Dear Enemy Recognition in Captive Brown Anoles (Anolis sagrei)

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Abstract - Six male Anolis sagrei were paired so that we had three sets of familiar lizards with adjacent cages and visual contact with only the male in the adjacent cage. After a minimum of seven days to habituate to the new neighbor, the test lizard had a cardboard partition placed between his cage and his neighbor's cage. The neighbor was either left in place or replaced with an unfamiliar lizard and its cage. The partition was left in place for six hours and then removed. The test lizard was observed for 15 minutes and display behaviors tallied. Each lizard was observed with his neighbor and with an unfamiliar male. We hypothesized that males would exhibit fewer display behaviors toward familiar individuals than toward unfamiliar individuals even if the lizards were confined in cages. We determined that male brown anoles could distinguish between familiar and unfamiliar conspecific males without having physical contact with the other male. Anoles displayed significantly more total aggressive behaviors (P = 0.02; df = 5) and dewlap extensions (P = 0.02; df = 5) at unfamiliar males than at familiar males.

Introduction

Brown anoles, Anolis sagrei, are small, diurnal lizards (Vigil, 2006) that are polygynous, and sexually dimorphic (Kaiser and Mushinsky, 1994). The males are seasonally territorial (Calsbeek and Marnocha, 2006) with territorial behavior coinciding with the breeding season (Vigil, 2006; Partan et al., 2011). This species inhabits the trunk-ground niche, is a sit-and-wait predator (Tokarz et al., 2003), and is found in the southeastern U.S. and the Caribbean (Simon, 2011).

Anole species employ a number of visual displays to communicate with conspecifics (Orrell and Jeness, 1998). Brown anoles use combinations of headbobs, pushups, dewlap extensions, and infrequently, dorsal crest extensions to make themselves look bigger (Vigil, 2006). Headbobs are often the most frequent display used to communicate to other males (Paterson and McMann, 2004) and may include oscillations of just the head and the head and front part of the body (Simon, 2011). Pushups involve movement of the head and forelegs and sometimes all four legs (Partan et al., 2011). Pushups may be a more aggressive display than headbobs (McMann and Paterson, 2003a; Partan et al., 2011). Dewlap extensions perform a number of functions including species recognition, communication to conspecifics, display used during competition for territories, female mate choice, and predator defense (Tokarz et al., 2003). Dorsal crest extensions are normally reserved for use in highly escalated aggressive bouts with other males (Paterson and McMann, 2004). The displays performed by a particular male vary with the length of time the male has held his territory, the signaler's location within his home range, and the male's familiarity with his rival (McMann and Paterson, 2003b).

Several hypotheses exist to explain differential aggression toward familiar and nonfamiliar individuals. Unfamiliar lizards may pose a greater threat to the territory holder and thus elicit more aggression from the resident or the resident may have more information about a neighbor and vice versa (Paterson and McMann, 2004). The resident would not need to waste effort displaying to assess the neighbor, but would need to gain information about an unfamiliar lizard.

The dear enemy effect explains the change in aggression levels that occur when neighboring lizards recognize each other. Initially, when a new male takes a territory it must expend much energy displaying and defending its territory from other male brown anoles. After boundary lines between adjacent territories have been settled both lizards can reduce their display effort saving their energy for other endeavors. Once the borders are agreed upon it is much less costly for neighbors to maintain their relationship than to have to establish a new relationship with an unknown lizard (Alcock, 2009).

Male brown anoles are able to recognize the difference between a familiar and an unfamiliar male conspecific when both are placed in a natural area that belongs to neither male (Paterson, 2002). When assessing rivals, territory holding male brown anoles view threats from non-territory holders as more serious than threats from neighboring territory holders (Paterson and McMann, 2004). In addition, male brown anoles perceive intrusion into some parts of their territories as more threatening than intrusion into other, possibly less valuable, portions of their territories (Calsbeek and Marnocha, 2006).
Territory defense is common in insectivorous lizards that are sit-and-wait foragers (Pough et al., 2004). The benefits include an increase in mate and food acquisition and access to a retreat safe from predators. Costs of territoriality include physical harm done to the lizard because of its behavior and loss of time that could be devoted to other behaviors (Calsbeek and Marnocha, 2006).

