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BEHAVIOURAL OBSERVATIONS OF THE CHAMELEON CALUMMA OSHAUGHNESSYI OSHAUGHNESSYI IN MADAGASCAR

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One of the most important questions in behavioural research is how animals distribute themselves in space. The area regularly inhabited by an individual is known as its home range, the size and spacing of which depend on several factors, including food availability, habitat structure, social organization and population density (Stamps, 1977). A territory can be described as that part of the home range which is defended (Maher & Lott, 1995). Over the last thirty years, territoriality has been discussed primarily in terms of benefits to individual fitness through priority of access to limited resources and costs incurred through the exclusion of competitive conspecifics. More recent work, however, emphasizes the complexity of interaction between social and spatial factors, including possible benefits of living adjacent to conspecifics (Stamps, 1994).

Much of the information regarding territoriality in chameleons comes from studies of captive (Kästle, 1967; Bustard, 1965, 1966; de Vosjoli, 1979) and semicaptive (Parcher, 1974) individuals. Parcher (1974) attempted a field study of social behaviour in rain forest species during the wet season but due to the scarcity of interactions between individuals, resorted to artificial manipulation. These studies give detailed descriptions of territorial display between both males and females but provide little information about the characteristics of territories. Descriptions of territorial behaviour from the field are much rarer presumably due to the difficulty of observing these solitary and well camouflaged animals in dense habitats. Exceptions include studies of desert and grassland species (Burrage, 1973) and rain forest species during the dry season (Kauffmann, 1994). Burrage found both sexes of the terrestrial Chamaeleo namaquensis rigorously defended territories, but the arboreal species Bradypodium pumilum (as

C. pumilus) defended only roosting sites. Kauffmann reported that *Calumma brevicornis* and *C. oshaughnessyi ambreensis* maintained small, discrete home ranges (without the need for defence) often remaining faithful to a single roosting site on consecutive days.

Many species of lizards follow a cycle of daily activity, centred around behavioural thermoregulation. Basking takes place during the early morning and late afternoon to maximise heat uptake while the hottest hours of the day are spent in the shade or posturing at an angle which reduces heat absorption (Heatwole, 1976). In chameleons, thermoregulation has been studied primarily in species which are adapted to temperature extremes (Burrage, 1973; Reilly, 1982). These species were active throughout the day, maintaining remarkably constant body temperatures despite the fluctuating external environment, by using a range of physiological temperature controls such as colour lability, changes in lung volume and cardio-vascular adjustment (Burrage, 1973; Walton, Bennett & Losos, 1993).

As part of a wider study of chameleons in the eastern rain forest of Madagascar (Ranomafana National Park), we carried out some behavioural observations on *Calumma o. oshaughnessyi*. Our prime interests were spatial organization and daily activity patterns.

The study site (approximately 38x25 m) was situated in primary forest within the Ranomafana National Park. It encompassed a flat area of fairly uniform forest at an altitude of 1090 m. The canopy is closed and the understorey rich with lianes, palms and tree ferns. Research was carried out during the wet (breeding) season between 23.11.93 and 21.12.93. In order to investigate the spatial organization of this species, roosting sites of individuals were recorded on successive nights (after Kauffmann, 1994). The main path which ran through the study site was mapped, allowing the initial roosting sites (origins) of all chameleons to be measured in relation to the path. Chameleons were individually marked using typewriter correction fluid. The study site was searched regularly, new chameleons recorded and the roosting sites of known chameleons measured in relation to their origins. In addition, one of four focal chameleons was chosen for continuous observation during the day. This individual, located at night, was found roosting the next morning and watched from 06.00 to 1800 hr, in shifts of 1.5 hours. Observations were divided into 15 minute blocks within which a number of variables were recorded to determine the relationship between movement, foraging and time of day: total distance moved (estimated by eye); timing of a single 'pace' (defined as the complete cycle of movement by all four feet and measured once at the beginning of each period); number of strikes (tongue flicks) and miscellaneous observations. To obtain more detailed information about the use of space by individuals we measured the maximum height, minimum height, distance and bearing from the roost at each 1.5 hour change-over. Four adult chameleons (three fe-



FIG. 1. *C. o. oshaughnessyi* roosting sites (with occupation dates), during the behavioural study period.

males, F1-F3 and one male, M1) were watched over 13 days for a total of 114 hours.

