

EXPERIMENTAL ANALYSIS OF GROUPING BEHAVIOUR IN CORDYLID LIZARDS

LOUISE VISAGIE¹, P. LE FRAS N. MOUTON¹ AND DIRK BAUWENS^{1,2}

¹Department of Botany and Zoology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa

²Present address: Institute of Nature Conservation, Kliniekstraat 25, B-1070 Brussel, Belgium

Although the majority of cordylids are solitary, some species display prominent grouping behaviour. We tested whether limited shelter availability is a factor responsible for the grouping behaviour observed in *Cordylus cataphractus* and *C. macropholis*, using the solitary-living *C. polyzonus* as control. In an experimental setup, individuals of each species were provided with an excess of shelter sites and the observed patterns of shelter occupation were compared among the three species. *Cordylus cataphractus* consistently aggregated, occupying fewer shelters than its two congeners. Grouping behaviour in *C. cataphractus* in the wild is not the result of a limitation of refuge sites. In contrast, shelter occupation by *C. macropholis* and *C. polyzonus* was random, hence non-aggregative. Thus, although the aggregative behaviour observed in *C. macropholis* in its natural habitat might be influenced by limited shelter availability, other causal factors can not be excluded empirically.

Key words: *Cordylus cataphractus*, *Cordylus macropholis*, *Cordylus polyzonus*, Cordylidae, refuge availability

INTRODUCTION

Although squamates are not generally group-living, temporary aggregations have been described in several species. In temperate zone species, these aggregations may occur during periods of reduced activity, for example during the winter as in certain *Eumeces*, *Urosaurus* and *Sceloporus* species (Neill, 1948; Worthington & Sabath, 1966; Weintraub, 1968; Ruby, 1977). Alternatively, such aggregations serve as a focal point for specific activities and have been termed accordingly. Sheltering (Hoofien, 1962; Myres & Eells, 1968) and basking (Hoofien, 1962; Myres & Eells, 1968) aggregations serve a strict thermoregulatory purpose, while mating (Pope, 1937; Hoofien, 1962) gestation (Graves & Duvall, 1993; Seburn, 1993) and nesting (Rand, 1967; Bock & Rand, 1989) aggregations are associated with reproductive behaviour. Feeding aggregations have also been described (Vitt, 1974; Arnold & Wassersug, 1978). Some authors have even linked the formation of temporary aggregations to possible anti-predatory (Vitt, 1974) and water conserving behaviour (Pope, 1937; Myres & Eells, 1968).

In contrast, few lizard species exhibit long-term or permanent aggregative behaviour. Long-term pair-fidelity has been reported in the viviparous skink, *Tiliqua rugosa* (Bull, 1994; Bull *et al.*, 1998). The Australian scincid genus *Egernia* also contains several gregarious species, with aggregations of individuals sharing rock crevices or burrows (Bull *et al.*, 2000). The gidgee skink (*Egernia stokesii*) forms stable social aggregations of up to 17 individuals that share the same rock crevice for several years (Main & Bull, 1996; Bull *et al.*, 2000).

The African cordylid genus *Cordylus* contains at least two species displaying aggregative behaviour (Mouton *et al.*, 1999), namely, the armadillo girdled lizard (*C. cataphractus*) and the large-scaled girdled lizard (*C. macropholis*). In both species, grouping is not restricted to any particular season or time of day, but occurs throughout the year. In addition, these groups are unlikely to represent family units as there is a high degree of intergroup movement (Visagie *et al.*, 2002; Nieuwoudt *et al.*, 2003a). *Cordylus cataphractus* presents one of the clearest manifestations of grouping behaviour observed within any lizard species to date. It is endemic to the arid and semi-arid areas along the west coast of South Africa (Mouton, 1988; Branch, 1998) where groups of up to 60 individuals may inhabit a single crevice in small sandstone outcrops (Visagie, 2001; Effenberger, 2004). Groups of two to six individuals are, however, the norm (Peers, 1930; Branch, 1998; Mouton *et al.*, 1999). Groups containing less than nine individuals usually include only one adult male plus several adult females and juveniles, but larger groups often include more than one adult male (Mouton *et al.*, 1999). *Cordylus macropholis* also occurs along the South African west coast. Although the succulent *Euphorbia caput-medusae* seems to be the preferred microhabitat of this species (Branch, 1998; Mouton *et al.*, 2000a; Nieuwoudt *et al.*, 2003a,b), it is not uncommon to find individuals sheltering in limestone cracks or alternative refuges (Branch, 1998). Aggregations of two to five (and occasionally up to 11) lizards can be found sheltering between the stems of a single succulent, and these aggregations rarely include more than one adult male (Mouton *et al.*, 2000a; Nieuwoudt *et al.*, 2003a,b).