Previous studies to test if male brown anoles could distinguish between familiar and unfamiliar conspecifics involved natural or semi-natural arenas, where males could have physical contact with each other (Paterson, 2002; Paterson and McMann, 2004). Our objective was to determine if captive males without the ability to physically contact each other would still exhibit dear enemy recognition. In spite of being housed within an artificial environment we felt this information was valuable because lizards are kept as research animals for lab experiments, by zoos and nature centers, in classroom settings and by individuals at home. Even if lizards are physically separated they may still have visual contact with other individuals and simply moving cages and exposing lizards to different neighbors could affect their stress levels. We hypothesized that even in an unnatural setting, male brown anoles would exhibit fewer display behaviors toward familiar individuals than toward unfamiliar individuals.

**Materials and Methods**

We purchased six adult, male brown anoles (*Anolis sagrei*) (Strictly Reptiles, Hollywood, FL.). Each lizard was placed in a 16 x 16 x 20 inch (20 x 20 x 50 cm) ReptiBreeze cage (Zoo Med, San Luis Obispo, CA.) upon arrival, allowed access to water ad lib., fed sub-adult crickets every other day, and maintained on a 14:10 L:D photoperiod with a 50W Reptile Basking Bulb (Zoo Med, San Luis Obispo, CA.). Each cage had a small repti hammock (Zoo Med, San Luis Obispo, CA.) for basking and artificial vegetation that could be sprayed with water for an additional source of water.

Lizard cages were positioned in pairs so that we had three sets of familiar individuals. Their cages were positioned next to each other without anything blocking the view between the cages. During this time a lizard could see only the lizard in the cage next to it, other cages were not visible. The cages were not moved and the lizards were not handled during our study.

Lizards were allowed seven days of habituation to the new cage and new neighbor before we started the first observation. The morning of an observation, a cardboard partition was placed between the test subject’s cage and that of its visual neighbor. For the observations between the test lizard and a familiar conspecific the neighbor’s cage was left in place. For observations between the test lizard and an unfamiliar conspecific the neighbor’s cage was replaced with a cage containing an unfamiliar male. The partition was left in place for six hours at which time the partition was removed and the test lizard’s behavior was recorded for 15 minutes. We recorded the number of headbobs, pushups, dewlap extensions, and dorsal crest extensions. After the test the original neighbor’s cage and the neighbor were placed next to the test lizard, if they had been moved.

Each lizard was the test male for one trial involving a familiar male and one trial involving an unfamiliar male. A single lizard was used as either a test lizard or rival lizard only once during a 24-hour period. There is ambiguity in how authors have defined headbobs and pushups of *A. sagrei* (Partan et al., 2011). Therefore, we defined a headbob as movement involving only the head and a pushup as movement involving bending the forelegs (Calsbeek and Marnocha, 2006) or all four legs (Partan et al., 2001).

We used paired T-tests to analyze the mean frequency of dewlap extensions, headbobs, pushups, and total display behaviors toward familiar and unfamiliar males. Due to the low number of dorsal crest extensions observed, this behavior was not analyzed. Display behaviors are given as mean ± SE and values are considered significant at P < 0.05.

**Results**

Brown anoles displayed significantly more total aggressive behaviors at unfamiliar males than at familiar males (P = 0.02; df = 5). During a 15 min session males displayed 5.6 ± 2.1 times (range = 0 - 14) per session to familiar males and 69.0 ± 21.0 times (range = 11 - 151) per session to unfamiliar males.

The males extended their dewlaps significantly more at unfamiliar males than at familiar males (P = 0.02; df = 5). They ranged from 0 to 13 extensions toward familiar males and seven to 59 extensions toward unfamiliar males (Fig. 1). Our males performed headbobs marginally more to unfamiliar males than to familiar males (P = 0.06; df = 5). They performed a range of zero to five headbobs in 15 minutes to familiar males and from four to 59 headbobs in 15 minutes to unfamiliar males (Fig. 1).

The number of pushups displayed toward familiar and unfamiliar males was not significantly different (P = 0.12; df = 5), but the trend of fewer pushups toward familiar males was noticed here too. Males performed 0 or 1 pushup toward familiar males and 0 to 36 pushups per trial toward unfamiliar males (Fig. 1). We observed only two dorsal crest extensions during the entire study (both were directed at an unfamiliar
male). Therefore, our sample size for these displays was insufficient for formal analysis.

