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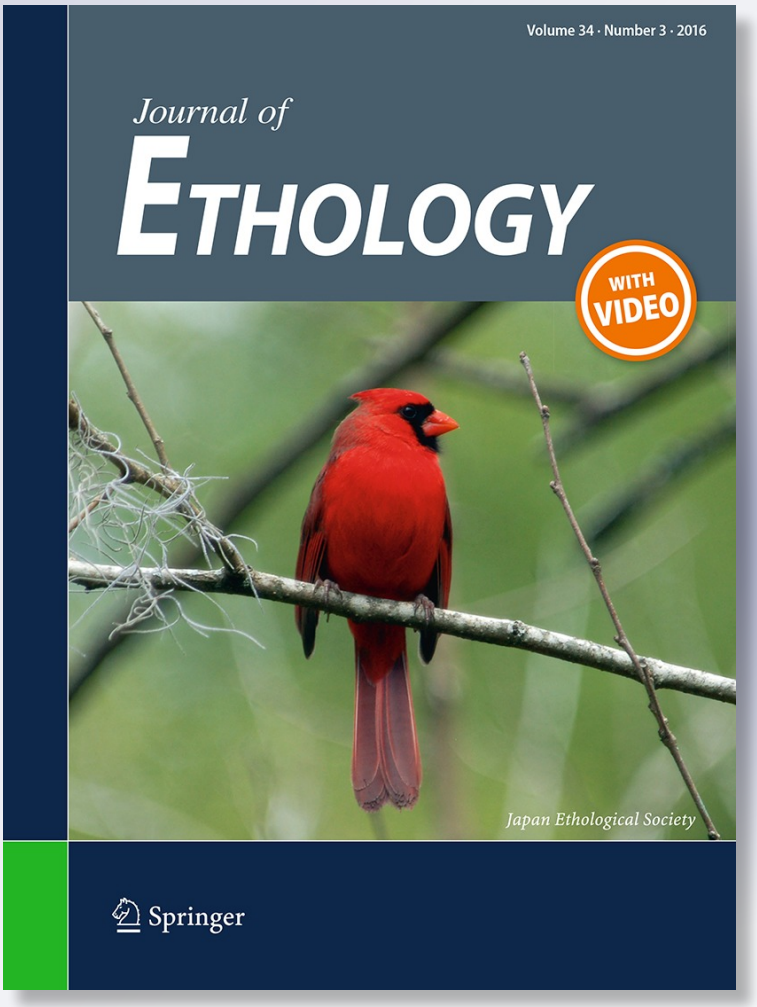


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ARTICLE

# Social networks in the Little Scrub Island ground lizard (*Ameiva corax*)

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**Abstract** *Ameiva corax* is a diurnal, widely foraging lizard endemic to a small (<2 ha) Caribbean island and is known for social foraging, whereby individuals aggregate at large food items (e.g., bird eggs and cactus fruits). We characterized the social network for *A. corax* through focal observations and surveys, which delineated associations for 82 known individuals. Lizards varied greatly in the extent to which they were linked to the social network. Approximately 31 % of individuals were not observed in any associations while one individual associated with 22 % ($n = 18$) of the animals in the study area. Larger lizards tended to be more central to the social network; body size was positively correlated with number of associations (degree) and centrality (betweenness), but negatively correlated with average distance between an individual and its associates (mean path length). Larger individuals were also associated with lower clustering coefficients, indicating that their associates were less closely interconnected. Sex was not related to number of associations (degree), but did help explain some patterns. The extent to which a lizard's associates were of the same sex (homophily) was related to both sex and body size. Females had lower homophily scores than males; within each sex larger lizards tended to have lower homophily.

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## Introduction

Some aspects of animal social systems are not evident when examining individual relationships, but are unveiled through patterns of association as depicted in a social network. Social network analysis can provide insight into processes such as the spread of information (Aplin et al. 2012; Atton et al. 2012) or disease (Godfrey et al. 2009; Wohlfiel et al. 2013). The adaptive nature of social systems can be addressed by examining how social network characteristics are influenced by environmental factors (Sundaresan et al. 2007; Chaverri 2010; Edenbrow et al. 2011), particularly food availability (Foster et al. 2012).

