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Does the Lizard *Platysaurus broadleyi* Aggregate Because of Social Factors?

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ABSTRACT.—**Aggregations are a common feature of many species although for most taxa, the mechanisms underlying these aggregations are poorly understood. The Augrabies Flat Lizard (*Platysaurus broadleyi*) is a sexually dimorphic lizard that experiences intense conflict as a result of sexual selection. In the wild, *P. broadleyi* share communal crevices and aggregate in the presence of large insect plumes. We experimentally tested whether lizards aggregate as a result of social factors. We also tested whether aggregative behavior differed between the sexes and depends on density. We found no evidence that Augrabies Flat Lizards preferentially group for social reasons in the absence of resources or thermoregulatory benefits. This was true for both sexes and at both densities (two-lizard and four-lizard trials). Although social factors did not promote grouping, males sheltered alone significantly more often than expected by chance, suggesting that males actively avoid one another. Therefore, social factors may work to promote social isolation rather than aggregation, under certain circumstances.**

The formation of aggregations is a behavior that has evolved in a number of different lineages, including mammals, birds, fish, insects, and reptiles (e.g., Brown, 1986; Griffiths and Magurran, 1998; Grether and Switzer, 2000; McGuire et al., 2002; Jeanson et al., 2005; Schradin and Pillay, 2005; Visagie et al., 2005). Recently, there has been increasing interest in reptilian aggregation behavior because it can provide insight into the evolution of sociality (e.g., Duffield and Bull, 2002; O'Connor and Shine, 2003; Shah et al., 2003; Chapple and Keogh, 2006; Lancaster et al., 2006). Grouping behavior has independently evolved numerous times in reptiles, but the mechanisms driving aggregation are poorly understood for the great majority of these lineages (O'Connor and Shine, 2003).

Aggregations may be driven by either ecological or social factors. Ecologically driven aggregations occur when access to key resources such as food, basking sites, oviposition sites, and mates is restricted because of their limited availability, their clumped spatial distribution, or their asynchronous availability (Graves and Duvall, 1995). As a consequence of patchy or limited resources, the costs to an individual of trying to exclude the rest of the population from a particular resource outweighs the benefits, and aggregations will form (Graves and Duvall, 1995). In contrast to ecological aggregations, social aggregations form when there is mutual attraction between conspecifics because the presence of conspecifics increases an individual's fitness (Graves and Duvall, 1995).

The structure of social groups is often sex-specific because of interactions within and between the sexes (Wikelski et al., 1996; Persaud and Galef, 2003; Pilastro et al., 2003; Dadda et al., 2005). For example, female eastern mosquitofish experience high levels of harassment from males and form larger, more closely knit aggregations as a result of male presence (Dadda et al., 2005; Pilastro et al., 2003). Because levels of intraspecific competition and sexual conflict are often density dependent (Fitze et al., 2005; Le Galliard et al., 2005), population density can influence the presence or nature of sex-specific grouping behavior. However, the effect of population density per se has seldom been tested.

The Augrabies Flat Lizard, *Platysaurus broadleyi*, presents a striking example of aggregation behavior. These lizards form large aggregations in the presence of plumes of black flies (their primary prey) and fruiting Namaqua fig trees (Greeff and Whiting, 2000) throughout the year. In addition, individuals may refuge communally with over 100 lizards in a single crevice, and often these aggregations are strongly male biased (MJW, unpubl. data). Small numbers of females refuge in these large, male-biased, communal crevices, but where most females refuge is unknown. One possibility is that females may refuge in smaller groups with resident males that have crevices on their territories. Therefore, social factors may play important roles in aggregation behavior in this

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system. *Platysaurus broadleyi* is highly sexually dimorphic (Branch and Whiting, 1997; Whiting et al., 2006). Competition among males for access to mates is intense (Whiting et al., 2003, 2006), and females are subject to high levels of sexual harassment (MJW, pers. obs.). Given the different selective pressures facing each sex, males and females may have evolved different patterns of aggregative behavior. We conducted experiments to examine whether social factors are driving the aggregative behavior in *P. broadleyi* and whether grouping behavior differs between the sexes. Specifically, we tested whether lizards preferentially share refugia when temperature is controlled and when resources (food and shelter) are not limited. In addition, we tested whether aggregative behavior differs between the sexes and whether it depends on density.

