

DISPLAY BEHAVIOR OF RESIDENT BROWN ANOLES (*ANOLIS SAGREI*) DURING CLOSE ENCOUNTERS WITH NEIGHBORS AND NON- NEIGHBORS

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Abstract.—There has been considerable interest in exploring how social relationships in territorial neighborhoods vary across contexts. In the lizard *Anolis sagrei* in southern Florida, dyads of males in a neutral arena behave differently depending on whether the lizards are prior neighbors, with prior neighbors exhibiting fewer bobbing relative to nodding forms of headbob displays than non-neighbors. Here we test whether free-living territory residents show similar display differences when faced with a close-range encounter with a neighbor versus a non-neighbor, and examine display behaviors not examined in the previous study. During each of 20 encounters, we exposed a focal animal to either a neighbor or a non-neighbor that had been placed in a cage and moved to a location approximately 1 m from the focal animal. We then recorded display behavior of the focal animal for 30 min. We found that neighbors elicited lower proportions of headbob displays that were bobbing displays and fewer bobbing displays than non-neighbors. Encounter types did not differ in the number of nodding displays, the proportion of headbob displays with crest erection, or the number of dewlap extensions. Our findings indicate that the response of a focal animal to neighbor is different, and likely less intense, than the response to a non-neighbor. This is consistent with what is often called the dear enemy phenomenon, and suggests that this phenomenon in male *Anolis sagrei* has at least a proximal basis that can be present regardless of whether the animals are in a natural territorial neighborhood.

Key Words.—Dear enemy phenomenon; differential aggression; display behavior; lizards; signaling; territoriality

INTRODUCTION

When animals form territories, they often divide space such that a number of individual territories are in close proximity, forming territorial neighborhoods that are the subject of increasing research interest (e.g., see Stamps and Krishnan 1999; Paterson 2002). Within such neighborhoods, social interactions are more complex than the simple exclusion of competitors from territories. In at least some cases, territory owners have been found to interact with potential competitors differently in different contexts. For example, in what has been called the “dear enemy phenomenon,” a territory owner may treat neighbors with less aggression than non-neighbors (e.g., Fisher 1954; Temeles 1994). However, relationships can be more complex than is implied by the simplest formulation of the dear enemy phenomenon. For example, this reduction in aggression towards neighbors may be inhibited in at least some contexts where the neighbor is not on its own territory (e.g., Falls 1982; Fox and Baird 1992; Giraldeau and Ydenberg 1987; Husak and Fox 2003; Olendorf et al. 2005), when a neighbor has previously intruded on the resident’s territory (Akçay et al. 2009), or when a neighbor has previously intruded on another individual’s territory (Akçay et al. 2010). Additionally, some studies have not found dear enemy behavior, and, in fact, neighbors can be treated with more aggression than non-neighbors in at

least some situations (e.g., see discussion in Temeles 1994). Although an increasing number of studies have examined the dear enemy phenomenon, relatively few have examined how relationships within territorial neighborhoods vary across contexts within one species.

We have been studying male Brown Anoles (*Anolis sagrei*; Fig. 1) in southern Florida to understand social behavior in multiple contexts within the territorial neighborhoods that they form during their breeding season (e.g., McMann 2000; Paterson 2002; McMann and Paterson 2003a; Paterson and McMann 2004). We previously found that dyads of former neighbors interacted differently than dyads of non-neighbors during close encounters within a neutral arena (Paterson and McMann 2004). That study established that male *A. sagrei* can distinguish former neighbors from non-neighbors. However, as the lizards were experimentally placed outside their territories, the previous study did not indicate whether neighbors are treated differently than non-neighbors within an established territorial neighborhood. Studies conducted in neutral arenas may have limited utility for describing behavior patterns in territorial neighborhoods (e.g., see Fox and Baird 1992). Competitors in such an arena may be less aggressive if they are already familiar with each other, even in animals that are not territorial. For example, familiar individuals may have previously assessed their relative fighting abilities and established a dominance relationship.



