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Islands in a sea of sand: use of *Acacia* trees by tree skinks in the Kalahari Desert

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In the Kalahari desert the tree skink *Mabuya striata sparsa* occupies *Acacia* trees separated by areas of open sand. On a single day in austral spring, the effects of tree size and structural complexity, presence of colonial nests of weavers, and fallen limbs on lizard abundance, and of time of day and air temperature on numbers of lizards active, location on trees, ground, or ground cover, and occupation of sunny, shaded, or partially shaded sites were examined. Multiple regression showed that the numbers of adult and total lizards increased with tree size, amount of ground cover, and air temperature. Neither number and size of sociable weaver nests nor complexity of tree shape affected lizard abundance. Proportions of lizards on trees and ground did not vary with time of day; neither did height above ground among individuals on trees. The proportions of lizards fully exposed to the sun was higher early and late in the day than at midday, when more lizards occupied shaded sites.

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Introduction

In arid zones, large trees may be important microhabitats for many animals and necessary ones for others. In the Kalahari Desert, large *Acacia* trees are often surrounded by open sand with sparse vegetation. The trees and the ground cover beneath them can provide a refuge from predators and relatively abundant invertebrate food for arboreal and semi-arboreal lizards. The most abundant semi-arboreal lizard in parts of the Kalahari Desert is the lygosomine skink, *Mabuya striata* (Peters), locally known as the svart turk. During a brief visit to the Kalahari Desert, we observed abundant *Mabuya striata sparsa. Mabuya striata sparsa* coexists with *M. spilogaster* (Peters), but is far more abundant at our study site. We noted a strong association between *Mabuya striata sparsa* and *Acacia* trees and made observations to investigate factors that affect the distribution of lizards among trees, lizard activity, and microhabitat selection.

The phylogeny, ecology, and behaviour of a large majority of species of the genus *Mabuya* remain poorly known, particularly in Africa, but more information is becoming available for a few African species, including species from arid zones of South Africa and Namibia. Pianka (1986) summarizes data on diet, habitat use, air and body

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temperatures, reproduction, and morphology for four Kalahari Desert species. Recent work on an assemblage of *Mabuya* in north-western Namibia has provided important information on diet, foraging, activity and microhabitat on a few species (Castanzo, 1991; Castanzo & Bauer, 1993).

Mabuya striata is one of the ecologically best known species of its genus. It is an insectivorous, viviparous species with a mean litter size of 5·4, and mean snout-vent length of 70·1 mm (Huey & Pianka, 1977; Branch, 1998). Several aspects of the natural history of *M. striata sparsa* have been investigated to some extent, including its foraging behaviour, diet, reproduction, body temperature, microhabitats occupied, and social organization (Brain, 1969; Huey & Pianka, 1977; Branch, 1998; Cooper & Whiting, 2000). *Mabuya striata sparsa* forages actively on the ground near trees which it uses for refuge, basking and foraging (Brain, 1969; Huey & Pianka, 1977; Cooper & Whiting, 2000). Mean body temperature is approximately 34°C (Brain, 1969; Huey & Pianka, 1977), with lowest temperatures recorded in the morning.

Although the microhabitat and diel activity of *M. striata sparsa* have been studied, scant attention has been paid to factors other than temperature that affect microhabitat selection and degree of activity. We investigated the relationships between numbers of individuals observed per tree and several features of the trees they occupied, as well as time of day and air temperature. In a previous study with a sample size too small for statistical analysis, Brain (1969) noted a possible increase in lizard abundance with tree size and presence of weaver nests and fallen limbs. We hypothesized that tree size, structural complexity, weaver nests, and availability of ground cover might affect the number of lizards occupying trees.

