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Original Article

Social foraging in the lizard *Ameiva corax*

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The diet of the lizard *Ameiva corax* includes bird eggs and fruit, which are items that represent more food than a single individual typically consumes; lizards often congregate at these large food items. We examined the extent to which lizards aggregate and to which locating food might be facilitated by social factors. During surveys, individual *A. corax* were most commonly seen in association with other conspecifics, sometimes as many as seven. Experiments indicated that lizards were recruited to noteworthy items in the environment (fruit or a novel nonfood object) and that recruitment to food was greater than to a novel, nonedible object. Use of visual displays varied with experimental conditions; aggressive displays were not used by animals visiting nonfood objects or abundant food but were observed when food was moderately limited. A nonaggressive display, which may signal the presence of food and invite others to join, was most commonly used by lizards at food and decreased in frequency as the number of lizards present increased. Their pattern of aggregation and use of behavioral displays demonstrate social foraging in *A. corax*; the potential role of social networks merits further investigation.

Key words: ***Ameiva*, displays, food sharing, lizard, social foraging.**

INTRODUCTION

A forager's success is sometimes dependent on the foraging decisions of others (i.e., social foraging); possible benefits include gaining information about the availability of food, obtaining food initially secured by other foragers, or joining efforts to obtain food only available to multiple foragers. Foragers can use the presence of conspecifics as a cue to food location (Buckley 1996; Otis et al. 2006) and conspecific cues may be essential for the long-term foraging success of some animals (Jackson et al. 2008). The use of conspecific cues is a first step toward the development of more elaborate forms of social foraging. Animals foraging in proximity are not necessarily engaged in social foraging, as animals may aggregate simply because of the distribution of food (Eifler 1995, 1996). Well-documented examples of social foraging are unevenly distributed across taxa although the phenomenon may be more widespread and extend to animals typically not considered social (Brockmann and Barnard 1979; Barnard 1984; Giraldeau and Caraco 2000). Likewise, there are many aspects of social foraging that require empirical examination (Giraldeau and Caraco 2000; Waite and Field 2007). Expanding the information available on the organisms that participate in social foraging and the characteristics of their interactions can lead to a more general understanding of how social foraging develops.

The nature of described social foraging in lizards is less elaborate than for other organisms. Most instances involve kleptoparasitism, with the lizards cued into the possession of food by others. The lizard *Diploglossus millepunctatus* may rely on both conspecific and heterospecific cues when feeding, possibly showing an attraction to the calls of nestling Blue-faced Boobies (*Sula dactylatra*) from whom they snatch any food dropped by the birds; they also seem attracted to "running" conspecific individuals (Kiester 1975). Cape flat lizards, *Platysaurus capensis*, when attempting to feed on figs, will attempt to steal food from each other and seem to cue into the activity of nearby lizards and birds (Whiting and Greeff 1997, 1999). In experimental feeding trials of the lizard *Podarcis lilfordi*, kleptoparasitism or kleptoparasitic attempts were common when animals were in associations (Cooper and Pérez-Mellado 2003). Empirical support of the potential for social foraging in lizards exists, but the limited number of examples implies constraints on the behavior's distribution. The purpose of our study was to characterize aspects of social foraging for the lizard *Ameiva corax*, particularly the role of conspecifics as sources of information about food availability.

Lizards in the genus *Ameiva* are diurnal, terrestrial, active foragers (Magnusson et al. 1985; Lewis and Saliva 1987; Perry 1999; Simmons et al. 2005; Rudman et al. 2009). *Ameiva* are not territorial (Hodge et al. 2003); in some species, individuals have been observed to forage in close proximity (Rudman et al. 2009). The lizard *A. corax* is endemic to Little Scrub Island, a 1.2-ha island off the coast of Anguilla, British West Indies. Approximately 60% of Little Scrub Island is bare rock, whereas the remainder has vegetation cover dominated by prickly pear (*Opuntia dillenii*) and moon vine (*Ipomoea violacea*; Hodge 2000). There are no mammal and few arthropod residents; the only other reptile occurring on the island is a small gecko that is rarely encountered (Hodge 2000). During