FIGURE 1. An adult male *Anolis sagrei* lizard extending a dewlap. (Photographed by Ann Paterson)



FIGURE 2. An adult male *Anolis sagrei* showing erection of a dorso-nuchal crest during an agonistic interaction. This photo also shows the paint marking used to individually identify lizards during this study. (Photographed by Stephen McMann)

Territoriality requires that relationships among individuals differ among contexts, notably spatial contexts. For example, both members of a dyad may each be dominant in its own territory. Therefore, behavior patterns that occur in a neutral arena may not occur within an established territorial neighborhood.

In the current study, we tested whether territory residents behaved differently during close encounters with neighbors versus non-neighbors. Social interactions in *A. sagrei* are conducted largely via high rates of conspicuous visual displays including headbob displays and dewlap extensions accompanied by modifiers such as different degrees of limb extension during headbobs, occasional lateral flattening, and, during the most escalated fights between males, erection of dorsal and nuchal crests (e.g., Greenberg 1977; Jenssen 1979; Scott 1984; see Fig. 2 for an example of crest erection). In the southern Florida *A. sagrei* that we have studied, the headbob displays can be readily classified into two strikingly different forms that we call bobbing displays and nodding displays. In the current study, we were particularly interested in the relative frequencies of these two forms because we have previously shown them to vary between social contexts (McMann 2000; McMann and Paterson 2003a) and, notably, we have found that they differ between dyads of neighbors and dyads of non-neighbors in neutral arenas (Paterson and McMann 2004). Additionally, other workers have found that the characteristics of headbob displays may correspond to aggressiveness in this species (e.g., Simon 2011), other anoles (Hurd 2004), and other iguanian lizards (Labra et al. 2007). Detailed descriptions of bobbing and nodding displays in our population can be found in McMann (2000), and these descriptions are similar to, but not necessarily identical to, descriptions of displays in *A. sagrei* by other authors (see Discussion). We describe bobbing and nodding displays briefly below.

A bobbing display is a discontinuous series of alter-

nating up-down dorsoventral motions of the front of the body and tail, where each upstroke (movement in a dorsal direction) is called a bob. Bobbing displays can vary greatly in amplitude and number of bobs, but have following stereotyped features. The third bob is separated from the subsequent downstroke by a longer pause than the pauses that separate the first and second bobs from their subsequent downstrokes. Then, if a fourth bob is present, it is followed immediately by a downstroke. Then there can be a variable number of additional bobs, where each bob is followed by a distinct pause of about 1 sec prior to any subsequent downstroke. During each bob, the front of the body is raised by an extension of the forelimbs, and higher amplitude bobs will also involve substantial extension of the hindlimbs.

A nodding display is a continuous series of rapid dorsoventral oscillations of the head, where each downstroke is called a nod. Unlike bobs, nods are accomplished mainly by movement of the head relative to the trunk, and, while forelimbs may flex during nods, the hindlimbs and tail move little if at all. Nodding displays vary in their amplitude and number of nods per display.

In this study, we tested whether encounter type affected the proportion of headbob displays that were bobbing displays, due to the significance of this variable in previous studies (McMann 2000; McMann and Paterson 2003a; Paterson and McMann 2004). However, because of their potential significance in communication (see Discussion), we also examined whether the proportion of headbob displays with crest erection, the number of bobbing displays, and the number of bobbing displays differed between encounter types. The results of encounters in neutral arenas suggest that these behaviors could also differ for encounters between former neighbors and encounters between former non-neighbors (Paterson and McMann



FIGURE 3. Typical pathway at Fairchild Tropical Botanic Garden where we studied aggressive interactions of adult male *Anolis sagrei*. The study took place in the vegetation away from the main pathways. (Photographed by Stephen McMann)

2004; unpubl. data). We also tested whether the frequency of dewlap extension differed between encounter types because the function of dewlap extension in particular has been of considerable recent interest (e.g., Tokarz et al. 2003, 2005; Nicholson et al. 2007; Vanhooydonck et al. 2009; Henningsen and Irschick 2011).