Grouping behaviour in squamates is viewed as the result of either limited resource availability or mutual attraction of conspecifics, although these two causes are not necessarily mutually exclusive (Stamps, 1988; Graves & Duvall, 1995; Kearney *et al.*, 2001). In our

Correspondence: P. le Fras N. Mouton, Department of Botany and Zoology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa.
E-mail: pnm@maties.sun.ac.za

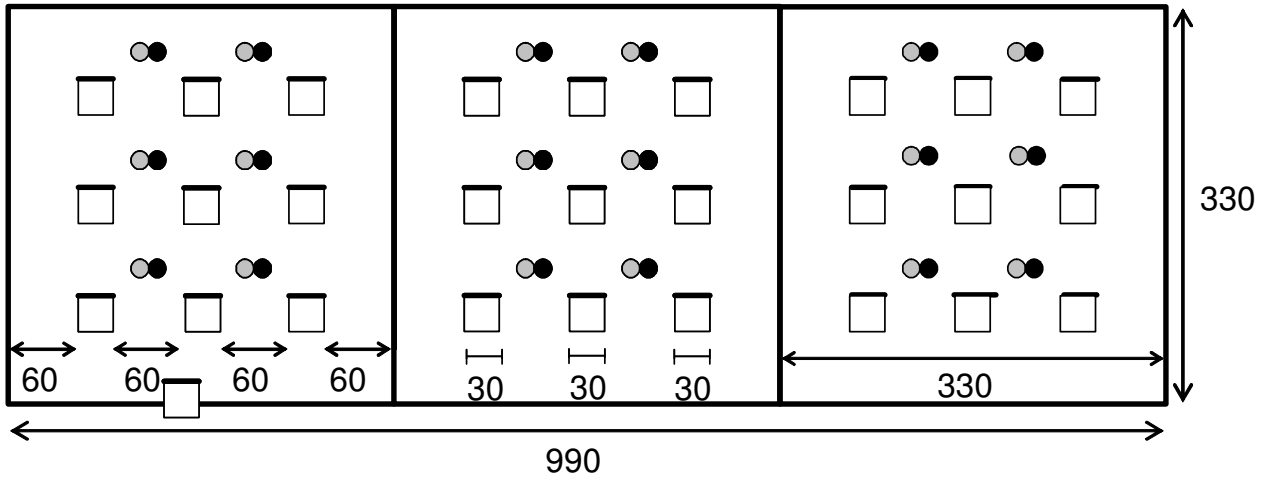


FIG. 1. Diagram of the experimental setup used to determine whether limited shelter availability influences aggregation in *Cordylus cataphractus*, *C. macropholis* and *C. polyzonus*. Enclosure walls are from asbestos sheets. Small squares represent individual shelters (30 × 30 cm) with darker lines representing the north-facing shelter entrance. Solid circles represent food dishes and open circles water dishes. All measurements are in centimeters.

study, we aimed to test the hypothesis that limited shelter availability is a factor inducing aggregative behaviour in *C. cataphractus* and *C. macropholis*. Over a large part of the range of *C. cataphractus*, specifically along the western coastal lowlands, rock outcrops appear to be a limited resource. Likewise, the distribution of *Euphorbia* plants, considered to be the preferred refuge of *C. macropholis*, is extremely patchy over most of this lizard's range.