To test these hypotheses, we observed the number of active lizards on the tree and nearby on ground or surface debris throughout the activity period on a single day in October. Because many individuals may not have been active at a particular time, our data may greatly underestimate the number of lizards present for some trees, but the numbers observed should be correlated positively with numbers present (suggested by limited data; Brain, 1969). By recording time of day and air temperature for each tree, we were able to assess the effects of these variables on the number of lizards observed. This permitted an examination of diel or thermal variation in activity and statistical removal of such effects from relationships between the number of lizards and tree variables. To detect any diel variation in microhabitat use, we also examined the positions of lizards on trees, ground, or ground cover and location in sun, shade, or mixed sun and shade.

Methods

After noting an apparent association between lizards and large camel thorn *Acacia* trees (*Acacia erioloba* Mey) on the previous day, we observed *M. striata sparsa* on 21 October 1994, a sunny spring day, at an arid site near Aroab (Farm Arabi, 26° 25′S, 18° 45′E) in south-eastern Namibia. Much of the site consisted of sparse clumps of grass and isolated trees on open sand. We searched the habitat visually for lizards from 08 30 to 18 50 h. This interval began nearly an hour before we observed the first lizard and ended with the sun just over the horizon.

To assess factors affecting the number of lizards observed per tree, we recorded the following variables: the number of individuals (LIZ) and number of adults (ADULTS) associated with each tree, including those on the tree or on the ground or debris beneath the tree; the circumference of the tree in cm at ground level (CIRC), the number of branching points where the diameter was $\geqslant 50$ cm on each branch at heights $\leqslant 2$ m; the time of day; the air temperature (TEMP) at 1 m above ground; the number of distinct trunks of the tree; the presence, size, and number of sociable weaver (*Philetairus socius* Latham) nests; and the degree of cover (COVER) available on the

Table 1. *Importance of communal masked weaver (Philetairus socius) nests in trees and availability of ground cover under trees*

Weaver nests	Ground Cover
0 - None	0 - None
1 - One to a few very small nests	1 - Grass clumps 2 m away
2 - One small nest	2 - Sparse
3 - More than one small nest	3 - Small branches
4 - One intermediate sized nest	4 - Fallen limb, part of weaver nest, or branches and debris
5 - More than one intermediate nest	5 - Part of weaver nest and limb; nest and branches or debris
6 - One large nest	6 - Nest and limb; $\geqslant 2$ limbs
7 - One very large nest	7 - Two or more limbs plus debris or nest
8 - Several large nests	8 - Extensive cover including fallen limbs, branches, nests, and/or debris

ground under the tree. Ordinal scales were constructed to indicate the presence of weaver nests in trees, not including fallen nests on the ground, and the degree of ground cover (Table 1). To detect any diel variation in microhabitat use, for each lizard we recorded its location (including height above ground) and degree of exposure to sunlight.

Multiple regression was used to assess the effects of variables on the total number of lizards and number of adults observed per tree (Sokal & Rohlf, 1995). For variables found to affect numbers of lizards, partial correlations were conducted to determine the strength of association of the variables with number of lizards independent of variation in the other variables. To determine whether lizard locations and exposure to sun varied with time of day, we used chi-square tests in which locations were compared in three time intervals (early morning–early afternoon: 09 45–13 00; mid-afternoon: 13 46–17 00; and late afternoon: 17 01–18 40 h). Initial site categories were ground, log or fallen nest, and standing tree. Categories for insolation were sun (complete exposure), mixed (partially in sun, partially in shade), and shade (entire body shaded). For those individuals on trees, possible variation in tree height with time of day was examined by single-factor analysis of variance for the three time categories. All tests were two-tailed, with $\alpha = 0{\cdot}05$.

Results

Lizards were observed in association with standing or fallen trees, either on the trees or on ground or litter associated with trees, such as fallen weaver nests and limbs. Those not on trees were under the canopy or only a short distance beyond it. The majority were found on or close to camel thorn *Acacia* trees, which are dominant in the area. There is no evidence that the lizards prefer camel thorn *Acacia* trees because they were associated with 0·62 (40/65) of camel thorn *Acacia* trees and 0·60 (6/10) of two other less abundant, unidentified tree species, one of them another *Acacia* tree.