MATERIALS AND METHODS

We staged encounters at Fairchild Tropical Botanic Garden in Miami-Dade County Florida (Fig. 3), a location that supports a dense population of *A. sagrei* where we have conducted previous studies of this species (e.g., McMann 2000; Paterson and McMann

2004). We staged the encounters between 20 May and 12 June 2009 during this species' breeding season in southern Florida, when mature males exclude other mature males from breeding territories (Lee et al. 1989; Tokarz et al. 1998). Encounters were between 20 free-living focal males and 20 caged stimulus males and were divided into two treatments based on the kind of stimulus male that we presented. In each of 10 neighbor-encounters, we presented a focal male with a stimulus male that we had captured within 5 m of the focal male and that was the closest visible male to the focal male at the time of capture. In each of 10 non-neighbor encounters, we presented a focal male with a stimulus male captured at least 50 m from the focal male at a time when one or more other males were visible closer to the focal male and in the general direction of the stimulus male. An adult male *A. sagrei* typically maintains a territory of a few square meters (Schoener and Schoener 1982; Tokarz 1998; McMann and Paterson 2003a), indicating that our protocol very likely selected individuals with adjacent territories for the neighbor treatment, while lizards in the non-neighbor treatment were extremely unlikely to have adjacent territories. *Anolis sagrei* males are typically most active in the morning and then in the later afternoon to evening (pers. obs.). When weather conditions during the morning were appropriate for high levels of lizard activity (see McMann and Paterson 2003a), we generally staged 1–2 encounters during each day's first activity period, and alternated between neighbor and non-neighbor encounters.

Shortly before each encounter, we chose a focal male from a population of marked males at the study site by choosing the first eligible marked male that we saw after arriving at the site or after finishing the previous encounter. The marked population was a subset of all of the males living at the site, and we established it by capturing each constituent male with a noose at the end of a fishing pole, measuring its snout-vent length (SVL), and marking it with a number on each side with a white acrylic marker (Speedball Painters markers, Hunts Manufacturing Co., Statesville, North Carolina, USA). We released each marked lizard within 1 m of its capture location, and we waited until at least the next day before using it in an encounter. Our marking method was designed to be minimally stressful but it had the drawback that markings were lost when lizards shed within a few weeks of capture. While this might result in a male being marked and used more than once, we minimized this possibility by capturing all males at least 25 m from any location where a male used in a previous encounter had previously resided but was no longer visible. In a previous study, Tokarz et al. (2003) found that males remained within a few meters of their capture location for at least several weeks with average maximum movement of < 4 m in the control group, suggesting that 25 m was a sufficient distance.

For each encounter, the observer captured, measured, and marked a stimulus male using the method described above for focal males. Then we placed the stimulus male in a cloth bag. As it is possible that capturing stimulus males disturbed focal males in the neighbor treatment more than in the non-neighbor treatment, we created a roughly similar potential disturbance in the non-neighbor treatment by having the observer approach the focal male and walk around with the capture pole within a few meters of the focal animal immediately after placing the stimulus animal in a bag. In both treatments, the observer then sat quietly several meters from where the focal animal had last been seen for at least 10 min to reduce the effects of disturbance on subsequent behavior. Other studies have shown that male *A. sagrei* appear to behave normally when an observer sits several meters away (McMann and Paterson 2003b). While focal animals sometimes hid when they were disturbed, they typically quickly re-emerged and perched in conspicuous locations near the ground (as is typical of male *A. sagrei* during the breeding season).