Materials and Methods

Study Population.—*Platysaurus broadleyi* is a relatively small cordylid lizard (64–84 mm adult snout–vent length, SVL) restricted to rocky outcrops in the Gordonia-Kenhardt districts of Northern Cape Province, South Africa (Branch and Whiting, 1997). We used captive lizards from Augrabies Falls National Park (28°35′S, 20°20′E), hereafter referred to as Augrabies. The area is xeric, and the habitat consists of continuous granite sheets and boulders flanking the Orange River, sparsely dotted with Namaqua fig trees (*Ficus cordata*). Lizards shelter communally in crevices at night and during the hottest parts of the day, with over 100 lizards having been observed in a single crevice (MJW, unpubl. data). Lizards travel from crevices (normally <100 m per day) to feeding areas (where there are plumes of black flies or a fruiting fig tree) or, in the case of resident males, to a territory that they vigorously defend (Branch and Whiting, 1997; Whiting et al., 2006). Although males are preferentially territorial, the high density of lizards, particularly in preferred areas near the river, results in many males adopting a ''floater'' tactic. Because females must travel through the territories of multiple males on their way to and from feeding areas and regularly encounter floater males, levels of sexual harassment are high (MJW, pers. obs.).

Lizard Husbandry.—For experiments, we used a captive colony of 23 adult males and 30 adult females, which had been in captivity for 3–4 years. Twelve weeks prior to the experiments, all the lizards were placed in separate, 30 × 30 × 30 cm glass tanks, in rooms maintained at 29°C on a 12:12 (light:dark) diel cycle. We cannot be sure that 12 weeks was sufficient to nullify previous social interactions that might influence a lizard's propensity to aggregate. However, we believe any effect of social history would be negligible because lizards were previously housed in small groups of only a few individuals. These tanks were separated by opaque dividers to prevent visual contact among individuals. Lizards were provided with fresh, folded newspaper for refuge, fed vitamin-supplemented cat food and mealworms three times per week, and provided with water ad libitum. Lizards were individually numbered using a nontoxic xylene-free marker pen.

Experimental Design.—Experiments were performed in a heated room, maintained between 32.5 and 33.5°C. The suspected preferred body temperature of *P. broadley* is 35°C (D. Bauwens, unpubl. data). Although the lizards were maintained at slightly lower room temperatures, *P. broadleyi* are active in the field at even lower temperatures and grouping for thermoregulatory reasons can likely be ruled out. A 12:12 (light:dark) diel cycle was used to mimic the natural photoperiod. The room contained six 120 × 90 × 75 cm enclosures lined with a thin layer of plastic and containing shelters consisting of a 20 × 20 cm terracotta tile raised 3 cm in the front and sloping down to ground level at the back. The number of shelters in each enclosure corresponded to the number of lizards for a given trial (i.e., one shelter per lizard). The shelters were arranged equidistant from each other and the sides of the enclosures. This experimental design controlled for all environmental variables that could promote grouping, allowing us to investigate whether social factors are involved in *P. broadleyi's* spatial behavior.

We ran 20 trials for each of six treatments: (1) two males; (2) four males; (3) two females; (4) four females; (5) one male, one female; and (6) one male, three females. To ensure that differences between treatments were not caused by the order in which they were conducted, all six treatments were run concurrently. Lizards were randomly allocated in the first set of trials and used in multiple trials (mean ± SD = 6.15 ± 1.20, range 3–8) but never in the same combination. Thus, no lizard encountered the same individual more than once in any of the trials across all six treatments. To minimize stress, lizards were not used on consecutive days (i.e., they were given at least one day of rest between trials).

Trials were conducted from 1300–0800 the following morning. At the start of each trial, lizards were released one by one into their respective treatments, and the shelter (i.e., the tile) they selected was noted. The following morning, their final shelter site selection was

TABLE 1. To test for aggregative behavior in the lizard *Platysaurus broadleyi*, we ran 20 trials for each of six treatments (listed in text). Three treatments consisted of four lizards. In each trial, the number of lizards equalled the number of refugia. The trials involving four lizards had five possible arrangements. For each arrangement, there were a number of possible outcomes depending on which refuge a lizard occupied (256 total outcomes). The probability of each outcome was calculated as the number of possible outcomes for a spatial arrangement/256.

Arrangement	% lizards alone	No. possible outcomes	Probability
1) One lizard under each tile	100	24	0.0938
2) Two lizards under one tile, two lizards under separate tiles	50	144	0.5625
3) Three lizards under one tile, one lizard alone	25	48	0.1875
4) Two lizards under one tile, two lizards under another tile	0	36	0.1406
5) Four lizards under one tile	0	4	0.0156

recorded after which lizards were returned to the holding facility. Between trials, both the plastic lining and the tiles were changed. All tiles were cleaned thoroughly before reuse. Tiles were left to soak in soap water for two hours, thoroughly scrubbed with a wire brush, soaked for another half an hour, and then scrubbed again before being left to air dry. This technique has been shown to be effective in removing the scent of snakes and/or lizards (Downes and Shine, 1998).