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certain times of year, seabirds (Laridae) nest on the island: Brown Noddies (*Anous stolidus*), Bridled Terns (*Sterna anaethetus*), Common Terns (*Sterna hirundo*), Sooty Terns (*Sterna fuscata*), and Laughing Gulls (*Larus atricilla*). Seabirds are known to eat *A. corax* (Censky and Powell 2001; Hodge et al. 2003). *Ameiva corax* forages in the nests of seabirds, eating eggs and fish scraps, as well as eating the leaves and flowers of various plants, the fruit of prickly pear, and invertebrates (Hodge 2000; Censky and Powell 2001; Hodge et al. 2003). Large food items such as seabird eggs and prickly pear fruit represent more food than a single lizard typically consumes. These items are not easily located or accessed, creating a situation where opportunistic foragers could benefit from cueing into the activities of other foragers. We investigated the extent to which foragers were in contact with other lizards, the extent to which they responded to the activities of others, and the potential influence of food quantity on activity and foraging behavior.

MATERIALS AND METHODS

We collected data from 12 to 20 June 2009 in the morning, 0730–1230 h, on Little Scrub Island (18.30833°N, 62.9667°W), situated approximately 1.5 km NE of Anguilla in the British West Indies. We conducted surveys to assess patterns of association: on 12–13 June, one of us walked slowly and systematically across the island, recording the presence of lizards. For each sighting, the first lizard detected was designated the focal lizard and we recorded the number of other associated lizards. Lizards were considered in association if they were within 50 cm of each other or linked by a chain of individuals, with each lizard being within 50 cm of the next (Croft et al. 2008).

Experiments were conducted to test the hypotheses that 1) a feeding lizard recruits other lizards to a food source and 2) the amount of food present influences the characteristics of recruitment. We selected 20 sites on the island to conduct experiments. The sites were not randomly selected; rather, we made a point of selecting sites where lizards had been previously observed that were separated by at least 10 m from the nearest other experimental site. Lizards were not individually identifiable, nor was information available concerning distances moved by individuals, so we cannot guarantee complete independence among sites, but the sites were chosen to minimize the possibility of individuals visiting more than 1 experimental site. We placed a stimulus object at an experimental site and recorded the arrival of lizards to the area as well as their subsequent behavior. Three stimulus types were used: 1) control (red Swiss Army pocket knife), 2) whole ripe prickly pear fruit (*Opuntia* sp.), and 3) partial ripe prickly pear fruit. For whole fruit trials, a single ripe fruit cut longitudinally and folded open was presented; for the partial fruit trials, one half a fruit with half of the pulp scooped out (= quarter of a fruit's pulp) was used. We used a red Swiss Army pocket knife for control trials because previous experience indicated a readiness by *A. corax* to approach and inspect novel objects and the knife we used approximated the size and color of a prickly pear fruit. Prickly pear fruit was selected because our preliminary observations indicated that lizards readily ate and congregated at fruits. Lizards do not easily obtain these fruits; we observed them unsuccessfully trying to break into fruits. An open fruit placed on the ground assured that discovery of a fruit represented access to food. We obtained ripe fruits from plants on the island immediately prior to each experiment and used new fruit for each trial. We ran trials for multiple experimental treatments at each site, separating treatments by at least 1 day, and randomly determining the order in which each site was used for each treatment. Due to time constraints, we were unable to do all 3 treatments at every site. At the start of each trial, we placed the test object on the ground and started a stop watch; trials lasted 10 or 20 min depending on latency to item discovery; trials at a particular site were of the same duration. From 5 to 10 m away, we recorded when each animal arrived and when any of the lizards present performed 1 of 2 distinctive behaviors: 1) pushup, where the limbs were quickly extended leading to a rapid elevation of the body and 2) lateral compression, where an individual stood on 4 extended limbs and laterally compressed its body. We began recording these behaviors partway through the study, so this information is not available for every trial. We recorded association size, defined as the number of lizards that were within 50 cm of at least one other individual in a chain, and every time 1 of the 2 behaviors occurred. From our recorded data, we were able to assess time to initial discover of the item, latency for other lizards to arrive once an experimental item was discovered, the amount of time spent at different association sizes, and display frequency for associations of different sizes.