Our approach consisted of exploring whether *C. cataphractus* and *C. macropholis* individuals continue to display aggregative behaviour when presented with an excess of shelters, while controlling for alternative factors which might prompt aggregation. Thus our null-hypothesis predicts that the lizards will not exhibit grouping behaviour when an excess of shelter sites are provided. Patterns of shelter occupation by these two species were compared to that obtained for a solitary-living congener, *C. polyzonus* (Branch 1998). This controls for any possible "Allee effect", i.e., where species display unnatural aggregations under experimental conditions in contrast to their field behaviour (Allee, 1931; Stamps, 1988). All three cordylids are territorial, sit-and-wait feeders (Cooper *et al.*, 1997; Mouton *et al.*, 2000a; Mouton *et al.*, 2000c; Effenberger & Mouton, 2003). Our experiment was conducted outside the mating season of these species (Flemming & Van Wyk, 1992; Mouton *et al.*, 2000a; Flemming & Mouton, 2002) to minimize the effects of territoriality and agonistic behaviour. Lizards of all three cordylids were collected and exposed to trials in identical sex ratios. Lastly, excess water and food supplies were distributed throughout the test arena to counter for the effects of patchy or limited availability of these resources.

MATERIALS AND METHODS

COLLECTION OF SPECIMENS

Lizards were collected during late November 1998 near Lambert's Bay, along the west coast of South Af-

rica and approximately 300 km north of the University of Stellenbosch where the experiments were conducted. Seven adult males and eight adult females of each species were collected using noosing techniques. Size at sexual maturity were taken as 95 mm for *C. cataphractus* (Mouton *et al.*, 1999; Flemming & Mouton, 2002), 58 mm for *C. macropholis* (Mouton *et al.*, 2000a) and 89 mm for *C. polyzonus* (Flemming & Van Wyk, 1992). Males were distinguished by the presence of large hemipenial bulges, broad heads, and the presence of a relative large number of generation glands (Van Wyk & Mouton, 1992). All lizards were released at their site of capture upon completion of the experiment.

HOUSING OF SPECIMENS

Specimens were transported to the University of Stellenbosch where they were housed singly in glass terraria in a laboratory prior to experimentation. An arbitrary period of four weeks was allowed for acclimation to captive conditions. A laboratory window allowed exposure to the natural photoperiod. Room temperature was maintained at 29 °C during daytime, and was allowed to follow ambient temperature at night. Each terrarium was provided with newspaper substrate and shelter sites constructed from two ceramic tiles separated by two wooden strips. Water and food, primarily tenebrionid larvae, were available *ad libitum*.

EXPERIMENTAL SETUP

An open-air experiment was conducted on the roof of a building on the university campus. This provided exposure to the natural photoperiod and weather conditions, and limited human interference. Three adjacent 3.30 m² enclosures were constructed using asbestos sheets held upright with bricks (Fig. 1). Crushed stone was added as substrate. Nine artificial shelters were spaced out in a symmetrical block pattern in each of the three enclosures. A shelter consisted of (top to bottom): a styrofoam cover (30 × 30 × 8 cm) to reduce radiation

heat from the sun; a plywood board (30 × 30 × 2 cm) as shelter cover; three plywood side strips (two 30 × 2 × 2 cm and one 26 × 2 × 2 cm) leaving one side open as a shelter entrance; and an asbestos base (30 × 30 × 0.2 cm). Crevice size was selected to be large enough to house all five lizards, but at the same time also small enough to ensure physical contact among lizards occupying a crevice. All shelter entrances were north facing. A brick was placed on top of each shelter to stabilize the structure. Only horizontal crevices were provided because of the preponderance of this type of crevice in the area where the lizards were collected (see also Mouton *et al.* 1999). One food and one water dish was placed in front of and between two shelter openings (Fig. 1).

EXPERIMENTAL PROCEDURE

We conducted three consecutive week-long trials (i.e. replicates), with species assigned randomly to one of the three enclosures at the onset of every trial. Five conspecific lizards were released at a single location within the designated enclosure of each species. Lizards were allowed to acclimate to conditions for a period of 24 hours. During the following seven days, the number of lizards residing under each shelter was recorded per enclosure at 20.00 hrs, when all activity for the day had ceased. Fresh water and food were also supplied at this time. On days exceeding 28 °C, the entire experimental area was irrigated at 12.00 hrs and additional drinking water was supplied. All shelters as well as the crushed stone substrate were thoroughly washed with water and cleaning agent between trials. Five novel lizards of each species were introduced into the experimental arena for every trial, in other words, a total of three groups and thus 15 lizards were tested per species. Two of these groups consisted of two males and three females, while the remaining group consisted of three males and two females. In the case of *C. cataphractus* and *C. macropholis*, these artificial groups never consisted of more than one member of the natural groups collected.

