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Characteristics of grouping in the Dominican Ground Lizard, *Pholidoscelis fuscatus* (Fitzinger, 1843)

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Abstract. Animals form groups when membership provides a net benefit, but environmental conditions can contribute to intraspecific variation in sociality. We observed grouping behaviour in the Dominican Ground Lizard *Pholidoscelis fuscatus* (Fitzinger, 1843; formerly *Ameiva*) in two adjacent habitats differing in vegetation density to assess group characteristics and their environmental correlates. Demographic structure differed between sites, with the more open site having a preponderance of large individuals. Group size differed significantly between our two habitats, with larger groups occurring in the more open area. The spatial distribution of groups was not random, although we did not detect specific habitat characteristics associated with group formation. Groups tended to be composed of similar-sized individuals. Our study revealed differences in demographic structure and sociality; given the nature of the groups we observed, predation risk and foraging constraints may promote group formation. The balance of costs and benefits stemming from predator avoidance and finding food may serve to link ecological conditions and intraspecific variation in sociality.

Keywords. *Ameiva*; Dominica; foraging; habitat structure; predation risk; size assortivity; sociality

Introduction

Animal groups represent a set of individuals who are close in space and time, and can form through a variety of mechanisms. Animals might, for example, group due to common attraction to an environmental condition or resource (= aggregation) or due to an attraction to conspecifics (= social group). Groups form in situations where there is a net benefit to membership, with their size and composition mediated by environmental circumstances (Krause and Ruxton, 2002). However, the degree of observed variation in grouping may challenge attempts to generalize about factors associated with groups and their characteristics. Animal taxa, even those that are closely related, may differ in their propensity to form groups – both social groups and aggregations (Rolland et al., 1998; Brashares et al., 2000; Fleischmann and Kerth, 2014), and the strength of grouping tendencies may vary with time of day or year (Blundell et al., 2002; Halley and Mari, 2004; Brent et al., 2013). Furthermore, intrapopulational differences in grouping may relate to age, sex, and reproductive status (Blundell et al., 2002; White, 2010). Ecological conditions also can lead to intraspecific variation in grouping, with the formation of groups possibly being prompted by environmental factors such as high predation risk (Caro, 2005; Creel et al., 2014) or limited access to resources such as food, water, or shelter (Krause and Ruxton, 2002). Examining grouping among taxa with a low propensity to group may be especially useful for increasing our understanding of the factors leading to grouping behaviour. Further, identifying the mechanisms prompting grouping can help address broader issues in spatial ecology (Grear and Schmitz, 2005).

Non-avian reptile sociality has received less attention than other vertebrate taxa, perhaps because the diversity and complexity of their social tendencies has been underestimated (Doody et al., 2013; Gardner et al., 2016). Among lizards, studies of grouping have focused on aggregations commonly attributed to

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limited resources such as shelter or to considerations of kinship and reproduction (Graves and Duvall, 1995; Chapple, 2003; Mouton, 2011). However, lizards sometimes use conspecific activity as a cue to resource availability and are attracted to active conspecifics (Kiester, 1975; Whiting and Greeff, 1997; Eifler and Eifler, 2014; Pérez-Cembranos and Pérez-Mellado, 2015). *Pholidoscelis corax* (formerly *Ameiva corax*) forms social groups at food resources; not only do they sometimes signal the presence of food to conspecifics but they also exhibit an attraction to each other even in the absence of food (Eifler and Eifler, 2014; Eifler et al., 2016). Work on *Pholidoscelis fuscatus* (Fitzinger, 1843) (formerly *Ameiva fuscata*) suggested that individuals can be found in groups and although non-territorial, the population studied seemed to exhibit some spatial structure (Rudman et al., 2009a). Our own observations of *P. fuscatus* suggest that groups move through the environment as cohesive units and exhibit coordinated escape trajectories (Eifler et al., in review). The observed behaviour in *P. fuscatus* alludes to the existence of social groups with complex interactions not limited to the immediate existence of a resource. To investigate the extent of grouping and the possibility of social grouping, we studied *P. fuscatus* on the site where grouping was originally reported and on an adjacent site. The two sites differed in habitat structure, with one having sustained significant damage due to a recent tropical storm (Erika, 2015), which allowed us to begin addressing the link between grouping and environmental conditions.