All trials were completed in June 2005. One trial in each of the single-sex treatments and three trials in each of the mixed-sex treatments had to be discarded (because lizards escaped their enclosure), leaving 19 and 17 trials, respectively, for statistical analysis.

Statistical Analysis.—For all treatments, we compared frequencies of observed spatial arrangements of lizards with the frequencies expected if the lizards distributed themselves randomly using chi-squared tests with Yates' correction for contingency tables with only two categories. To derive expected frequencies, we multiplied the expected probabilities of arrangements by the number of successful trials in a treatment. Arrangements and their expected probabilities differ according to treatment and are detailed below.

In all two-lizard treatments (same and mixed sex), there are only two possible spatial arrangements: either both lizards can shelter together, or each lizard can occupy a separate shelter, with each arrangement having an equal expected probability (0.5). For the four-lizard treatments, there are five possible spatial arrangements with different expected probabilities (Table 1). Given that some arrangements have a very small expected probability, arrangements were grouped into the following categories: (1) 50% or more of the lizards are found alone; and (2) 75% or more of the lizards are found together. The probabilities of these arrangements are 0.6563 and 0.3447, respectively. This grouping was necessary to meet assumptions of the chi-squared test (given the small probability of some arrangements, we would have needed to perform at least 321 trials for each treatment to avoid violating the assumption that expected frequencies of all the cells must be greater than five). Finally, for the one-male, three-females treatment, there are four different arrangements with regards to sex: the male alone or the male with either one female, two females, or three females under a single tile. These can be grouped into arrangements in which males are found alone and those in which the male is found with one or more females. The expected probabilities of these arrangements are 0.4219 and 0.5781, respectively.

RESULTS

Approximately half the lizards moved in each trial (mean proportion across all trials ± SD = 0.56 ± 0.20), and as a result, the final arrangement of the lizards differed from their initial arrangement in almost all trials (mean proportion across all trials ± SD = 0.80 ± 0.37).

All Male Treatments.—In the two-male treatment, the lizards' distribution was not random, and males sheltered alone significantly more often than expected by chance (79% alone, 21% together, $N = 19$; $\chi^2 = 6.42$, df = 1, $P = 0.02$). Similarly, in the four-male treatment, the observed frequencies were significantly different to that expected if the lizards distributed themselves randomly among the shelters (Fig. 1A; $N = 19$; $\chi^2 = 5.17$, df = 1, $P < 0.03$).

All Female Treatments.—In the two-female treatment, the lizards' distribution was random (42% together, 58% alone, $N = 19$; $\chi^2 = 0.53$, df = 1, $P = 0.49$). Similarly, in the four-females treatment, the observed frequencies were not significantly different to that expected if the lizards distributed themselves randomly among the shelters ($N = 19$, $\chi^2 = 0.75$, df = 1, $P = 0.82$).

Mixed Sexes Treatments.—In both mixed-sex treatments, the lizards' spatial pattern did not differ significantly from that expected by chance (Fig. 1B; 59% alone, 41% together, $N = 17$; $\chi^2 = 0.31$, df = 1, $P = 0.47$ and $\chi^2 = 0.59$, df = 1, $P = 0.67$ for the two-lizard and four-lizard treatments respectively). Furthermore, when arrangements were analyzed specifically with respect to the distribution of the male in relation to females (one-male, three-female trial), the observed frequencies did not differ significantly from those expected by chance (Fig. 1C; $N = 17$, $\chi^2 = 1.92$, df = 1, $P = 0.16$).

DISCUSSION

Our results indicate that Augrabies Flat Lizards do not preferentially group when resources and thermoregulatory benefits are controlled for. This was true for both sexes at both densities (two-lizard and four-lizard trials). Instead, males appear to actively avoid sheltering together when given the opportunity to occupy separate overnight refugia. This is consistent with male spatial arrangements in natural populations during the day. During the breeding season, males are preferentially territorial and are intolerant of other males (Whiting et al., 2006). It would appear that this carries over to some degree outside of the breeding season. The aggregations of male flat lizards in the wild are, therefore, likely to be resource driven. Social factors are involved in the spatial arrangements of males, but they are promoting a solitary rather than a group existence.