Food availability can influence social behavior in several ways: spacing patterns may be influenced by food dispersion (Eifler 1996), social interactions may be linked to the immediate presence of food (Eifler and Eifler 2014) and the ability to find food may depend on social connections. Many foragers use the presence of conspecifics as a cue to food presence (Buckley 1996) and models reveal that conspecific cues may be essential for the long-term foraging success of some animals (Jackson et al. 2008). Once food has been found, an individual forager may need conspecifics to successfully access the food item (Kruuk 1972; Giraldeau and Lefebvre 1986; Stander 1992). Social relationships, including the components of individual recognition and repeated interaction, can be important in promoting food sharing (Dubois and Giraldeau 2003). With the occurrence of social foraging, social network characteristics can influence individual foraging success, even for animals displaying simple forms of connectedness.

The presence of extensive social networks is little known among lizards. Many species are territorial (Stamps 1977; Martins 1994) and are not likely to display elaborate social networks. One attempt at elucidating a lizard social network focused on a species whose social system largely consisted of unconnected pair-wise associations (Leu et al. 2010, 2011). But reptile social systems can be more elaborate, with a fair number of species forming aggregations (Graves and Duvall 1995; Chapple 2003; Davis et al. 2011; Mouton 2011). While some aggregations may be driven by access to limited resources such as shelter or basking sites (Mouton 2011), instances of kin association (Huang 2006; McAlpin et al. 2011), non-random aggregation membership (Kearney et al. 2001) and individual recognition (Bull et al. 1999, 2000) indicate that some lizard species aggregate for social reasons and in instances where social network structure may be linked to environmental factors.

We sought to characterize the social network for the lizard *Ameiva corax*, a diurnal active forager that does not defend territories (Eifler and Eifler, personal observation) and is known for social foraging, whereby individuals aggregate at large food items such as bird eggs and cactus fruits (Eifler and Eifler 2014). Opening large food items is most often accomplished by larger individuals (Garrison, Phillips, Eifler and Eifler, unpublished results); *A. corax* foraging behavior raises the possibility that social network characteristics influence access to food and that some individuals may fill different roles in the network. We start by describing the social network of *A. corax*. Based on their propensity for social foraging and the fact that larger individuals may play an important role in providing access to food to others, we hypothesized a structured (nonrandom) social network in which larger individuals were more central than others.

## Materials and methods

The lizard *A. corax* is endemic to Little Scrub Island, a small (<2 ha) island off the coast of Anguilla, British West Indies (18°17′45.55″N 62°57′24.02″W). Approximately 60 % of Little Scrub Island is bare rock of volcanic and coral reef origin; on the remainder of the island, rock is overlain with vegetation cover dominated by prickly pear (*Opuntia dillenii*) and moon vine (*Ipomoea violacea*) (Hodge 2000). Our study area consisted of a combination of bare rock and vegetated areas, encompassing approximately 25 % of the island. There are no mammal and few arthropod residents on Little Scrub Island; the only other reptile occurring there is a small gecko (*Sphaerodactylus sputator*) that is rarely encountered (Hodge 2000). During certain times of the 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*). Laughing gulls are known predators of *A. corax* (Censky and Powell 2001; Eifler and Eifler 2014). *A. corax* forages in the nests of seabirds, eating eggs and fish scraps as well as leaves and flowers of various plants, prickly pear fruit and invertebrates (Hodge 2000; Censky and Powell 2001; Eifler and Eifler 2011, 2014). Large food items such as seabird eggs and prickly pear fruit represent a bigger single item of food than one lizard typically consumes, and are not easily located or accessed, creating a situation where opportunistic foragers could benefit from cueing into the activities of other foragers.