To compare changes in latency to arrive within a trial, we ranked the length of the intervals between arrivals within each trial and combined all trials within a treatment for use in Spearman rank correlation analyses. Discovery times and the number of lizards recruited during a trial were not normally distributed; we used Wilcoxon signed-rank tests to compare these metrics among treatments. Survival analyses were used to examine the latency of item discovery and the arrival of subsequent individuals; initial survival curves were compared using nonparametric log-rank tests, and general linear models (GLMs), assuming a Weibull distribution, were used to examine subsequent arrivals. For lateral compressions and pushups, we determined the number of displays performed during a trial when the association was of a specific size and calculated the per capita display rate for the different size associations. A single trial may have involved associations of several sizes and generated several display rates for use in analyses. We used GLMs to examine the relationship between display rates, treatment, and association size.

RESULTS

During our study, *A. corax* exhibited a tendency to associate with conspecifics. Two days of surveying resulted in the sighting of 281 lizards, in 192 associations of 1–7 lizards. Slightly more than half of lizards (50.5%) were in association with at least one other lizard (Figure 1). The distribution of association sizes differed significantly from random (Poisson) expectations ($\chi^2 = 32.57$, degrees of freedom [df] = 2, $P < 0.001$); most notably, associations of 4 or more lizards occur much more frequently than expected (Figure 2). Combining survey information with incidental observations, we found that feeding typically involved lizards in association with others. In the 29 instances where lizards were observed feeding or at a potential food source (i.e., in a bird nest), 18 involved solitary lizards, and 11 were associations involving a total of 50 lizards. Further, in 5 of the solitary instances, the lizard was feeding on small items (insects, flower parts, and bird scat) and being approached by other lizards. Feeding on large food items such as eggs and prickly pear fruit can present foraging *A. corax* with challenges. Lizards were sometimes unsuccessful at opening prickly pear fruits or eggs. Seabirds were observed aggressively repelling lizards from nests; in 2 instances, lizards were killed by nesting birds.

The time required for test items to be discovered was not dependent on stimulus type. Prickly pear fruit was discovered no more quickly than the control (Wilcoxon signed rank: $W = 68.0$, $N = 17$, $P = 0.705$) nor was full fruit discovered any more quickly than partial fruit (Wilcoxon signed rank: $W = 45.0$, $N = 13$, $P = 1.000$). Discovery times (seconds) for the 3 treatments were control 330 (77–1216), partial fruit 201 (15–1124), and full fruit 217 (72–565). Survival curves for initial discovery times did not differ among treatments (log-rank test: $\chi^2 = 1.511$, df = 2, $P = 0.47$). Lizard activity, whether at fruit or control objects, recruited other lizards to the site; after discovery, the appearance of subsequent lizards to the site occurred with decreasing interval length (Spearman rank correlation—full fruit: $r_s = -0.362$, $P = 0.002$; partial fruit: $r_s = -0.383$, $P = 0.007$; control: $r_s = -0.398$, $P = 0.018$; Figure 3). Survival analyses indicated that latency to arrive at test items was significantly related to order of arrival and trial site ($Z = -6.26$, $P < 0.001$; $Z = 3.04$, $P = 0.002$) but was not influenced by treatment type ($Z = -0.16$, $P = 0.873$).

Once a test item was discovered, the number of visiting lizards depended on the treatment. The total number of lizards visiting a site was influenced by the presence of food (full fruit vs. control: Wilcoxon signed rank, $W = 106$, $N = 19$, $P = 0.010$) but was not related to the amount of food (full vs. partial fruit: Wilcoxon signed rank, $W = 35.5$, $N = 13$, $P = 0.139$). The maximum number of lizards simultaneously at a site was also influenced by the presence of food (full fruit vs. control: Wilcoxon signed rank, $W = 86.5$, $N = 15$, $P = 0.005$) but less so by the amount of food (full vs. partial fruit: Wilcoxon signed rank, $W = 16.5$, $N = 11$, $P = 0.249$).