**Discussion**

Despite being in a small, artificial habitat, the lizards still monitored and recognized their neighbors. They quickly assessed the adjacent cage when the partition between the cages was removed at the onset of the behavioral trials and if they did not recognize the individual in the cage, they responded much more aggressively than if they were familiar with the lizard. This difference is consistent with observations made on lizards in outdoor settings where the lizards could freely move and interact with other males (Paterson, 2002; Paterson and McMann, 2004). Even when the test lizard was placed in a neutral area outside of his territory and presented with either a former neighbor or non-neighbor the male could distinguish to which category the other male belonged and responded more aggressively to the non-neighbor (Paterson and McMann, 2004).

We observed aggressive behaviors in *A. sagrei* similar to those observed in past studies (Vigil, 2006; Paterson and McMann, 2004; Calsbeek and Marnocha, 2006). Dewlap extensions were the most frequently used visual display toward both familiar and unfamiliar lizards (Fig. 1). Males always extended their dewlaps in the presence of an unfamiliar lizard, but not always when presented with a familiar male. The purpose of extending the dewlap at a conspecific is not understood (Tokarz et al., 2003). No difference was found in behaviors between male *A. sagrei* presented with normal male rivals or with males that had been surgically altered to prevent dewlap extension (Tokarz et al., 2003). Although dewlap displays had no impact on a rival's display behavior, male *A. sagrei* extended their dewlaps more frequently when a rival was one m away than when it was three m away Tokarz et al. (2003). Additionally, the extension of the dewlap had no effect on a male's ability to get females to become receptive and copulate (Tokarz et al., 2005).

The rate of headbobs was 15 times greater toward an unfamiliar male than toward a familiar male. Similar results occurred when *A. sagrei* was placed in a natural habitat that was unfamiliar to that lizard and then presented with either a familiar or unfamiliar male (Paterson and McMann, 2004). Our males always directed headbobs at unfamiliar lizards, but did not always perform them at familiar lizards.

Pushup displays were employed less frequently than dewlap extensions and headbobs. Despite a trend toward more pushups directed at unfamiliar males, during some observations males did not use pushup displays. Jenssen et al. (2000) compared headbob and pushup displays to a whisper and a shouted signal. The amplitude of a pushup is much greater than that of a headbob and because our lizards were in close proximity to each other they may not have needed to use pushup displays to communicate.

Only twice did we observe dorsal crest extensions in our test males and both were directed at an unfamiliar male. This behavior only occurs in sexually mature males during aggressive encounters (Tokarz et al., 2003). In a laboratory setting, males that could physically contact each other extended their dorsal crests while individuals who could only see each other did not (Tokarz et al., 2003).

Two of the test animals arrived with broken tails, but this had no noticeable effect on their behavior toward other males. A survey of 287 *A. sagrei* in central Florida found that about 38% of the wild anoles had broken and/or regenerated tails (Kaiser and Mushinsky, 1994). In a study where pairs of male brown anoles were brought to an outdoor enclosure one always became the dominant male, and removing part of the dominant male’s tail did not change the lizard’s dominance status or his aggressive behavior (Kaiser and Mushinsky, 1994).

We have no evidence that our presence during the experiment influenced the lizards’ behaviors. How-
ever, some of the males paired with a familiar male spent part of the experimental period looking at the observer and not the other lizard. This was not the case with males paired with unfamiliar males. Male *A. sagrei* behaved similarly in the field if handled 1 - 2 hours before the study began or 1 - 2 days before the study began (McMann and Paterson, 2003b). We did not handle the lizards before or during the observation period and were careful to sit quietly before and during the time data were gathered. McMann and Paterson (2003a) saw no effect of observer presence on lizard behavior in the field.

Our lizards displayed a clear difference in their behavior toward familiar versus unfamiliar lizards despite being in an unnatural environment where they did not have physical contact with a rival male. Male *A. sagrei* performed dewlap extensions and aggressive behaviors significantly more frequently in response to unfamiliar males. These results have implications for housing brown anoles in laboratory or public display settings where cages may be moved frequently. Being confronted with new neighbors likely creates a more stressful situation and is energetically more costly to the lizard.

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**Literature Cited**