Materials and Methods

Our study took place from 8–24 June 2016 on the central west coast of Dominica near the mouth of the Batali River (15.451914° N, 61.446489° W). We used two study sites that were forested with similar tree species but differed in their density of vegetation near ground level, one open (site 1: approximately 5161 m^2, Fig. 1A) and the second, situated across the road from site 1 along the edge of a streambed, that was more dense (site 2: approximately 2537 m^2, Fig. 1B). In both sites, vegetation consisted of a mixture of trees dominated by mango (*Mangifera indica*), papaya (*Carica papaya*), cacao (*Theobroma cacao*), tamarind (*Tamarindus indica*), and coconut (*Cocos nucifera*) with some herbaceous understory. Sand and leaf litter covered the ground and was interspersed with large boulders. Although not quantified, the sites differed dramatically in structure. Site 1 had a relatively open understory and fruiting trees scattered throughout; a *P. fuscatus* on the ground would have good visibility. Site 2, by contrast, had been damaged by a tropical storm less than a year prior to the study; it had many downed trees and vegetation debris close to the ground. Almost none of the trees were bearing fruit. An animal moving on the ground at site 2 would have limited visibility (Fig. 1).

We collected data from 0900–1330 each day and visually assigned lizards to the size categories small (< 100 mm snout-to-vent length [SVL]), medium (100–150 mm SVL) or large (>150 mm SVL) when sighted in the field. We captured a small subset of the population to associate SVL with size categories. To assess the

Figure 1. (A) Site 1 and (B) Site 2.

prevalence and size of groups, we completed two surveys per day on each of the study sites, randomizing the direction and origin of each search. Surveys were started no earlier than 10.00 h, when lizards were active. During surveys, we recorded the size class (small, medium, large) of each individual encountered and the number of conspecifics within a group. We considered lizards to be in a group 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; Eifler and Eifler, 2014). We waited at least 90 min after a survey was completed before conducting an additional survey on the same site.

On site 1, we also determined the spatial distribution of groups and their location relative to microhabitat features by conducting a series of sweeps through the site, randomizing the direction and starting location of each sweep. We established a series of waypoints for measurements that we later used to assign Cartesian coordinates to group sightings. During the sweeps, we systematically searched the study site by having three researchers, separated by approximately 10 m, walk transects throughout the site. For each group sighted, we recorded the number of individuals in the group, size class of group members, location of the group relative to the nearest waypoint, distance to the canopy edge of the nearest mango tree within 10 m, and distance to nearest understory vegetation that was 30–100 cm high and occupied an area of at least a 1 m^2. In addition, we recorded whether, at the time of sighting the group, mangos were on the ground or sunlight was available within a 3-m diameter of the group's location. We focused on mangos because they represent a potential food source and attractant for invertebrate prey (Rudman et al., 2009b). To determine whether group location reflected environmental conditions, each group was paired with a random location that was a random distance away (range = 3.5–10 m) and in a random direction from the group's location. Random locations were characterized by the same criteria as group locations: sun exposure, presence of mangoes on the ground, and distance to the nearest mango tree canopy and understory vegetation.

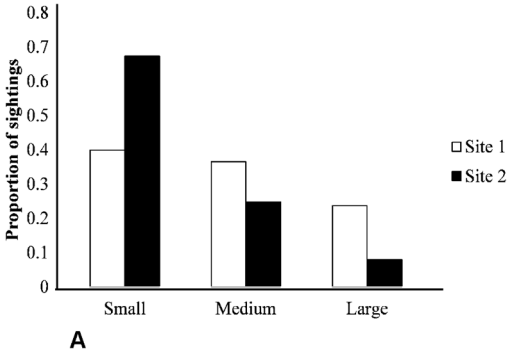
Analyses.—We compared the size structure of lizards on the two sites as well as size-composition of groups in contrast to random expectations using Chi-square tests. For each site, we determined random expectations for the size-composition of groups (pairs) using the proportion of sightings for each size class; we assumed groups would form independently of body size.