Behaviorally, the frequency of lateral compressions varied with treatment but was unrelated to association size (GLM: $R^2 = 30.78\%$, treatment: $F_{2,86} = 19.04$, $P < 0.001$, association size: $F_{1,86} = 0.25$, $P = 0.618$, Figure 4). Lateral compressions never occurred during the control trials and occurred infrequently during full fruit trials but were common during the partial fruit trials. Pushup displays varied with both treatment and with association size (GLM: $R^2 = 47.63\%$, treatment: $F_{2,86} = 34.99$, $P < 0.001$, association size: $F_{1,86} = 31.01$, $P < 0.001$, Figure 5); pushup displays were less frequent in the control condition than in either fruit condition, and lower pushup display rates were associated with increasing group size. In the presence of food, there was a negative correlation between pushup and lateral compression events ($r = -0.263$, $P = 0.032$).

DISCUSSION

Our findings indicate that *A. corax* foraging is influenced by the activities of other lizards. Individual *A. corax* routinely associate with others and show a strong tendency to associate during feeding events. The benefits seem to include gaining information about the availability of food as well as possibly access to food acquired by others. At least 2 factors that promote social foraging are present in *A. corax* but not widespread among lizards, shedding light on the presence of social foraging among *A. corax* despite its apparent absence among lizards in general. First, many lizard species are territorial, leaving relatively little chance of interaction (Stamps 1977; Martins 1994). Although home range defense seems to be the ancestral condition for lizards, *Ameiva* belongs to a family not typically thought to exhibit home range defense (Martins 1994). No spacing information is available for *A. corax*, but our observations suggest that individuals tolerate each other's presence and exhibit extensively overlapping home ranges. In dense captive situations, lizards may respond to the feeding of conspecifics by increased attention, attempts at food stealing, and even consumption of novel food items (Greenberg 1976; Auffenberg 1983). The role of social structure and population density in promoting social foraging needs to be more fully explored. Second, social foraging is influenced by food characteristics (Giraldeau and Caraco 2000). *Ameiva corax* seems to exhibit a tolerance for sharing and possibly cooperation in acquiring food. Food sharing has been predicted to be more likely

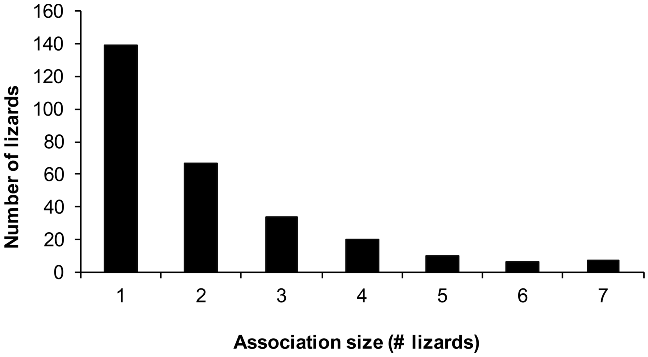

Figure 1

Number of lizards observed in different size associations during surveys. Total number of lizards sighted = 281.

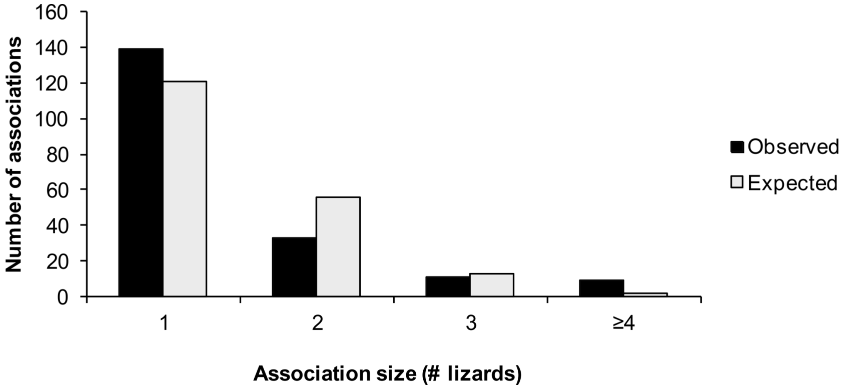

Figure 2

Number of observed and expected associations of different sizes. Expected values are for a Poisson distribution. The observed number of associations ≥ 4 represents: 5 of size 4, 2 of size 5, and 1 each of size 6 and size 7. Total number of associations sighted = 192.