In contrast to males, females distributed themselves randomly among the shelters, suggesting that social factors are not involved in their spatial behaviors. The difference in male and female spatial arrangements is probably because of different levels of conflict within each sex (Whiting et al., 2003). In contrast to males, females do not compete with one another for resources or mates, although mild aggression between females is occasionally observed. However, they do not experience the same selective pressures as males. The relative lack of

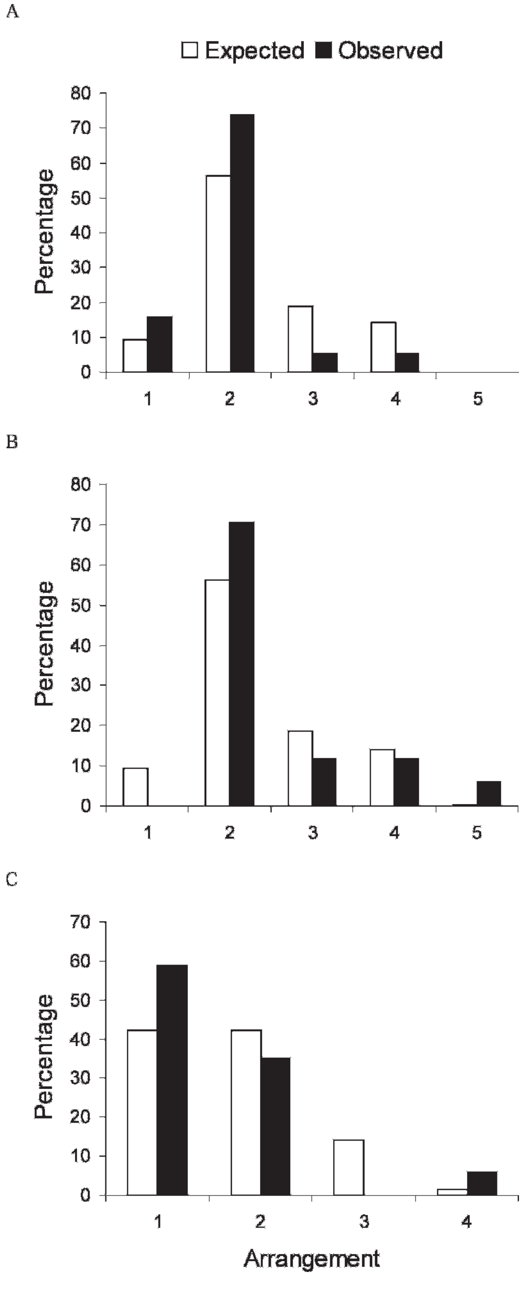

FIG. 1. The observed and expected spatial arrangement of *Platysaurus broadleyi* in selected grouping experiments in which the number of available refugia equalled the number of lizards. (A) Four males; (B) one male and three females; and (C) one male and three females in which the possible spatial distribution is in relation to the male (i.e., male and one female together under same tile, male and two females under same tile, etc.). Males avoided grouping with other males significantly more than expected by chance, whereas male:female grouping was not significantly different from chance (see text for statistical analysis). For (A) and (B) the x-axis numbers correspond to the following arrangements: (1) one lizard under each tile; (2) two lizards under one tile, two lizards under separate tiles; (3) three lizards under one tile, one lizard alone; (4) two lizards under one tile, two lizards under another tile; and (5) four lizards under single tile. For (C), the x-axis numbers correspond to the following arrangements: (1) male alone; (2) male with one female; (3) male with two females; and (4) male with three females under a single tile.

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competition among females has promoted a system where females neither seek each other out nor actively avoid one another.

Given the high levels of sexual harassment in natural populations, females may be expected to avoid males or group together to decrease the chances of being harassed by males (Wikelski et al., 1996; Persaud and Galef, 2003; Pilastro et al., 2003). However, our study was conducted outside of the breeding season of *P. broadleyi*. Outside of the breeding season, males are not territorial, and aggressive interactions occur at a much lower frequency. This may also explain why population density did not influence spatial arrangements. Given the intensity of male-male competition during the breeding period and harassment of females by males, a contrasting social arrangement might be found in the breeding season.

Our results suggest that aggregations of *P. broadleyi* in the wild are likely to be caused by ecological rather than social factors, in particular, the spatial clumping of food resources and limitation of suitable overnight crevices. Because of the higher concentration of food resources near the river, lizard densities within 50 m of the river can be exceptionally high (MJW, unpubl. data). The narrow crevices preferred by Augrabies Flat Lizards as shelters may also be a limiting resource, necessitating the use of communal crevices. Currently, evidence that aggregation in lizards is resource-driven is mixed. For example, resource limitation is likely to drive aggregation in *Cordylus macropholis* (Nieuwoudt et al., 2003b; Visagie et al., 2005), yet the congener *Cordylus cataphractus* preferentially aggregates in the presence of excess shelters (Visagie et al., 2005). The great variation in factors driving aggregative behavior in reptiles and even within lizard families such as the Cordylidae, highlights the need for additional studies on the selective forces shaping the evolution of reptilian grouping behavior and, ultimately, sociality.

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