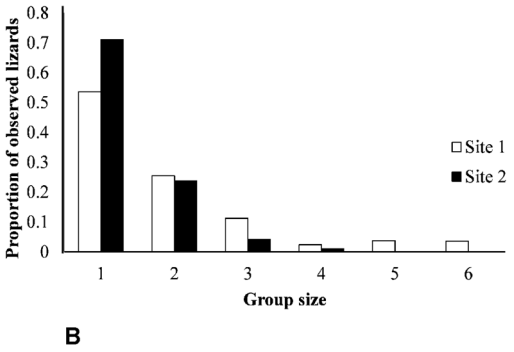
We looked for environmental correlates to the presence of groups by comparing proximity to mango trees and understory at group and random locations using Wilcoxon signed-rank tests. Chi-square tests were used to compare group and random locations for sun exposure and mangos on the ground. We used Spearman rank correlations to explore the relationship between group size and habitat characteristics. We tested data for normality (Anderson-Darling test) and, where appropriate, used non-parametric tests; statistical analyses were performed using Minitab 17 (College Park, Pennsylvania, USA), with a significance level of 0.05.

Results

We sighted *P. fuscatus* 1031 times during surveys. The population size structure on the two sites differed (Chi-square $\chi^2 = 74.3$, df = 2, $P < 0.001$); larger lizards were less common on site 2 (Fig. 2A). Grouping was more common on site 1 than site 2 (46% vs. 29% lizards sighted; Chi-square $\chi^2 = 30.5$, df = 1, $P < 0.001$). In addition, the distribution of group sizes differed between sites 1 and 2 (Chi-square $\chi^2 = 54.5$, df = 5, $P < 0.001$; Fig. 2B), with site 1 having a higher proportion of large groups than site 2. The size-class composition of groups differed from random expectations on both sites (site 1: Chi-square $\chi^2 = 17.3$, df = 5, $P = 0.004$; site 2: Chi-square $\chi^2 = 14.4$, df = 5, $P = 0.013$). Further, the size-class composition of groups differed between sites (Chi-square $\chi^2 = 26.4$, df = 5, $P < 0.001$; Fig. 2C). We were unable to perform similar analyses for larger groups due to limited sample sizes.

Based on our sweep data, the spatial distribution of groups was not evenly dispersed in study site 1 (Fig. 3). Although we did not collect spatial information, solitary lizards occurred throughout the site. We did not observe any environmental correlates with the presence or size of groups. Proximity to understory and mango trees did not differ from random (Wilcoxon signed-rank tests: understory $W = 1048$, $P = 0.950$; mango $W = 775$, $P = 0.685$). When we compared locations where groups were found to their random pairing, we found no differences in sun exposure nor whether mango fruit was present (sun: $\chi^2 = 0.9$, df = 1, $P = 0.343$; mango fruit: $\chi^2 = 1.6$, df = 1, $P = 0.193$). Group size was not related to proximity to understory or proximity to mango canopy (Spearman rank correlation: $\rho = -0.025$, $P = 0.825$; $\rho = 0.093$, $P = 0.397$; respectively).





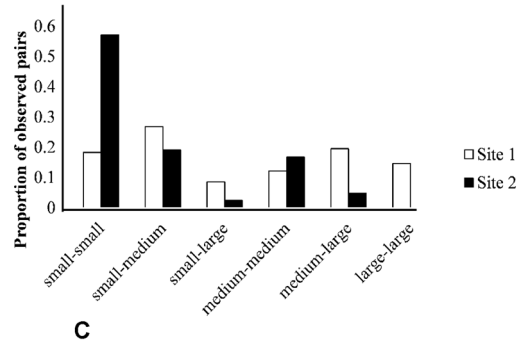


Figure 2. From surveys on each site, Dominican Ground Lizard, *Pholidoscelis fuscatus* (A) demographic structure, by body size, expressed as proportion of individuals we counted in each size class, (B) frequency distribution of the proportion of lizards in groups of different sizes and (C) size-based distribution for pairs composing groups.

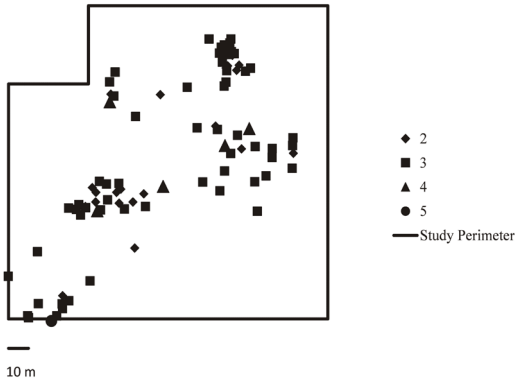


Figure 3. Spatial distribution of Dominican Ground Lizard (*Pholidoscelis fuscatus*) groups, observed during sweeps of the entire Site 1. Bold line represents the boundary of site 1 and symbols represent groups of different sizes.