As soon as the focal male was visible after the 10-min waiting period, the observer collected baseline behavioral data on the focal male for 10 min. The behavioral data included the number of headbob displays, the type of each headbob display (bobbing or nodding; see McMann 2000 for detailed descriptions), the presence or absence of crest erection during each headbob display, and the number of dewlap extensions during the observation period. We then presented the stimulus male to the focal male once the focal male was in a location that allowed us to properly present the stimulus male (see below). We removed the stimulus male from the bag and placed the stimulus male in a 30 cm³ cage constructed of bridal veil attached to a frame of wooden dowels (Fig. 4). While not completely transparent, any effects of opaqueness would likely have made our experiment more conservative by inhibiting recognition of another individual. Male *A. sagrei* will display and behave more naturally when in a cage than on a tether (Ann Paterson, pers. obs.), and pilot data indicated that male *A. sagrei* respond strongly to stimulus males in cages with this design. The cage was attached with a string to a 250 x 5.0 x 2.5 cm pine furring strip, which we used to move the cage into a position that presented the stimulus male to the focal male. The cage was placed in a stable location on the ground where the portion of the cage closest to the focal animal was visually estimated at 1 m away from the location of the focal animal's head at the start of the presentation, and where the focal animal could likely clearly see the stimulus male. Exact measurement of the distance between the cage and the focal male was not possible without disturbing the animals, but under similar conditions the observer could estimate a 1-m distance to



FIGURE 4. Mesh cage (arrow) used during trials of aggressive behavior of adult male *Anolis sagrei* at Fairchild Tropical Botanic Garden, Florida. (Photographed by Stephen McMann)

within a few centimeters (unpubl. data). The location of the cage was also in a direction as close as possible to the direction towards the capture location of the stimulus male. Once the cage was in position, the observer recorded the behavior of the focal lizard during the next 30 min using the same behavioral variables as for collecting the baseline data. At the end of the 30-min observation period, we removed the cage and subsequently released the stimulus male at its capture location.

We analyzed the data using PC SAS (Rel. 9.2, Williams Baptist College, SAS Institute, Inc., Cary, North Carolina, USA, 2002–2011). We used a Wilcoxon signed rank test to compare male to female SVL. We also used two-tailed Wilcoxon two-sample exact tests to test whether the treatment groups differed in the proportion of headbob displays that were bobbing displays, as well as the numbers of bobbing and nodding displays, the proportion of headbob displays accompanied by crest erection, and the number of dewlap extensions. For the above five comparisons, we adopted the conservative approach of using a Bonferroni correction for five comparisons and considered an alpha of < 0.01 to be significant (Sokal and Rohlf 2012). We did not perform a multivariate analysis because of the restrictive assumptions required by such tests and because the results of such tests are often difficult to interpret in terms of easily recognizable behaviors (Sokal

and Rohlf 2012). We did not use parametric tests because of their restrictive assumptions (Sokal and Rohlf 2012).

We wanted to be sure that the encounter types did not differ significantly with respect to baseline behavior before encounters or other characteristics of encounters. Therefore, we tested whether SVLs of focal and stimulus males, SVL difference between focal and stimulus males, the time of day of each encounter, the waiting period before baseline behavioral observations could begin, and the length of the wait between baseline data collection and the start of the encounter differed between encounter types using two-tailed Wilcoxon two-sample exact tests. Because we did not have any *a priori* reason to expect a difference between the treatment groups and were more concerned with type II than with type I error, we adopted a non-conservative approach of considering an alpha of 0.05 to be significant. We did not use parametric tests because of their restrictive assumptions (Sokal and Rohlf 2012).

RESULTS

Our protocol resulted in stimulus lizards that we designated as neighbors being captured at distances that were much closer to the locations of focal males than lizards that we designated as non-neighbors. Neighbors were caught a median of 4.1 m (mean \pm SE; 4.0 ± 0.3 m) from focal males, with distances ranging from 2.1 to 4.9

TABLE 1. Behaviors of focal male *Anolis sagrei* at Fairchild Tropical Botanic Garden, Florida, during 30 min encounters with neighbors or non-neighbors.