We collected data from 13 to 29 June 2011, beginning when animals became active in the morning until their activity ceased due to midday heat, between approximately 0630 and 1100 hours. Seabird eggs and prickly pear fruit are seasonally available on Little Scrub Island; our study overlapped with the period during which both were present. Lizards were captured by hand or noose, sexed and measured (snout-to-vent length), and given unique color codes by applying nontoxic paint to the base of the tail and body; animals were processed and released within 30 min of capture. Data were collected through daily surveys, focal observations, and incidental encounters. We conducted surveys to assess patterns of association: several times each morning, we walked slowly and systematically throughout the study region, recording the presence of marked 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). For each sighting, the identity of lizards in association and the nature of any interactions were recorded. During focal observations, from a distance of 3–10 m, a single observer watched a marked individual for 10 min. Each time the focal animal was observed in association with another lizard, the associating individual was identified and the nature of the interaction was recorded. If the associate was unmarked, we captured, measured, and marked the animal at the end of the observation period. Associations encountered while we moved around the island (incidental encounters) were also recorded.

### Analyses

To describe the social network, each lizard was treated as a node and pairs of individuals seen in association at least once during the study were connected by an edge. Edges were non-directional. Network density refers to the proportion of possible edges that were present. A network component is a set of nodes that are interconnected but not connected to the rest of the network. The social network

was characterized using several measures of node centrality. An individual's degree is the number of its associates, while a weighted degree is sum of the number of times an individual was seen in association with all other lizards. Path length is the number of edges separating two nodes, using the shortest sequence of edges. Mean path length is the average number of edges separating an individual and each network member. The clustering coefficient is the proportion of an individual's associates which are themselves associated. Node betweenness, a measure of how central an individual is to the entire network, is determined by calculating the number of shortest paths between all possible pairs of nodes in the network that actually pass through that individual; homophily refers to the proportion of an individual's associates that are of the same sex. Network measures were calculated using Ucinet 6 (Borgatti et al. 2002). We assessed the relationship between lizard characteristics (sex and body size) and position in the social network using Minitab 17 (Minitab, State College PA).

Using $\chi^2$-tests, we compared network degree distribution to expected degree distribution when degree was assigned according to a random (Poisson) distribution. We used logistic regression tests to examine the characteristics of individuals belonging to the main network component and linear regression models to assess the relationship between lizard characteristics (sex and body size) and network metrics. We assessed relationships between network measures with Pearson correlations and examined the relationship between degree weight and association type by categorizing each network edge as either female–female, male–female or male–male, using ANOVA to compare edge weight among different types of pairings. We present summary statistics as mean ± SE.

## Results

Over the course of the study 82 adult individuals were captured in the study area: 56 males, 24 females and two of unknown sex. By the end of our study, surveys were no longer yielding unmarked lizards, suggesting that most lizards in our study area had been sampled. Males were larger than females (mean snout-to-vent length, 106.9 ± 1.2 and 90.7 ± 0.8 mm, respectively, $T = 10.6$, $p < 0.001$; mean mass, 41.5 ± 1.4 and 24.0 ± 0.6 g, respectively, $T = 11.17$, $p < 0.001$). We identified 127 network edges (associations), for an overall network density of 3.8 %. Of the 82 animals in the study, 56 (68.3 %) were in the main component (Fig. 1), while the remaining 26 (31.7 %) were not observed in any associations. Membership in the main component did not depend on body size or sex (logistic regression—mass, $\chi^2 = 0.72$, $df = 1$, $p = 0.699$; sex, $\chi^2 = 0.49$, $df = 1$, $p = 0.482$; Fig. 1). Mean degree was 3.14 ± 0.43; the overall degree distribution differed from the expectations of a random (Poisson) distribution ($\chi^2 = 182$, $df = 6$, $p < 0.001$).

