Herpetological Monographs 9:63–74.

Liang, K., and S. L. Zeger. 1986. Longitudinal data analysis using generalized linear models. Biometrika 73:13–22.

Licht, P., and G. C. Gorman. 1970. Reproductive and fat cycles in the Caribbean *Anolis* lizards. University of California Publications in Zoology 95:1–52.

Losos, J. B. 1985. An experimental demonstration of the species-recognition role of *Anolis* dewlap color. Copeia 1985:905–910.

Maynard Smith, J., and D. Harper. 2003. Animal Signals. Oxford University Press, Oxford.

McMann, S. 1993. Contextual signalling and the structure of dyadic encounters in *Anolis carolinensis*. Animal Behaviour 46:657–668.

McMann, S. 2000. Effects of residence time on displays during territory establishment in a lizard. Animal Behaviour 59:513–522.

McMann, S., and A. V. Paterson. 2003. Relationship between location and displays in a territorial lizard. Journal of Herpetology 37:414–416.

Meyers, J. J., D. J. Irschick, B. Vanhooydonck, and A. Herrel. 2006. Divergent roles for multiple sexual signals in a polygynous lizard. Functional Ecology 20:709–716.

Ophir, A. G., K. N. Persaud, and B. G. Galef, Jr. 2005. Avoidance of relatively aggressive male Japanese quail (*Coturnix japonica*) by sexually experienced conspecific females. Journal of Comparative Psychology 119:3–7.

Ord, T. J., and C. S. Evans. 2003. Display rate and opponent assessment in the Jacky dragon (*Amphibolurus muricatus*): an experimental analysis. Behaviour 140:1495–1508.

Ord, T. J., R. A. Peters, C. S. Evans, and A. Taylor. 2002. Digital video playback and visual communication in lizards. Animal Behaviour 63:879–890.

Orrell, K. S., and T. A. Jenssen. 2002. Male mate choice by the lizard *Anolis carolinensis*: a preference for novel females. Animal Behaviour 63:1091–1102.

Pan, W. 2002. Goodness-of-fit tests for GEE with correlated binary data. Scandinavian Journal of Statistics 29:101–110.

Paterson, A. V., and S. McMann. 2004. Differential head-bob displays towards neighbors and nonneighbors in the territorial lizard *Anolis sagrei*. Journal of Herpetology 38:288–291.

Perry, G., K. Levering, I. Girard, and T. Garland, Jr. 2004. Locomotor performance and social dominance in male *Anolis cristatellus*. Animal Behaviour 67:37–47.

Persons, M. H., L. J. Fleishman, M. A. Frye, and M. E. Stimphil. 1999. Sensory response patterns and the evolution of visual signal design in anoline lizards. Journal of Comparative Physiology A, Sensory, Neural, and Behavioral Physiology 184:585–607.

Rand, A. S., and E. E. Williams. 1970. An estimation of redundancy and information content of anole dewlaps. The American Naturalist 104:99–103.

Ruibal, R., and R. Philibosian. 1974. Aggression in the lizard *Anolis acutus*. Copeia 1974:349–357.

Schoener, T. W., and A. Schoener. 1980. Densities, sex ratios, and population structure in four species of Bahamian *Anolis* lizards. Journal of Animal Ecology 49:19–53.

Scott, M. P. 1984. Agonistic and courtship displays of male *Anolis sagrei*. Breviora 479:1–22.

Sigmund, W. R. 1983. Female preferences for *Anolis carolinensis* males as a function of dewlap color and background coloration. Journal of Herpetology 17:137–143.

Simon, V. B. 2002. The influence of predation pressure on the signaling behavior of an *Anolis* lizard. Unpubl. Ph.D. diss., Duke University, Durham, North Carolina.

Simon, V. B. 2007. Not all signals are equal: male Brown Anole lizards (*Anolis sagrei*) selectively decrease pushup frequency following a simulated predatory attack. Ethology 113:793–801.

Stamps, J. A. 1977. The relationship between resource competition, risk, and aggression in a tropical territorial lizard. Ecology 58:349–358.

Stamps, J. A. 1983. Sexual selection, sexual dimorphism, and territoriality, p. 169–204. *In*: Lizard Ecology: Studies of a Model Organism. R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.). Harvard University Press, Cambridge, Massachusetts.

Stamps, J. A., and G. W. Barlow. 1973. Variation and stereotypy in the displays of *Anolis aeneus* (Sauria: Iguanidae). Behaviour 47:67–93.

Stamps, J. A., and V. V. Krishnan. 1994. Territory acquisition in lizards. II. Establishing social and spatial relationships. Animal Behaviour 47:1387–1400.

Stamps, J. A., and V. V. Krishnan. 1998. Territory acquisition in lizards. IV. Obtaining high status and exclusive home ranges. Animal Behaviour 55:461–472.

Tokarz, R. R. 1985. Body size as a factor determining dominance in staged agonistic encounters between male

Brown Anoles (*Anolis sagrei*). Animal Behaviour 33: 746–751.

Tokarz, R. R. 1992. Male mating preference for unfamiliar females in the lizard, *Anolis sagrei*. Animal Behaviour 44:843–849.

Tokarz, R. R. 1995. Mate choice in lizards: a review. Herpetological Monographs 9:17–40.

Tokarz, R. R. 1998. Mating pattern in the lizard, *Anolis sagrei*: implications for mate choice and sperm competition. Herpetologica 54:388–394.

Tokarz, R. R. 2002. An experimental test of the importance of the dewlap in male mating success in the lizard *Anolis sagrei*. Herpetologica 58:87–94.

Tokarz, R. R., A. V. Paterson, and S. McMann. 2003. Laboratory and field test of the functional significance of the male's dewlap in the lizard *Anolis sagrei*. Copeia 2003:502–511.

Tokarz, R. R., A. V. Paterson, and S. McMann. 2005. Importance of dewlap display in male mating success in free-ranging Brown Anoles (*Anolis sagrei*). Journal of Herpetology 39:174–177.

Vanhooydonck, B., A. Herrel, R. Van Damme, and D. J. Irschick. 2005a. Does dewlap size predict male bite performance in Jamaican *Anolis* lizards? Functional Ecology 19:38–42.

Vanhooydonck, B., A. Herrel, R. Van Damme, J. J. Meyers, and D. J. Irschick. 2005b. The relationship between dewlap size and performance changes with age and sex in a Green Anole (*Anolis carolinensis*) lizard population. Behavioral Ecology and Sociobiology 59:157–165.

Williams, E. E., and S. Rand. 1977. Species recognition, dewlap function and faunal size. American Zoologist 17:261–270.

Ydenberg, R. C., L. A. Giraldeau, and J. B. Falls. 1998. Neighbors, strangers, and the asymmetric war of attrition. Animal Behaviour 36:343–347.

Zahavi, A. 1975. Mate selection—a selection for a handicap. Journal of Theoretical Biology 53:205–214.