Behavior	Treatment	Median	Mean \pm SE	Range
Proportion of Headbob Displays that are Bobbing Displays	Neighbor	0.05	0.11 \pm 0.04	0.00–0.31
	Non-Neighbor	0.42	0.45 \pm 0.09	0.10–0.86
Number of Bobbing Displays	Neighbor	2.5	3.9 \pm 1.6	0–17
	Non-Neighbor	8.0	9.9 \pm 1.9	3–20
Number of Nodding Displays	Neighbor	31	39.4 \pm 11.1	1–104
	Non-Neighbor	18	18.1 \pm 4.2	1–42
Proportion of Headbob Displays with Crests	Neighbor	0	0.25 \pm 0.11	0–0.93
	Non-Neighbor	0.19	0.36 \pm 0.13	0–0.93
Number of Dewlap Extensions	Neighbor	44	63.6 \pm 20.5	0–191
	Non-Neighbor	97	86.8 \pm 15.7	0–167

m. Non-neighbors were collected a median of 185.5 m (209 ± 30 m) from focal males, with distances ranging from 81 to 346 m.

When we presented stimulus lizards to focal males, neighbors elicited different behavioral responses than did non-neighbors. Notably, focal males presented with neighbors produced lower proportions of headbob displays (bobbing displays) than did focal males presented with non-neighbors ($S = 67$, $P = 0.003$) with the sample median proportion more than eight times as large in the neighbor treatment as in the non-neighbor treatment. Focal males presented with neighbors also produced fewer bobbing displays than those presented with non-neighbors ($S = 70.5$, $P = 0.007$) with the sample median of the neighbor treatment less than one-third that of the non-neighbor treatment. There were no significant differences between the treatments in the number of nodding displays ($S = 122.5$, $P = 0.196$), the proportions of headbob displays accompanied by crest erection ($S = 98.5$, $P = 0.616$), or the number of dewlap extensions ($S = 89.5$, $P = 0.255$; Table 1).

The treatments were similar in several ways that we measured but did not directly control (Table 2). The treatments did not differ significantly with respect to snout-vent lengths of focal males ($S = 106.5$, $P = 0.927$) and stimulus males ($S = 105$, $P = 1.000$), the difference in snout-vent length between focal and stimulus males ($S = 110.5$, $P = 0.630$), the time of day of each encounter ($S = 116$, $P = 0.425$), the waiting period before baseline behavioral observations could begin ($S = 100$, $P = 0.722$) or the length of the wait between baseline data collection and the start of the encounter ($S = 109$, $P = 0.786$). Snout-vent lengths of focal lizards averaged 57.3 ± 0.70 mm while those of stimulus males averaged 57.0 ± 0.49 mm, and the difference was not significant ($S = 7$, $P = 0.775$). Stimulus males were presented at $10:33.45 \pm$

8.83 (h:min EDT \pm min), the waiting period before baseline observations averaged 39.22 ± 7.85 min. and the wait before baseline observations and encounters averaged 7.4 ± 2.48 min.

The behavior of focal lizards was also similar in the two treatment groups during the 10 min of baseline observations prior to our presenting stimulus males (Table 3). While all of the focal lizards produced headbob displays after presentation of the stimulus male, only nine of the 10 focal lizards in the neighbor treatment and eight of the 10 focal lizards in the non-neighbor treatment produced headbob displays during the observation period prior to their encounters. Among the lizards that produced headbob displays, there were no significant differences in the proportion of headbob displays that were bobbing displays ($S = 66.5$, $P = 0.615$) or the proportion of headbob displays accompanied by crest erection ($S = 68$, $P = 1.000$). Among the 10 lizards in the neighbor treatment and the 10 lizards in the non-neighbor treatment, there were no significant differences in the number of bobbing displays ($S = 98$, $P = 0.615$), the number of nodding displays ($S = 106$, $P = 0.939$), or the number of dewlap extensions ($S = 92.5$, $P = 0.361$). The proportion of headbob displays that were bobbing displays averaged 0.277 ± 0.06 . The number of bobbing displays averaged 6.90 ± 1.38 . The number of nodding displays averaged 28.75 ± 6.29 . The proportion of headbob displays accompanied by crest erection averaged 0.306 ± 0.08 . The number of dewlap extensions averaged 75.2 ± 12.85 .