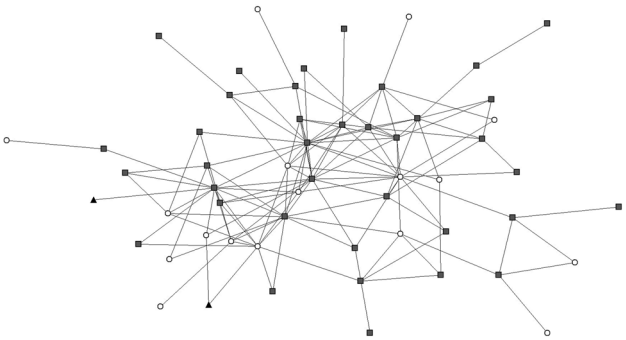

**Fig. 1** Social network of *Ameiva corax*. Depicted are the 56 individuals in the main component. *Squares* represent males, *circles* represent females, and the *triangle* represents an individual of unknown sex

### Main component

The main network component of the study population consisted of 56 individuals (37 males, 17 females, two of unknown sex) and was relatively sparse with a density of 8.2 % and an average degree of 4.6 ± 0.5 (range 1–18; Fig. 1). The degree distribution of the main component included many individuals with a few associates, while a small number of lizards had many associates and differed from the expectations of a random (Poisson) distribution ($\chi^2 = 47$, $df = 7, p < 0.001$; Fig. 2). Sex was not significantly related to degree, weighted degree, clustering coefficient, betweenness or mean path length (linear regression models; $p > 0.05$). Among network measures, degree, clustering coefficient, betweenness and mean path length were related to body size (mass); larger lizards tended to have higher degree and betweeness while having lower clustering coefficients and mean path length (Table 1). As a measure of network centrality, betweenness values (average 51.0 ± 11.2) indicated

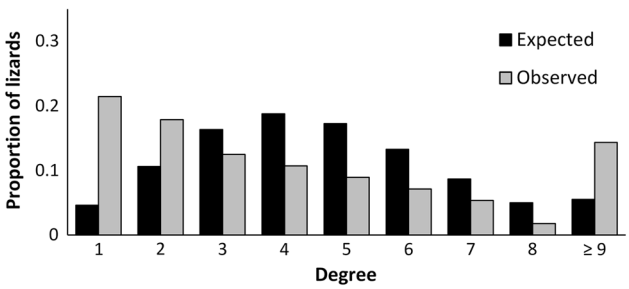


**Fig. 2** Degree distribution for the main component of the *A. corax* social network (observed values). Expected values are from a Poisson distribution

**Table 1** Pearson correlations among network characteristics and lizard size (weight) for main component *Ameiva corax*

| | Body size | Clustering coefficient | Degree | Degree (weighted) | Betweenness |
|---|---|---|---|---|---|
| Clustering coefficient | −0.309 (0.044) | | | | |
| Degree | 0.286 (0.038) | −0.196 (0.203) | | | |
| Degree (weighted) | 0.255 (0.065) | −0.147 (0.339) | 0.936 (0.001) | | |
| Betweenness | 0.294 (0.032) | −0.309 (0.041) | 0.891 (0.001) | | |
| Mean path length | −0.292 (0.034) | 0.118 (0.242) | −0.799 (0.001) | −0.703 (0.001) | −0.641 (0.001) |

Values represent the correlation coefficient ($r$) and the associated probability ($p$)

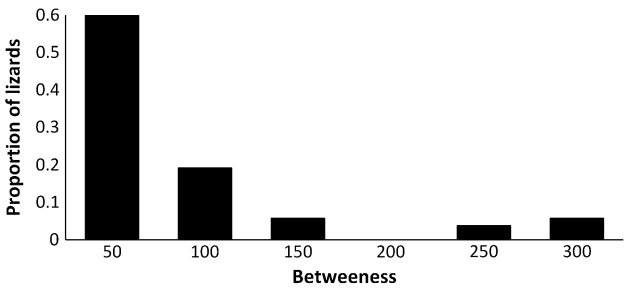


**Fig. 3** Betweenness value distribution for the main component of the *A. corax* social network

that a relatively small proportion of the individuals in the main component were central to the network (Fig. 3). Clustering coefficient averaged 0.36 ± 0.04 (range 0.0–1.0), while average mean path length was 2.85 ± 0.07 (range 1.8–4.1). Weighted degree averaged 7.3 ± 1.1 (range 1–43). Betweenness and degree (weighted and unweighted) were positively correlated (Table 1). Mean path length was negatively correlated with both degree (weighted and unweighted) and betweenness (Table 1).