In the multiple regression models, the number of lizards observed on or under a tree increased with the amount of cover on the ground beneath the tree, tree circumference, and air temperature (Figs 1–3). Preliminary models including all variables revealed no significant effect of number of large branching points on the trees, weaver nests,

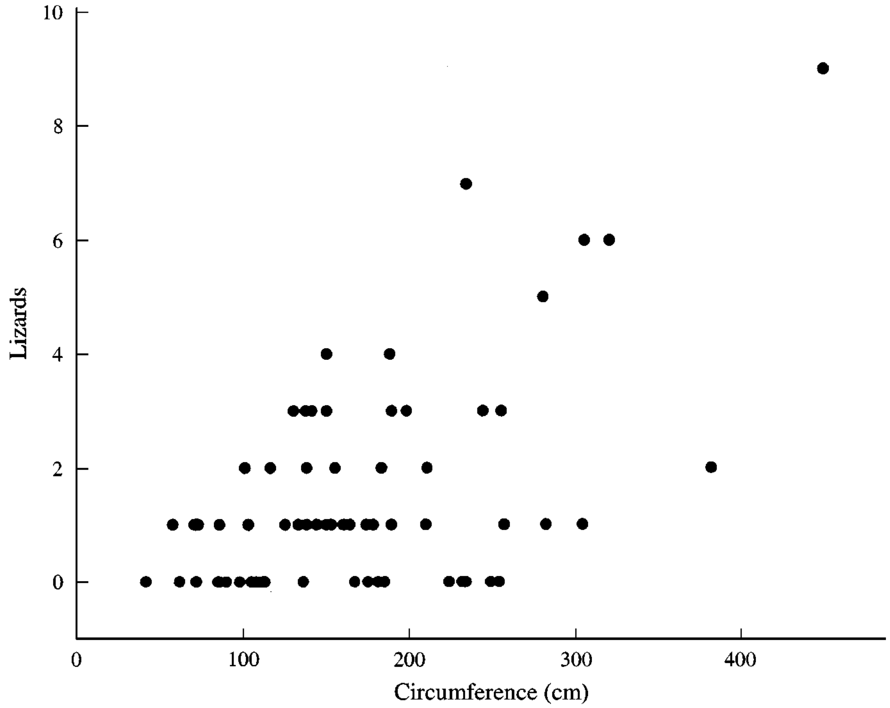

Figure 1. Number of individuals of *Mabuya striata sparsa* observed on or closely associated with camel thorn *Acacia* trees in relation to tree circumference.

number of separate trunks, or time of day. The final multiple regression model for number of lizards was highly significant ($F = 26{\cdot}41$; df. = 3, 61; $p < 0{\cdot}0001$), accounting for 54·4% of the variance. The model is:

$$\text{LIZ} = 0{\cdot}010\ \text{CIRC} + 0{\cdot}308\ \text{COVER} + 0{\cdot}258\ \text{TEMP} - 7{\cdot}618.$$

All model components were significant. For CIRC $t = 4{\cdot}77$, df. = 61, $p < 0{\cdot}0001$; for COVER $t = 5{\cdot}08$, df. = 61, $p < 0{\cdot}0001$; for TEMP $t = 3{\cdot}72$, df. = 61, $p = 0{\cdot}0004$; for the constant $t = -4{\cdot}08$, df. = 61; $p = 0{\cdot}0001$. Figures 2 and 3 show that although the maximum number of lizards observed per tree increased with tree circumference and air temperature, there was little change in the minimum number of lizards even for large trees (at least up to 300 cm circumference) and high temperatures. The temperature effect remains highly significant when the individual with the single lowest temperature value is removed ($t = 3{\cdot}59$, df. = 60, $p = 0{\cdot}0007$). The partial correlations between number of lizards and each of CIRC, COVER, and TEMP, with the other two of these independent variables held constant, are 0·52 for CIRC, 0·55 for COVER, and 0·43 for TEMP (df. = 61 each). Analysis restricted to adults reveals a pattern of significance identical to that for all lizards.

