

Experimental analysis of retreat-site selection by thick-tailed geckos *Nephrurus milii*

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Abstract Although animals use habitats non-randomly in the wild, complex correlations among environmental features mean that proximate influences on habitat selection can be identified only by experimental manipulation of potential cues. Thick-tailed geckos *Nephrurus milii* are large lizards that are widely distributed through southern Australia. These nocturnally active animals typically spend daylight hours under surface rocks. We presented captive geckos with alternative retreat-sites (rock crevices) differing in attributes potentially relevant to habitat selection. The lizards showed strong preference for shelter-sites that enhanced thermoregulation (warm rather than cool) and that reduced the animal's vulnerability to predators (narrow crevices with small openings and not containing the scent of a predatory snake). Horizontal rather than sloping crevices were also preferred. Overall crevice size and thickness of the overlying rock did not influence retreat-site selection in the laboratory, but could be important in the field because of their influence on thermal regimes under rocks. The present study supports the idea that nocturnal reptiles base their selection of diurnal shelters on multiple aspects related to the fitness consequences of occupancy of alternative available retreat-sites.

Key words: gecko, habitat selection, *Nephrurus milii*, retreat-site selection, thick-tailed gecko.

INTRODUCTION

Habitat requirements differ substantially among organisms, and can constrain their distribution and abundance (Schlesinger & Shine 1994; Jones 2001; Thery 2001). Some taxa exhibit very specific habitat preferences (Burger & Gochfeld 1981; Cowan 1989; Wilkinson *et al.* 1998), whereas others are far more generalized in this respect (Sol *et al.* 1997; Aiken & Coyle 2000; Jones *et al.* 2001). Extreme habitat specificity can reduce a species' ability to persist in the face of anthropogenically induced habitat change (Shine *et al.* 1998; Harwood 2001). Thus, the features of habitats that make them suitable for a particular species are of considerable significance for understanding phenomena such as the distribution, abundance and conservation status of that taxon.

There is immense complexity in actual patterns of habitat use. Commonly, different components of the habitat are differentially important for different activities. An animal might shelter while inactive in one site, forage in another and reproduce yet elsewhere. For species that remain sequestered within retreat-sites for a high proportion of the diel and annual cycle, the availability of suitable shelter will be a critical deter-

minant of habitat availability. This situation also has logistical advantages for study, because it is much easier to measure and manipulate attributes of a fixed retreat-site than to quantify and manipulate the range of habitats used by an actively moving animal. These factors have stimulated several recent studies on retreat-site selection by ectotherms, and the strong consensus from such studies is that the animals are indeed capable of making subtle choices among an array of attributes of alternative potential retreat-sites (Huey *et al.* 1989; Downes & Shine 1998b; Kearney 2002).

Although much can be learned from field surveys of habitat use, and especially from comparisons between sites occupied by animals compared to nearby unoccupied areas (Scott *et al.* 1998; Gamel & Brush 2001), the causal determinants of habitat selection might remain ambiguous because of complex correlations among variables. For example, under many circumstances, a rock's size and its thermal properties will covary, making it impossible to determine from field data whether animals that refuge under rocks select retreat-sites based on either or both of these criteria. We can gain further insight into the factors driving habitat selection by laboratory studies that tease apart these correlations to identify the cues that animals use to select retreat-sites (Hertz *et al.* 1994; Schlesinger & Shine 1994; Downes & Shine 1998b; Stow 1998; Webb & Shine 1998).

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The present study describes a laboratory-based experimental investigation of the cues used for diurnal retreat-site selection by a large nocturnally active gekkonid lizard, the thick-tailed gecko *Nephrurus milii* from southern Australia. These lizards typically spend daylight hours inactive under loose surface rocks. Their habitats usually contain an abundance of rocks that encompass a very wide range of physical attributes (Huey *et al.* 1989; Kearney 2002). Field surveys confirm that the rocks used as retreat-sites by thick-tailed geckos differ significantly from a random sample of available rocks in attributes such as rock size and thermal profiles in retreats (Shah 2002). Hence, we predicted that the lizards would exhibit non-random selection among alternative retreat-sites in the laboratory. Previous studies have suggested that the two most important aspects of a diurnal shelter-site for such a species are (i) protection from predators (Downes & Shine 1998a); and (ii) access to relatively high body temperatures that are generally unavailable to these nocturnal lizards during their foraging period (Huey *et al.* 1989; Schlesinger & Shine 1994; Downes & Shine 1998a; Webb & Shine 1998; Kearney & Predavec 2000; Kearney 2002). Thus, we focused on attributes of shelter-sites likely to influence those factors.