### Effect of sex on associations

The level of homophily was significantly related to both sex and body size (sex, $F_{1,51} = 68.44$, $p < 0.001$; mass, $F_{1,51} = 10.52$, $p = 0.002$; overall $R^2 = 0.62$; Fig. 1); females had lower homophily scores than males and within each sex larger lizards tended to have lower homophily (males, homophily = 1.223−0.01168 × mass; females, homophily = 0.475−0.01168 × mass). For the 127 edges observed in our network, the average weight was 1.6 ± 0.1 (range 1–8). There was no difference in average edge weight among female–female, male–female or male–male pairings (ANOVA, $F_{2,122} = 0.72$, $p = 0.48$).

## Discussion

Some individuals can play important roles in social networks because of the number of their social contacts (degree) or because their network centrality connects others [betweenness (Lusseau and Newman 2004; Croft et al. 2008)], resulting in single individuals able to dramatically influence social interactions and group dynamics (McComb et al. 2001; Flack et al. 2006; Manno et al. 2007). Our network analysis for *A. corax* indicated that a small number of lizards were central to their social network; high degree and betweenness values were found for a small percentage of individuals. For individual *A. corax*, foraging may provide a vehicle through which different social roles could arise. Food availability is known to influence foraging strategy and social networks in other species (Foster et al. 2012; Tanner and Jackson 2012), and *A. corax* is known to feed socially through aggregations forming at food sources (Eifler and Eifler 2014). *A. corax* open bird eggs and prickly pear fruit through a combination of biting efforts and pushing the items against hard objects (Eifler and Eifler, personal observation); lizards often fail in their attempts to open these food items (Eifler and Eifler 2014). With wider gapes, stronger bite force and greater ability to move food items forcefully, larger *A. corax* are expected to have an advantage when trying to open eggs and prickly pear fruit. Opening large food items such as bird eggs is most often accomplished by larger individuals (Garrison, Phillips, Eifler and Eifler, unpublished results), and larger *A. corax* tended to have higher degree and betweenness values, which means that the highly connected, more central individuals in the network tend to be larger in body size, raising the possibility that network centrality in *A. corax* may be food related. In a system where some foragers may provide access to food [producers (Giraldeau and Caraco 2000)] and others avail themselves of this food [scroungers (Giraldeau and Caraco 2000)], producers may receive higher levels of social attention. The greater connectedness of larger lizards may reflect the possibility that they are more likely to be producers in the community, at least during our study season when both bird eggs and cactus fruit were available on the island. If the social network we describe herein is influenced by food availability, further work is needed to determine whether and how network structure changes with season and diet.

Although only a small proportion of possible network edges were actually observed, most of the study population

was socially connected and degree distribution differed from random expectations, indicating that the *A. corax* social network is highly structured. While most of the lizards in our study area were sampled, these lizards were not necessarily restricted to the study area and are likely part of a larger network associated with a larger area. Social structure can be reflected in space-use patterns (Lusseau et al. 2006; Wolf et al. 2007; Mourier et al. 2012) and information on space use can provide insights into social structure not available from patterns of association alone (Leu et al. 2010, 2011). For example, larger *A. corax* tended to have lower clustering coefficients (loosely connected associates), but higher degree (more associates), which might occur if larger individuals have larger home ranges, and if space use differentially impacts network characteristics. Similarly, individuals in a social network may exhibit associative patterns where individuals of similar sex, size or network degree tend to preferentially associate (Croft et al. 2005; Carter et al. 2013; Hirsch et al. 2013). Within the main component of the *A. corax* social network, males and females exhibited a difference in the extent to which they were associated within their sex; females exhibited less homophily, and within each sex larger individuals tended to display lower homophily. Among *A. corax*, sex and size may influence social tendency or aspects of their use of the environment. Thus, understanding the role of individuals and classes of lizards in the *A. corax* social system may require combining network analysis with information about space use and resource distribution.

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**Compliance with ethical standards**

**Conflict of interest** The authors declare that they have no conflict of interest.

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