RESULTS

We explored whether individuals of the three species showed a tendency to aggregate in shelter sites at night. The test statistic was the number of shelters containing lizards on a given night, ranging between one (i.e. all five lizards under a single shelter) and five (i.e. each lizard sheltering individually). To detect grouping behaviour, the frequency distributions of observed scores for each species were compared to frequencies expected under the null hypothesis that lizards shelter randomly according to the urn or occupancy statistical model (Parzen, 1960). According to this model, the expected mean value is 4.01 occupied shelters. The three species displayed varying degrees of aggregation. *Cordylus cataphractus* used two to four shelters per night (Fig. 2), which is significantly less than expected under the occupancy model (Kolmogorov-Smirnov one-sample test, $d_{max}=11$, $P<0.01$). On all nights at least two individuals shared a shelter. The maximum number of lizards under

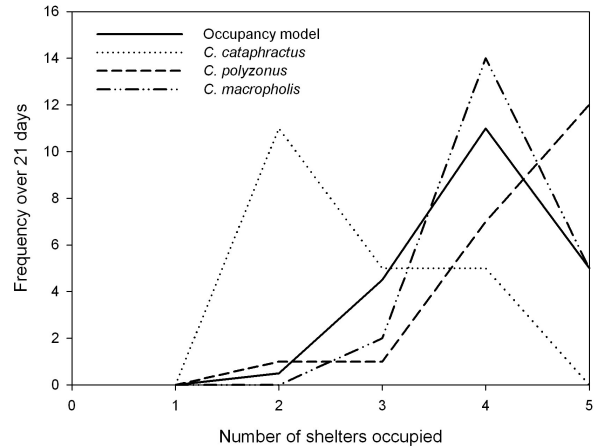


FIG. 2. Line graph depicting frequencies of shelter occupation by five *C. cataphractus* individuals, five *C. polyzonus* individuals, and five *C. macropholis* individuals for a period of 21 days – each day is considered a separate sample. The expected frequencies under the occupancy statistical model (Parzen 1960) are also depicted.

a single shelter was four, which was observed on five occasions. There was no significant difference in the number of shelters used by *Cordylus macropholis* and the number of shelters expected to be used under the occupancy model (Kolmogorov-Smirnov one-sample test, $d_{max}=3$, $P>0.05$). Although the majority of lizards sheltered singly, on rather frequent occasions two lizards shared the same shelter. We never found more than two *C. macropholis* lizards under a single shelter. *Cordylus polyzonus* occupied significantly more shelters than expected under the occupancy model (Kolmogorov-Smirnov one-sample test, $d_{max}=7$, $P<0.05$), which suggests mutual avoidance of individuals. Lizards predominantly sheltered singly or in pairs, except for one occasion where three *C. polyzonus* individuals were found together (Fig. 2).

The former results suggest that *C. cataphractus* exhibited a significant tendency to aggregate when provided with excess shelters, whereas *C. macropholis* and *C. polyzonus* did not. However, our analyses assumed that the data for each group of lizards on consecutive nights represent independent samples. This may increase the probability of falsely rejecting the null-hypothesis. To avoid this, a Repeated Measurements ANOVA was used to compare the pattern of shelter occupation by *C. cataphractus* to that of *C. macropholis* and *C. polyzonus*, the species that did not show any tendency to aggregate. Since the RM Anova only tests for relative differences and provides no point of reference for randomness of distribution, the null hypothesis simply predicts no difference in observed distribution patterns. This analysis treated the number of shelters occupied on consecutive nights by each experimental group as dependent variables, while “time” (i.e. consecutive nights) served as the within-subjects factor and species as the between-subject factor. We detected no significant interaction effect between species and the seven consecutive trial nights ($F_{12,36}=0.845$,

$P > 0.6$). In other words, any differences in shelter occupation among species remained approximately constant over the experimental period. The number of shelters used by each species did not vary significantly among different nights ($F_{6,36} = 0.270$, $P > 0.2$). A significant difference was however detected in the number of shelters occupied among the three species ($F_{2,6} = 8.166$, $P < 0.05$). A *post hoc* Newman-Keuls test indicated no difference in shelter occupation between *C. polyzonus* and *C. macropholis*, but *C. cataphractus* used significantly fewer shelters than both these species.