The proportions of lizards observed on trees, logs or fallen nests, and on the ground did not vary significantly with time of day (Fig. 4). Numbers of lizards on the ground and on fallen logs or nests were pooled to obtain adequate expected frequencies in all cells of the 3 × 2 table for analysis by chi square ($\chi^2 = 3{\cdot}50$, df. = 2, $p > 0{\cdot}10$), but the results were similar for unpooled data. Examination of the data shows that slightly more individuals were on the ground in the early afternoon (Fig. 4), but this effect was

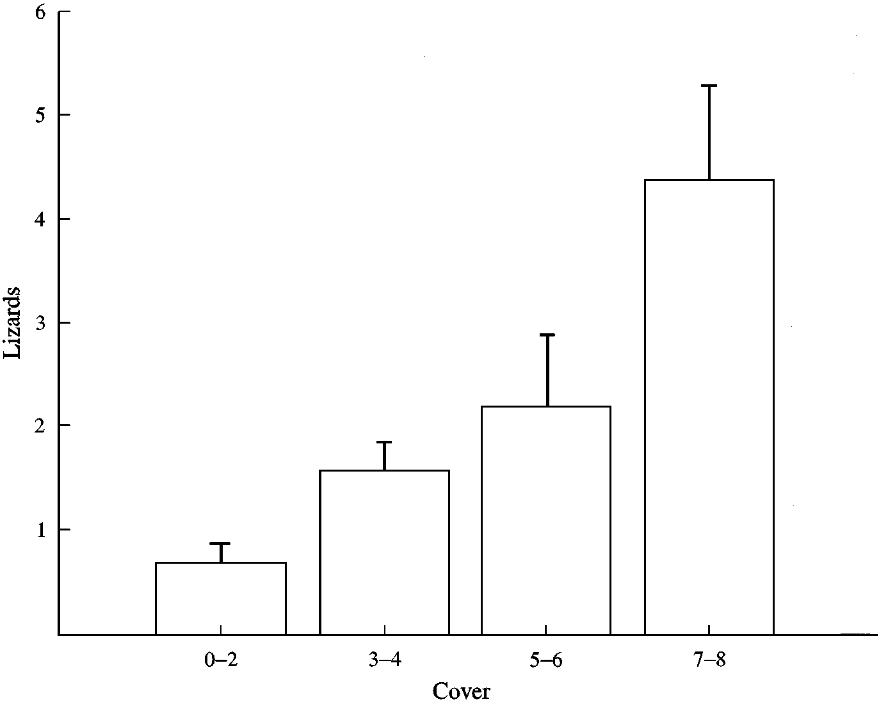

Figure 2. Number of individuals of *Mabuya striata sparsa* observed on or closely associated with camel thorn *Acacia* trees in relation to amount of ground cover, including fallen limbs, weaver nests, and bark.

not significant. Among those individuals on trees, height above ground did not vary significantly with time of day ($F = 0{\cdot}248$; df. = 2, 64; $p > 0{\cdot}10$).

Exposure of lizards to sunlight varied strongly with time of day (Fig. 5). Due to low expected frequencies for lizards not fully exposed to sun early and late in the day, frequencies of lizards in full and partial shade were pooled. Proportions of lizards fully exposed to the sun varied significantly with time of day ($\chi^2 = 35{\cdot}01$, df. = 2, $p < 0{\cdot}001$). The proportion of individuals in sun was higher early and late in the day than in the middle period, during which the number of individuals in shade or mixed sun and shade increased greatly (Fig. 5).