DISCUSSION

Our study indicates that resident male *A. sagrei* produced lower proportions of headbob displays that were bobbing displays towards neighbors than towards non-

TABLE 2. Characteristics of encounters between male *Anolis sagrei* at Fairchild Tropical Botanic Garden, Florida.

Variable	Treatment	Median	Mean \pm SE	Range
Snout-Vent Length of Focal Males (mm)	Neighbor	57.0	57.6 \pm 1.3	52–64
	Non-Neighbor	56.0	57.0 \pm 0.7	54–60
Snout-Vent Length of Stimulus Males (mm)	Neighbor	57.0	57.0 \pm 0.9	52–62
	Non-Neighbor	57.5	57.0 \pm 0.5	55–59
Snout-Vent Length Difference (mm)	Neighbor	0	0.6 \pm 1.1	-4 – +6
	Non-Neighbor	-1	0.0 \pm 0.8	-2 – +5
Time-of-Day of Encounter (h:min EDT)	Neighbor	10:50	10:42 \pm 12min	9:29–11:28
	Non-Neighbor	10:21	10:27 \pm 13min	9:34–11:57
Waiting Period before Baseline Observations (min)	Neighbor	21	43.8 \pm 13.8	10–135
	Non-Neighbor	24	35.3 \pm 8.2	11–84
Wait between Baseline Observations and Encounter (min)	Neighbor	5	5.7 \pm 1.2	2–14
	Non-Neighbor	4	9.1 \pm 4.9	3–53

neighbors. This result is similar to those of other field studies of *A. sagrei* from southern Florida in that social contexts affected the proportion of headbob displays that were bobbing displays (McMann 2000; McMann and Paterson 2003a), including our previous study of close encounters in a neutral arena in which neighbors elicited lower proportions of bobbing displays than non-neighbors (Paterson and McMann 2004).

Taken together with the results of other studies, the results of the current study suggest that the lower proportions of bobbing displays exhibited by focal males in the neighbor treatment corresponded to a lower aggressive arousal (see Arnott and Elwood 2009b for a recent discussion of aggressive motivation). A large literature indicates that fights have a lower tendency to escalate when between familiar individuals (e.g., Beaugrand 1997; Arnott and Elwood 2009a; Booksmythe et al. 2010; Reddon et al. 2011). Our previous finding that close encounters in neutral arenas exhibited lower proportions of bobbing displays when they were between neighbors (Paterson and McMann 2004) is consistent with lower proportions of bobbing displays among neighbors corresponding to lower aggressive arousal associated with lower escalation. A large literature also indicates that during fights over territories, longer-term residents are more willing to escalate and subsequently win fights (e.g., Waage 1988; Switzer 2004; Kokko et al. 2006). Therefore, a study of the effects of residence time on display behavior in *A. sagrei* (McMann 2000) supports the idea that the proportion of bobbing displays communicates aggressiveness because longer term-residents exhibited a higher proportion of bobbing displays and were more

likely to subsequently be seen occupying the patch than newly arrived opponents. A study by Simon (2011) that measured the frequencies of bobs and nods rather than the relative frequencies of bobbing and nodding displays found that individuals that bobbed more and nodded less were more likely to win aggressive interactions and were more likely to mate, suggesting that increased bobbing corresponds to increased aggressive and sexual arousal. Because the number of bobs per bobbing display does not seem to vary with social context (McMann 2000), Simon's (2011) finding suggests that individuals with aggressive or sexual arousal sufficient to be successful precede their success with more bobbing displays. In light of the above, our finding in the current study that lower proportions of bobbing displays occurred during close encounters with neighbors rather than non-neighbors is consistent with the "dear enemy effect" of neighbors eliciting less aggression than non-neighbors in at least some contexts.