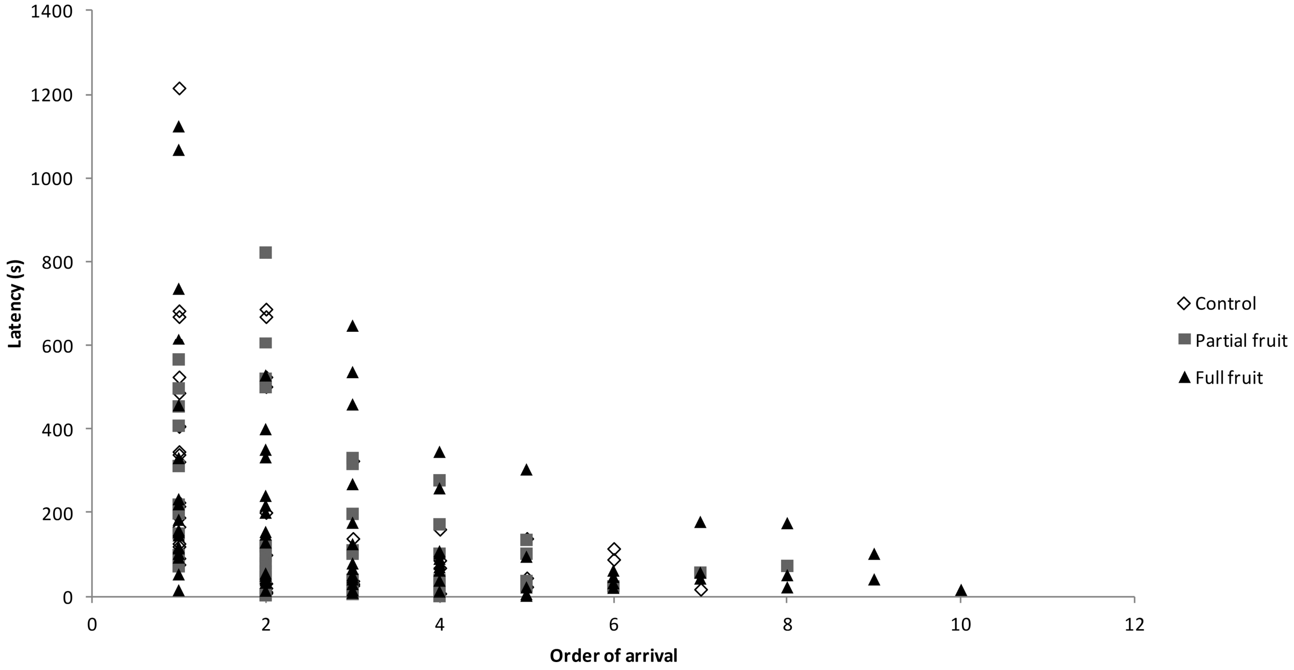

Figure 3
Relationship between the order of arrival at a trial item and latency to arrive. For lizards arriving first, latency is equivalent to discovery time. After the first arrival, latency is the duration of the time interval between the previous and current arrival.

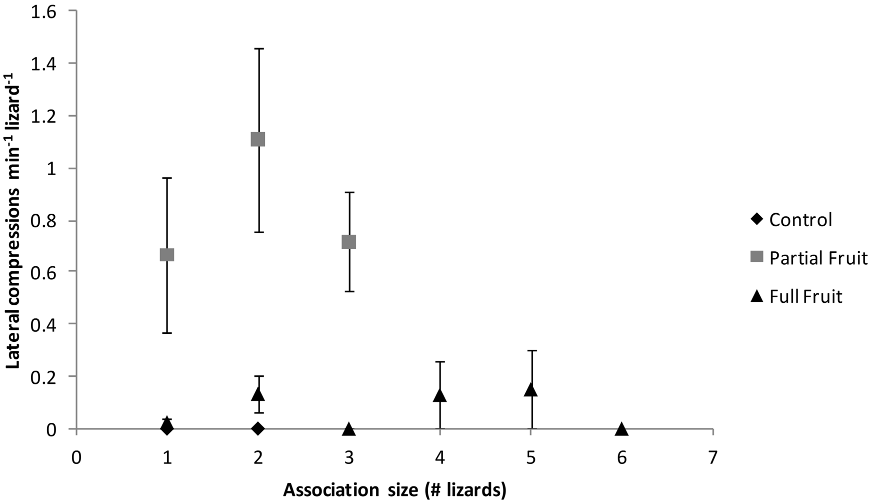

Figure 4
Lateral compression rates for different size associations. Values are presented as mean ± SE.

when food is divisible (Hadjichrysanthou and Broom 2012). Many lizard diets are composed largely of small indivisible food items, not suitable for sharing or kleptoparasitism (Vitt and Pianka 2007). By contrast, a large proportion of the observed *A. corax* feeding events involved food that was divisible, which may be important in defining how foraging *A. corax* interact.