Discussion

Trees appear to be necessary for *M. striata sparsa*, presumably due to a combination of factors such as abundance of prey, refuge from predators that are poor climbers, and retreat from harsh environmental conditions, especially high temperature. Although no data are available for *M. striata sparsa*, higher humidity in tree cavities and perhaps weaver nests might also provide some protection against desiccation. The lizards were very strongly associated with large trees, most being found on trees and fewer on the ground or on ground litter under or adjacent to trees. No lizards were observed in the areas between trees despite the much greater area occupied by sand than trees. The trees may be thought of as habitat islands in an otherwise unsuitable desert. Although the number of individuals seen on large trees was surprisingly great, up to 9 per tree, the actual numbers of lizards present were probably substantially greater based on removal sampling in the nearby Kalahari Gemsbok National Park (Brain, 1969).

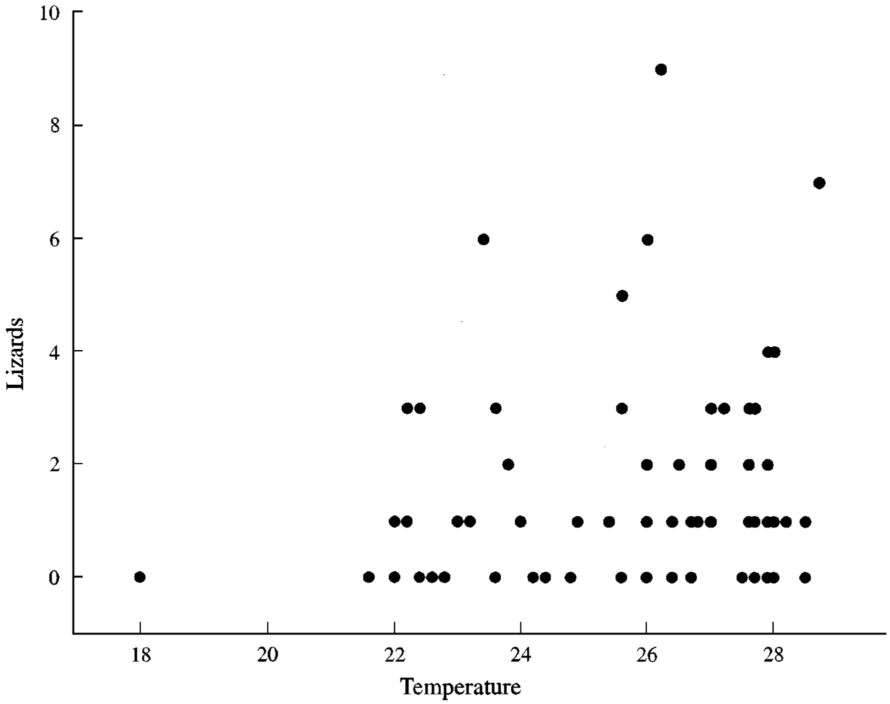

Figure 3. Number of individuals of *Mabuya striata sparsa* observed on or closely associated with camel thorn *Acacia* trees in relation to air temperature.

Of the three factors affecting the numbers of lizards observed per tree, two structural factors presumably affected the actual numbers present. Number of lizards observed increased with tree circumference, presumably because larger trees provide more space, greater structural complexity possibly permitting social separation, more refuges from predators, and a larger food supply. The greatest numbers of lizards were observed on or under trees with a large amount of ground cover, including fallen branches and weaver nests, presumably for the same reasons as for tree circumference. Increasing ground cover may be especially important for its effect on food supply because we observed active foraging at ground level.

Air temperature, the third major factor related to number of lizards, must affect the proportion of individuals active at a given time rather than the number that occupy a tree. Fewer individuals were active early in the morning when air temperatures were low than later in the day when air temperatures were higher and the lizards had completed basking. This finding agrees with the data of Huey *et al.* (1977), who found little activity in the early morning during spring, fall, and winter. Because our data were collected in spring when the maximum air temperature was relatively low (below 30°C), more lizards might be active on warmer days. However, because the number of active lizards was low at the lowest temperatures, but increased rapidly with temperature and then remained nearly constant over much of the observed temperature range, the major effect of temperature appears to have been depression of activity at temperatures too low for basking to reach the preferred body temperature. Once the initial period of morning basking has been completed, the lizards appear to be able to maintain a high body temperature (Brain, 1969), especially on sunny days with low wind speeds as during our observations. Previous studies of *M. striata sparsa* have shown that the mean body temperature is closely regulated (Huey & Pianka, 1977; Huey *et al.*, 1977; Pianka, 1986).