Our findings suggest that, during close encounters, male *A. sagrei* suppress aggression when opponents are neighbors, irrespective of whether the encounters occur within a neutral arena or within a territorial neighborhood. *Anolis sagrei* are highly territorial and it is likely that most or all focal males in the current study were within their own naturally established territories and that most or all of the stimulus males were within the focal males' territories. However, we did not map territory boundaries in this study, so we must use some caution in interpreting this context as necessarily always an intrusion into a focal male's territory. Nonetheless, our data suggest that when a stimulus lizard is near or within the territory of a focal lizard, its status as a neighbor

TABLE 3. Behaviors of focal male *Anolis sagrei* at Fairchild Tropical Botanic Garden, Florida before encounters.

Variable	Treatment	Median	Mean \pm SE	Range
Proportion of Headbobbing Displays that are Bobbing Displays	Neighbor	0.15	0.30 \pm 0.12	0.00–1.00
	Non-Neighbor	0.14	0.16 \pm 0.06	0.00–0.45
Number of Bobbing Displays	Neighbor	1.0	2.0 \pm 0.8	0–8
	Non-Neighbor	1.0	2.0 \pm 0.9	0–9
Number of Nodding Displays	Neighbor	6.5	10.4 \pm 5.4	0–58
	Non-Neighbor	8.5	7.8 \pm 2.0	0–18
Proportion of Headbobbing Displays with Crests	Neighbor	0	0.04 \pm 0.04	0.00–0.36
	Non-Neighbor	0	0.00 \pm 0.00	0.00–0.00
Number of Dewlap Extensions	Neighbor	18	18.0 \pm 4.7	0–49
	Non-Neighbor	28	26.7 \pm 7.08	0–72

neighbor suppresses aggression, as it does in a neutral arena. Therefore, behavior consistent with the dear enemy phenomenon occurs both in neutral arenas and in at least some contexts within a territorial neighborhood, and we can speculate that this phenomenon in male *Anolis sagrei* has at least a proximal basis that can be present regardless of whether the animals are in a natural territorial neighborhood.

Theoretical treatments of the evolution of signals used in conflicts indicate that honest signals of aggressive motivation can be evolutionarily stable when differences in motivation between individuals are generated by contested resources having different values to these individuals (e.g., see Grafen 1990; Searcy and Nowicki 2005; Laidre and Vehrencamp 2008; Szamados 2011). Some behaviors are more effective than others at winning a contested resource, but the more effective behaviors are also more costly in a way that the overall payoff is maximized by choosing behaviors of intermediate effectiveness and cost. In such a situation, individuals that value the resource more are likely to signal their higher motivation by choosing the more effective, costlier behaviors when all else is equal (Grafen 1990; Searcy and Nowicki 2005; Laidre and Vehrencamp 2008; Szamados 2011). This suggests that because bobbing appears to be more effective than nodding (Simon 2011), bobbing may be more costly. This may be so because bobbing displays are more energetically expensive or because they may provoke other individuals (see also discussion in Simon 2011).

The above framework also suggests that when individuals have already established conventions such as dominance or ownership of a given location, less costly behavior corresponding to low aggressiveness will be optimal, even when resource values are high. Our

current and previous studies have found lower proportions of bobbing displays in contexts where conventions are likely already established, such as when male *A. sagrei* have close encounters with familiar rather than unfamiliar individuals (current study; Paterson and McMann 2004). This may also be true for when unchallenged males are established residents rather than new arrivals (McMann 2000) and when unchallenged males are in cores rather than the peripheries of territories (McMann and Paterson 2003a).

In the current study, the lower proportion of bobbing displays in the neighbor treatment was associated with fewer bobbing displays rather than more nodding displays. A possible interpretation of this is that the rate of bobbing per se is a signal of aggression in *A. sagrei*. However, such an interpretation should be treated with caution as overall display rates are sensitive to weather conditions (see McMann and Paterson 2003a; Ord et al. 2010). During the current study, weather conditions appeared to be exceptionally conducive to display rates being consistently near their maximal levels. Notably, there were no windy days during the current study. In more typical years, the effect of social context on rates of bobbing could be overwhelmed by the effects of weather on overall display rates. Additionally, Simon (2011) found that males that were unsuccessful in aggressive encounters had both reduced rates of bobbing and increased rates of nodding, suggesting that the frequencies of bobbing and nodding together are important.