Fig. 1 shows the initial locations of the four study chameleons and the positions of subsequent roosting sites. It can be seen that there is considerable spatial overlap but almost no temporal overlap. With the exception of 2.12.93 (when M1, F2 and F3 roosted close together) chameleons occupied the same area but at different times.

The maximum distance travelled from the roosting site, measured every 1.5 hours, was obtained for F2 and F3. Since the chameleons were watched continuously, these points can be joined together to give the two-dimensional area traversed during the day. Maximum and minimum heights were recorded for the same individuals and can be used to estimate the volume of space used by these individuals on a daily basis (Table 1).

No direct interactions between individuals occurred but short bouts of head jerking, consisting of two or



FIG. 2. *C. o. oshaughnessyi* behavioural observations. Individual averages were pooled to give the overall mean $(\pm SE)$ for all four chameleons. (a), hourly movement; (b), no. prey strikes (successful and unsuccessful) per hour; (c), pace per hour; (d), % frequency distribution of pace (taken only from days on which observations were completed from 06.01 to 18.00 hrs).

three sharp upwards movement of the head, were observed on 11 occasions for M1 and once for F3. We were unable to see the recipient, but head jerks have only been described as part of courtship, not agonistic, display (de Vosjoli, 1979; Parcher, 1974).

Mean hourly movement, mean number of strikes/ hour, mean pace/hour and the % frequency distribution of pace were calculated from our observation data (Fig. 2). Despite considerable individual variation, some general patterns emerged. After one or two hours of basking, activity increased during the morning although the distance travelled was only 2-3 m per hour. Movement decreased again towards late-afternoon before a final surge of activity at sunset, coinciding with the search for a roosting site. Foraging occurred throughout the day but peaked between 11.00 and 12.00 hrs. If a single pace took longer than the 15 minute recording block, the chameleon was considered to be stationary. 'No movement' was most frequently

Chameleon	Date	Area (m ²)	Circumference (m)	Height (m)	Volume (m ³)	
F1	1.12.93	3.81	13.12	3.0	11.43	
F2	2.12.93	4.28	16.10	4.1	17.54	
F3	20.12.93	2.79	9.27	5.5	14.78	

TABLE 1. Use of space by individual chameleons.

recorded. For a moving chameleon, a single pace ranged from a few seconds to 13 mins, but was usually between one and three minutes. Movement during the afternoon was very slow whereas the return towards a roost at night was associated with an increase in speed.

The conclusions which can be drawn from our observations are clearly limited by the small sample size in this study. Nevertheless, use of space by the chameleons in this study was very different from that of two similar species (C. brevicornis and C. o. ambreensis) during the dry season (Kauffmann, 1994). Instead of maintaining small (mean size 29 m²) discrete home ranges, our study animals passed through the same area at different times, seldom returning to the same roosting site. Characteristics of the home range may vary with changes in the most sought-after resource. In seasonal habitats, an expansion of home range area is likely to occur during periods when there are high demands for food and/or mates (Rose, 1982). Burrage (1973) found that territories of male C. namaquensis increased during mate acquisition and those of females increased during egg-laying. The timing of reproduction in chameleons is varied (Lin & Nelson, 1981), but it is likely that breeding in most Malagasy species coincides with the rainy season. In this study, chameleons were occupying relatively large and overlapping home ranges, but the extent to which territories were held within these areas cannot be deduced. It is possible, for example, that the single male occupied a large territory through which the females travelled but much more information is needed on chameleon mating systems before this can be substantiated. Descriptions of chameleon agonistic display in the literature lead one to expect territorial behaviour but we saw no evidence of territorial or roosting site defence. It is interesting to note that territories are much more difficult to defend in visually complex habitats (Stamps, 1977). If territories are maintained, aggressive encounters are too rare to observe in the field (see Parcher, 1974).