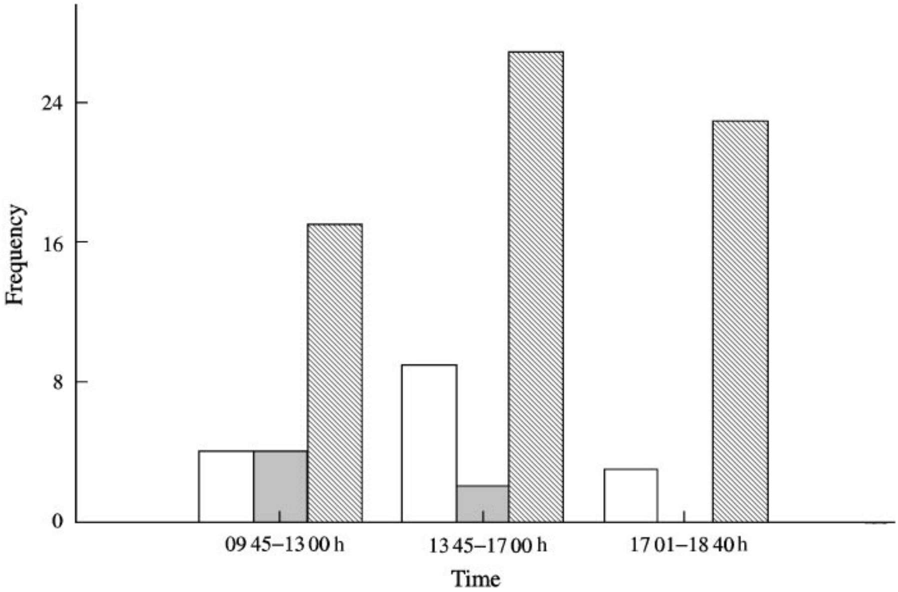

Figure 4. Number of individuals of *Mabuya striata sparsa* observed on camel thorn *Acacia* trees and on ground and ground cover nearby throughout a daily activity period. ☐ Ground; ▩ Log-nest; ▧ Tree.

Our predictions that the number of lizards observed would increase with the number of branching points of large diameter, the number of trunks per tree, and number and size of weaver nests were not confirmed. There was a slight, but non-significant tendency for the numbers of lizards observed to increase with the number of weaver nests in trees. We did not observe lizards on weaver nests in trees. Nevertheless, weaver