In conjunction with the first test, this indicates that *Cordylus cataphractus* displays aggregative behaviour even if presented with an excess of shelter sites. *Cordylus macropholis* displayed random shelter occupancy as expected by the occupancy model. Shelter occupation by *C. polyzonus* did not differ significantly from that of *C. macropholis* according to the RM ANOVA, thus the mutual avoidance detected for this species in the occupancy test must be interpreted with caution.

DISCUSSION

A significant difference was apparent in the pattern of shelter occupation among our three test species. *Cordylus cataphractus* consistently occupied fewer shelters than *C. macropholis* and *C. polyzonus* did under identical experimental conditions. Since this grouping behaviour was additionally exhibited in the presence of an excess of shelter sites, our working hypothesis is rejected for this species: grouping behaviour in *C. cataphractus* is not the result of limited shelter availability. In contrast, *C. macropholis* displayed a pattern of shelter occupation that did not differ significantly from that of *C. polyzonus*. Our working hypothesis is accepted in this case, in other words, limited shelter availability can not be excluded as a factor contributing to the aggregative behaviour naturally observed in *C. macropholis*.

These findings are well supported by field studies. Of 134 *C. cataphractus* collected by Mouton *et al.* (1999) along the western coastal lowlands, 85 % of individuals were found in groups of two or more, illustrating the strong tendency to aggregate in the species. The distribution of *C. cataphractus* is not restricted to these coastal lowlands, where rocky outcrops are limited, but also occur inland and in more mountainous areas, where there is an abundance of crevices. Individuals nevertheless still aggregate in groups in the latter areas (Peers, 1930; personal observations), indicating mutual attraction of conspecifics. Furthermore, members of a group not only share the crevice as a nighttime refuge, but during daytime the entire group utilizes the rock containing the home crevice as an elevated look-out point from where foraging attempts are launched, despite the fact that this promotes intraspecific food

competition (Mouton *et al.*, 2000c). In the case of *C. macropholis*, field studies have shown the incidence of lizards sharing plants to be as high as 89 % (Mouton *et al.*, 2000a). Unlike *C. cataphractus*, however, these lizards displayed mutual avoidance when provided with an excess of shelter sites in our experiment. The distribution of *E. caput-medusae* is extremely patchy across the range of *C. macropholis* and the plants can be considered a limited resource, thus forcing lizards to co-inhabit the same plant (personal observations). The high incidence of one *C. polyzonus* lizard per shelter in our experiment also correlates with field observations, where individuals are predominantly encountered singly (Branch, 1998; personal observations).

C. cataphractus displays several unique physiological and behavioural characters, which may be associated with energy constraints brought about by the permanent group-living lifestyle of this sit-and-wait forager. These characters include low fecundity, with females giving birth to only one young per year as opposed to two to nine in other cordylids (Flemming & Mouton, 2002), an extremely low resting metabolic rate (Mouton *et al.*, 2000b), and extremely low activity levels during dry summer months (Visagie, 2001) when other cordylids remain active. No such unique characters have been encountered in *C. macropholis* as of yet, once again enforcing our hypothesis that aggregative behaviour in *C. macropholis* is the result of limited availability of refugia.

In light of our evidence that different driving forces are responsible for the grouping behaviour observed in *C. cataphractus* and *C. macropholis*, it becomes questionable whether aggregations of *C. macropholis* should be classified as social groupings. The dense spatial arrangement of *E. caput-medusae* stems allows limited visual contact between individuals and mutual avoidance can easily be maintained. On the other hand, *C. cataphractus* lizards are in constant visual contact and, to a lesser extent, physical contact within their rock crevices (personal observations). Lizards are forced to interact socially and a complex social structure is to be expected.

In conclusion, limited crevice availability can be eliminated as being responsible for the strong grouping tendency in *C. cataphractus*. It will be difficult to assess whether the unique characteristics of *C. cataphractus* are the cause of its group-living behaviour or a consequence thereof. In contrast, aggregative behaviour observed in *C. macropholis* might be an artifact of limited refuge availability and social structure in this species is potentially not as complex as in *C. cataphractus*. These two species provide ideal opportunities for further investigations into social structure among reptiles.

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