Roosting site locations alone provide limited information about chameleon home ranges since the area visited during the day is not included. Kauffmann (unpub. data) found that during the dry season, the increase in home range area calculated using the outermost positions reached during the day was generally small (average increase for *C. o. ambreensis* = 12%). During this study chameleons followed a more irregular path between roosts indicating that home range size calculated using this method would have been severely underestimated. Nevertheless, roosting sites are obtained at night when chameleons are readily located and are useful in looking at relative differences between individual home ranges or within a population over time.

Home range size is particularly difficult to study in chameleons because of the three-dimensional nature of the arboreal habitat. Distribution within the vertical habitat may be an important means of resource partitioning within and between species of arboreal lizards. The difference between maximum and minimum heights recorded during the day gives a more accurate idea of the amount of space occupied by the chameleons. However, since chameleons sometimes ascended out of sight, these estimates of volume are probably conservative. F3 (20.12.93) moved further in the vertical plane than the horizontal, resulting in a larger overall space than F2 (1.12.93), although the area covered by F2 would have looked more extensive when presented on a two-dimensional map (Table 1). Improvements in canopy access techniques need to be applied to this area of study.

The pattern of daily activity shown here (Fig. 2) is consistent with behavioural thermoregulation to the extent that the cool early hours are spent basking and activity increases with increasing temperature. Maximum temperatures in this shady environment, however, are not sufficiently high to produce the midday inactive period typical of temperate lizards (Avery, 1993). Furcifer oustaleti exhibited similar activity patterns in warm secondary forest during the dry season in Madagascar (Kauffmann, unpub. data). This contrasts with the predominance of physiological thermoregulation described by Burrage (1973) and Reilly (1982) for desert and montane species. Perhaps in the relatively mild forest environment, the use of costly physiological thermoregulation is avoided. Further evidence for behavioural thermoregulation in rain forest species may come from observations during the dry/cold season in Madagascar (Kauffmann, 1994). In the early morning, chameleons travelled from their roost to a 'resting place' (either on a branch or under the leaf litter) where they maintained a long period of inactivity or torpor (up to 10 hours) before returning to roost. It is not certain, however, whether this behaviour resulted from low temperatures (daily mean 16°C) or food shortage. Reilly (1982) also noted differences between coldadapted chameleons which roosted in the interiors of shrubs/trees to avoid night time frost and warmeradapted species which roosted at the ends of branches in order to benefit from early morning sunshine. On many occasions, C. o. oshaughnessyi moved relatively large distances in the early evening just before arriving at their roosting site, suggesting such a preference for roost position.

Chameleons hunt by a combination of sit-and-wait predation and foraging while moving slowly through the habitat (Stamps, 1977; Burrage, 1973). This is confirmed by data from our study which shows that foraging occurred throughout the day, spanning periods with more and less movement (Fig. 2). However, the peak foraging time between 11.00 and 12.00 hrs was not accompanied by a large distance travelled, possibly due to the high activity of aerial prey. This, together with the most frequently recorded 'pace' of zero seconds, implies that sit-and-wait predation may be the predominant strategy in this species. There was no clear relationship between speed of movement and distance covered (Fig. 2) suggesting that chameleons travel with a combination of short bursts and slow, steady movements.

Some of the difficulties involved in the study of chameleon behaviour have been highlighted here. Without radio-tracking equipment, continuous observation is the only means of watching chameleons in the complex rain forest environment and may still result in the occasional focal individual disappearing from sight. Kauffmann (1994) used this method more successfully in the dry season, when chameleons were relatively inactive, but it is still a labour intensive and inefficient means of studying behaviour. More efficient sampling methods have been used successfully in open habitats: grassland and desert (Burrage, 1973); scrub (Lin and Nelson, 1981); montane scrub (Reilly, 1982). However, the use of radio-tracking is recommended for future studies, both for gaining information about chameleon spatial organization and to assist in finding and observing chameleons. Radio-tracking was used successfully in Kenyan scrub by Hebrard & Madsen (1984) and is currently being used to study the European chameleon in Spain (Loman, pers. comm.). However, even here there are a number of problems including high cost and poor signal reception in dense habitats. Nevertheless, with improved means of locating individuals in the field it will be possible to find out much more about the behaviour of these elusive animals

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