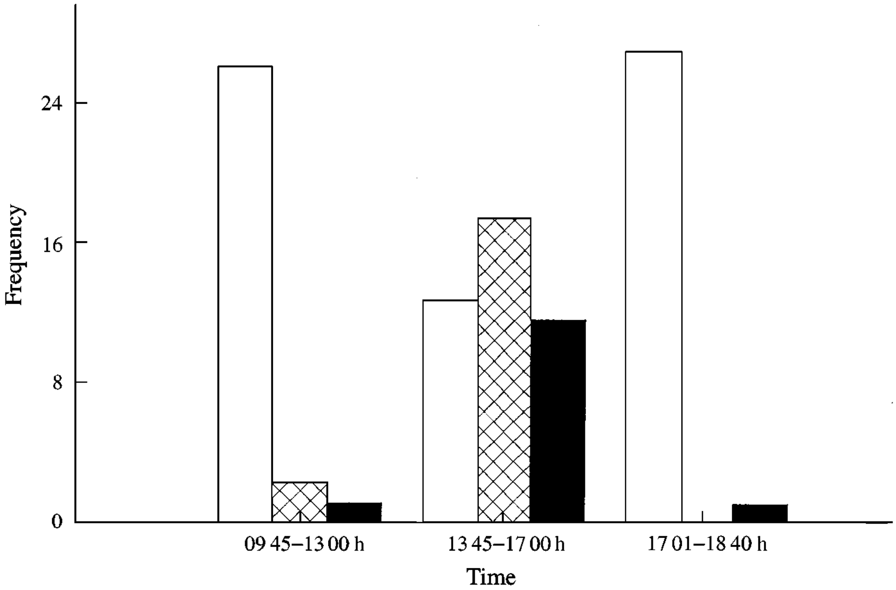

Figure 5. Variation in number of individuals of *Mabuya striata sparsa* observed fully exposed to sun, in partial shade, and fully shaded during a daily activity cycle. ☐ Sun; ⊠ Mixed; ■ Shade.

nests presumably affected lizard abundance via their strong contribution to the degree of ground cover by fallen nests.

Based on the assumption that the lizards would take shelter in the trees at night, bask, and then descend to forage, as does the skink *Eumeces laticeps* (Taylor) (Cooper, unpublished data), we expected that the proportions of lizards not on trees would increase during warm temperatures in the middle of the day and that lizards would be observed higher in trees early and late in the day. No such changes were observed. It remains possible that the lizards do behave this way, but that our few observations early in the day were inadequate to show it. Another hypothesis consistent with the data is that some lizards spend the night under ground cover or that some descend to bask at ground level. We observed several individuals basking at or very near ground level. Our observations of the use of trees vs. ground plus logs by *M. striata sparsa* on a warm spring day are almost identical with those of Huey *et al.* (1977) for summer in showing that 75·3% of lizards were on trees. Our data suggest somewhat greater use of trees and lesser use of ground and logs than did those of Huey *et al.* (1977) for spring and fall combined, which might be due to differences between localities or years, or to a variation specific to our single day of sampling.

The importance of thermoregulatory behaviour in *M. striata sparsa* is suggested by the variation in exposure to sunlight with time of day. Our data for one spring day conform to the pattern reported by Huey *et al.* (1977) in summer: A high percentage of individuals basked upon emergence in the morning, as is typical for heliothermic lizards (Huey, 1982), but by mid-afternoon, a large majority were in partial or full shade, suggesting maintenance of preferred body temperature by shuttling between sun and shade. In other seasons, the lizards typically emerge later, and a higher percentage are in full sun throughout the activity period (Huey *et al.*, 1977), suggesting thermoregulatory basking. That almost all individuals in our study were fully exposed to sunlight after 17 00 h suggests that basking was required to keep body temperatures high during the low air temperature and low angle of incidence of sunlight.

Our knowledge about the ecology and behaviour of *M. striata sparsa* is rudimentary, but this lizard offers great opportunities for further research due to its high abundance, ease of observation, and ready adaptability to laboratory conditions (Cooper, in press). Nothing is known of its social behaviour, but the isolation of small groups associated with each tree is ideal for studies of social organization, reproductive success, and dispersal. Variation in lizard density with tree size suggests the possibility of coincident changes in social behaviour and organization. The chemosensory ability revealed by identification of prey by tongue-flicking by *M. striata sparsa* (Cooper, in press) and the presence of well-developed pheromonal communication in *Eumeces* (Cooper & Vitt, 1986*a, b, c,* 1987*a, b*; Cooper, 1996) suggest that pheromones may be important to *M. striata sparsa.* Given the strong possibility of inbreeding in isolated groups, pheromonal kin recognition is a good possibility. The anti-predatory behaviour of *M. striata sparsa* is virtually unknown and would seem to provide a good opportunity for the detection of separate adaptations for evading aerial predators while on trees, and aerial and terrestrial predators on the ground.

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