We should also note that our classification of headbob displays into bobbing and nodding displays has allowed us to show that components of display behavior that are strikingly different from each other vary clearly among social contexts, although other authors have classified

displays of *A. sagrei* somewhat differently. For example, the signature displays described by Scott (1984) seem to be similar, but not identical, to the bobbing displays in our scheme. The quick, rhythmic bobbing described by Scott (1984) may correspond to a nodding display in our scheme, although our nodding displays exhibit a faster cadence. Additionally, a headbob pattern that we would classify as a nodding display, followed by a bobbing display, would appear to be a single signature display in Scott's classification. Potentially interesting differences exist between our displays and those described by Partan et al. (2011) in a central Florida population; our bobbing displays seem to correspond somewhat to the pushup displays in their scheme, but at least some of the pushup displays that they describe contain headbob patterns that do not appear to occur in southern Florida. While some of the differences between displays in our study and those of other authors may simply reflect differences in terminology, some differences may stem from inter-population variation for a given context. It is also at least possible that different contexts in different studies could lead to different display classification. For example, in our populations, nodding displays form the majority of displays that we observe in the field (all of our studies), but nodding displays are almost never observed when these lizards are brought into captivity (unpubl. data), suggesting that nodding displays might never have been seen if we had studied captive animals.

In the current study, the frequency of a focal male's dewlap extensions was not affected by whether a stimulus male was a neighbor or non-neighbor. Other work has found that social contexts affecting the relative frequencies of bobbing and nodding displays do not affect the frequency of dewlap extensions relative to headbob displays (McMann 2000). On the other hand, pilot trials for this study conducted in 2006 suggested that the frequency of dewlap extension could vary among some social contexts (unpubl. data). The function of the dewlap in this species and in other anoles has been the subject of considerable recent attention, although its function is still not well understood (e.g., Tokarz et al. 2003, 2005; Lailvaux and Irschick 2007; Nicholson et al. 2007; Vanhooydonck et al. 2009; Henningsen and Irschick 2011). The current study does not provide evidence for a function of dewlap extension within a dear-enemy context.

Our current study also did not find a treatment effect on the proportion of headbob displays accompanied by crest erection. Data from encounters in a neutral arena suggested that encounters between former neighbors had lower proportions of headbob displays accompanied by crest erection than encounters between former non-neighbors, although that variable was not subjected to a hypothesis test in the neutral arena study (Paterson and McMann 2004). In that study, the mean proportion of

headbob displays accompanied by crest erection was 0.04 among former neighbors and 0.25 among former non-neighbors. Thus, in the current study it is likely that a stimulus male's status as a neighbor did not suppress crest erection in the focal animals. Crest erection is characteristic of aggressive encounters between male anoles, and this suggests that an opponent's status as a neighbor was not as effective in suppressing aggressiveness in the current study as it was in the neutral arena study. A possible interpretation of this is that when a stimulus lizard is near or within the territory of a focal lizard, its status as a recent neighbor may suppress aggression less than in a neutral arena. However, this interpretation needs explicit testing.

It is also important to note that the stimulus males in the current experiment did not approach focal animals voluntarily, and in natural encounters the motivation of individuals may play a significant role in structuring encounters. For example, intruders into territories may only intrude when highly motivated to do so. A highly motivated intruder may produce behaviors such as displays that differ from those of a less motivated intruder, and residents may respond differently to a highly motivated intruder than to a less motivated intruder. Additionally, the structure and outcomes of natural territorial interactions can be strongly influenced by the nature of previous encounters (Stamps and Krishnan 1998; Akcay et al. 2010). Previous work observing naturally occurring territorial neighborhoods and artificially created territorial neighborhoods of *A. sagrei* showed that clear intrusions by neighbors into occupied territories were relatively uncommon (Paterson 1999, 2002). However, a description of the dynamics of relationships in territorial neighborhoods may be aided by the examination of the roles of motivation and histories of the participants.

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