Discussion

Our study revealed a tendency for *P. fuscatus* to form groups, to show variation in group size between sites, and for groups to be composed of similar-sized individuals. The formation and variability of animal groups is expected to reflect circumstances in which a net benefit accrues (Krause and Ruxton, 2002). Group formation is not widespread among lizards and most examples of group formation in lizards are related to access to a limited resource, such as food, shelter or warmth, or reproduction (Graves and Duvall, 1995; Chapple, 2003; Lancaster et al., 2006; Mouton, 2011). Our observations in *P. fuscatus*, of groups consisting of active individuals away from shelters, suggest that group formation does not depend on shelter, thermoregulation, or considerations of reproduction. Foraging-related grouping in the closely related *P. corax* coupled with the characteristics of *P. fuscatus* groups raise the possibility that the grouping observed in our study may have been prompted by foraging. Coordinated escape trajectories by *P. fuscatus* (Eifler et al., in review) raise the possibility for anti-predation related benefits to grouping.

Site differences in group size might be based on ecological conditions. Habitat structure can influence group formation, and vegetation for our two sites was qualitatively distinct (Fig. 1). Group size in the more densely vegetated site 2 was significantly smaller than on our more open site 1, perhaps because site differences

in vegetation influenced the ability of individuals to cue into conspecifics or detect predators. Habitat features, particularly tree cover, influence group size in Japanese macaques in a manner similar to *P. fuscatus*; smaller groups of macaques occurred in forested areas compared to more open areas (Izumiyama et al., 2003). Similarly, smaller groups of bison occurred in forested areas than in open meadows (Fortin et al., 2009).

Characteristics of food also can influence group size; certain food resources may be more easily acquired or detected by groups (Creel and Creel, 1995; Blundell et al., 2002), and the consumption of some foods may facilitate the formation of groups (Eifler and Eifler, 2014; Laursen et al., 2016). Food resources on the two sites seemed to differ; fruit trees were common on the site with large groups, but relatively scarce on the site with smaller groups. *Pholidoscelis fuscatus* eats mangos and presumably the invertebrates attracted to them (Rudman et al., 2009b). However, until more is known about diet and food preferences of *P. fuscatus*, the relationship between food availability and group size will remain unknown. Groups of *P. fuscatus* consisted of active individuals that behaved as if foraging, although we observed very few feeding events and cannot generalize about diet. However, lizards from several species cue into the foraging success of conspecifics to locate food (Keister, 1975; Whiting and Greeff, 1997; Eifler and Eifler, 2014; Pérez-Cembranos and Pérez-Mellado, 2015; Eifler et al., 2016). Indeed, when the closely related *P. corax* forms groups at concentrated food sources, some individuals in the groups are able to gain access to food not available to separate individuals (Eifler and Eifler, 2014; Eifler et al., 2016). These factors hint at the possible importance of food to group formation in *P. fuscatus*.

The composition of groups requires further investigation. Our two study sites appeared to differ in habitat structure (Fig. 1), which can lead to variation in the benefits of grouping (Caro, 2005). Specifically, group size may increase when predation risk increases, as can the tendency to form groups (Heard, 1992; Banks, 2001; Fortin et al., 2009). Grouping may reduce predation risk through a number of mechanisms, including improved threat detection and predator confusion (Magurran et al., 1985; Landeau and Terborgh, 1986; Turner and Pitcher, 1986). *Pholidoscelis fuscatus* groups were most often composed of similar-sized individuals, which differed from random expectations. The fact that disparate-sized lizards were sometimes in the same group suggests that size-based assortment was not due to aggression or threats. Rather, some benefits to assortivity may exist (Ranta et al., 1994; Conradt and Roper, 2000; Hemerlrijk and Kunz, 2005). Animals that are close in size may move at the same rate and have similar habitat and diet preferences. Positive size assortivity could decrease predation risk. Similar phenotypes within a group make distinguishing individuals more difficult for a predator and reduces attack success (Landeau and Terborgh, 1986). In schools of fish, like-sized individuals tend to maintain proximity in the presence of predators (Krause, 1994). Further investigation is needed to distinguish whether foraging or predation related benefits promote grouping, and to determine the specific conditions leading to group formation and its variability in *P. fuscatus*.

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