The 2 display types used by *A. corax* seem to serve different roles in the presence of food. Lateral compressions were often associated with chasing and other forms of agonistic behavior and were most commonly observed when food was present but limited. The pushup display was also minimal in the absence of food but was present for both partial and full treatments and did not seem to be associated with aggression; rather, the pushup may serve the function of advertising the presence of food to conspecifics. Peaceful food sharing is not always expected among foragers and is expected to be dependent on food clump characteristics (Dubois and Giraldeau 2003, 2007). We observed less aggression when *A. corax* foraged at clumps large enough to satisfy the number of foragers present. The fact that pushups decreased with increasing association size may reflect some function connected with relative food abundance, an idea consistent with a signal alerting others to a food source. House sparrows advertise when they discover a food source that is large enough to be shared, though the level of recruitment calling decreases with group size (Elgar 1986). Our initial observations suggest that signaling in *A. corax* may play a similar role.

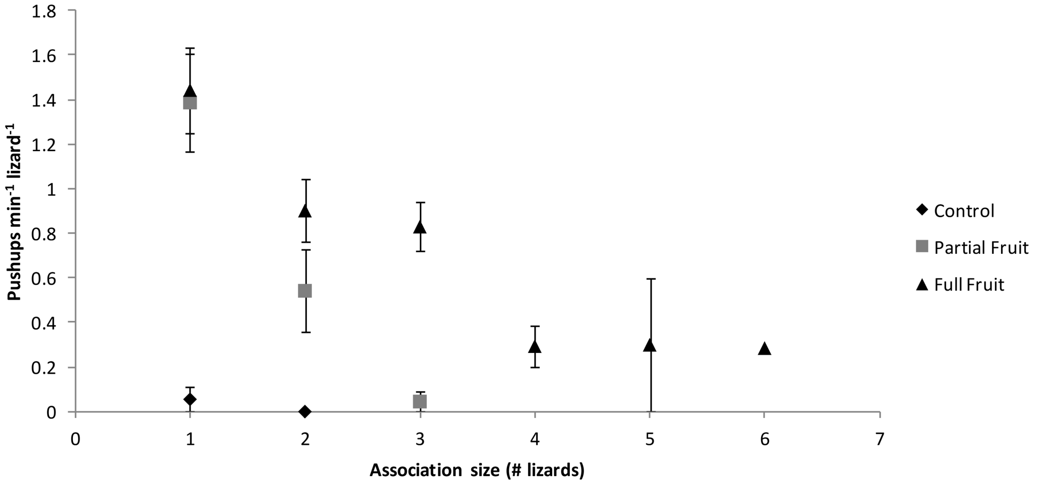

Figure 5
Pushup rates for different size associations. Values are presented as mean ± SE.

Ameiva corax uses conspecifics as a source of information concerning the availability of food, with foraging associations involving large, potentially difficult to access food items. That this can be done with relative tolerance of conspecifics raises the possibility that the full extent of social foraging in *A. corax* could be more extensive. Social foraging can be beneficial by allowing individuals to serve different roles (Giraldeau and Lefebvre 1986; Stander 1992). In several instances, multiple *A. corax* were simultaneously attending to an unopened egg; some food sources may be more easily accessed through the efforts of multiple foragers (Kruuk 1972). Further, some food sources may only be accessible to a subset of the population (e.g., larger individuals). Social relationships may also play a role in promoting food sharing; individual recognition and repeated interactions can be important (Dubois and Giraldeau 2003). Further information about how individuals benefit and contribute to social foraging will help understand the conditions that lead to food sharing in *A. corax*.

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