METHODS

Study species

Nephrurus milii are nocturnal terrestrial lizards. They are widely distributed across southern Australia from the east to the west coast (Cogger 2000). The lizards are found in a variety of macrohabitats from wet coastal heathlands and sclerophyll forests to arid scrublands and rocky hills (Swan 1990; Cogger 2000). Within these areas, they are usually found inactive during daylight hours under slabs of rock, in burrows and beneath loose bark (Swan 1990; Johnstone & Werner 2001). A detailed analysis of retreat-site use at our study site revealed that the rocks sheltering thick-tailed geckos were larger and more thermally stable than nearby (available but unused) rocks (Shah 2002). The geckos feed primarily on insects, spiders and scorpions but also take smaller lizards of other species (Cronin 2001). Thick-tailed geckos are large geckos; juvenile lizards in the present study ranged from 39 to 55 mm snout-vent length (SVL; 1.0–4.0 g), and adults ranged from 63 to 88 mm SVL (5.1–14.2 g).

Data collection

We collected 103 animals from Mount Korong (36°45'S, 144°17'E) in Victoria, approximately 250 km

north-west of Melbourne (Australia) in July 2001. The lizards were transported to the University of Sydney where they were maintained either in pairs or individually in plastic boxes measuring 220 mm × 220 mm × 70 mm (for paired juveniles and solitary adults) or 290 mm × 215 mm × 65 mm (for paired adults). Heating tape running beneath the back of each cage provided a thermal gradient from 20 to 29°C during daylight hours. At night the heating tape was switched off, allowing the cage to cool to room temperature (20°C). Two shelter-items (half plastic pipe: diameter 5 cm, length 12 cm) were provided within each cage. Crickets were provided twice weekly as food, and water was available *ad libitum*.

For habitat selection trials, our experimental units were halves of plastic boxes (each measuring 360 mm × 280 mm × 195 mm). The room was maintained at 20°C; photoperiod was 07.00–20.00 hours. Opaque covers with nine ventilation holes (diameter 5 mm) over each bin eliminated extraneous visual cues. Two shelters in each experimental unit (both consisting of the gaps between two ceramic tiles) differed with respect to a single trait as described below. Ceramic tiles (11 cm × 11 cm; 11 mm thick) at opposite ends of the unit provided substrates for shelters, with sand covering the substrate to the same height as the tile (11 mm). Tiles also formed the upper part of each shelter. Crevice height was 12 mm (just wide enough to allow ingress by geckos) for all experiments unless stated otherwise.

For each experiment, we used 50 geckos (26 juveniles, 12 adult males and 12 adult females), chosen randomly from the available 103 captive animals (60 juveniles, 24 adult males and 19 adult females). Only one gecko was placed in each experimental unit at a time. Where two different shelter-types were used, the positions (left or right) of these were also randomized, as was the order in which the animals were put into the experimental units.

Experiments were conducted between August and November 2001. Animals were placed in the experimental units between 16.00 and 19.30 hours, left overnight and removed between 08.30 and 11.00 hours the following morning, at which time we noted each lizard's location. If a gecko had not selected a shelter at this time, it was excluded from the results. Animals were given at least one night's rest between successive experiments, and each gecko was only used once per experiment. Following each experiment, all tiles were soaked in hot soapy water for a minimum of 30 min. They were then vigorously scrubbed, soaked for another 30 min in hot water, rinsed and air-dried.

Data on shelter-site use were analysed using contingency-table tests. Preliminary analyses revealed no significant differences in shelter-site selection by juveniles, adult females or adult males, so all data were pooled and total numbers only are reported. Because

some animals were used in more than one trial (to test different variables), we adopted the conservative approach of applying sequential Bonferroni corrections across the seven tests (one per variable; Hurlbert 1984; Cabin & Mitchell 2000).

We conducted seven separate experiments to test the role of various shelter characteristics in retreat-site selection. These attributes were as follows.

Crevice height

This experiment provided a choice between a crevice barely high enough for the lizard to squeeze into (8 mm for juveniles, 12 mm for adults, based on preliminary trials) versus a wider crevice that they could enter easily (12 mm for juveniles, 18 mm for adults).

Thickness of overlying rock

Shelters consisted of either three tiles or one tile above the crevice (i.e. 33 vs 11 mm thickness of overlying rock).

Crevice size

The large shelter was constructed of two substrate plus two shelter tiles placed side by side (22 cm × 11 cm), whereas the small shelter remained the same as in previous experiments (11 cm × 11 cm).

Slope of crevice

The substrate of one crevice was set at a slope of between 35° and 40°, with the other horizontal as in previous trials.

Crevice thermal regime

Thermal film (140 mm wide, 65 W m⁻¹, Thermofilm Australia Pty Ltd) was laid under half the shelters (one per unit), and the room temperature reduced to 16°C. Substrate tiles on the thermal film were maintained at 25–30°C (as measured by an infrared thermometer), with the unheated tiles at 16–19°C.

'Protected' crevice

We offered geckos shelter-sites that differed in the degree of concealment (i.e. visual exposure) of a lizard within a crevice by covering the gap beneath one shelter in each experimental unit on three and a half sides with strips of cardboard, leaving an opening of 5.5 cm at the front of the shelter. The other shelter was left with all sides uncovered, as in previous experiments.

Predator-scented crevice

Common blacksnakes (*Pseudechis porphyriacus*, Elapidae) are broadly sympatric with thick-tailed

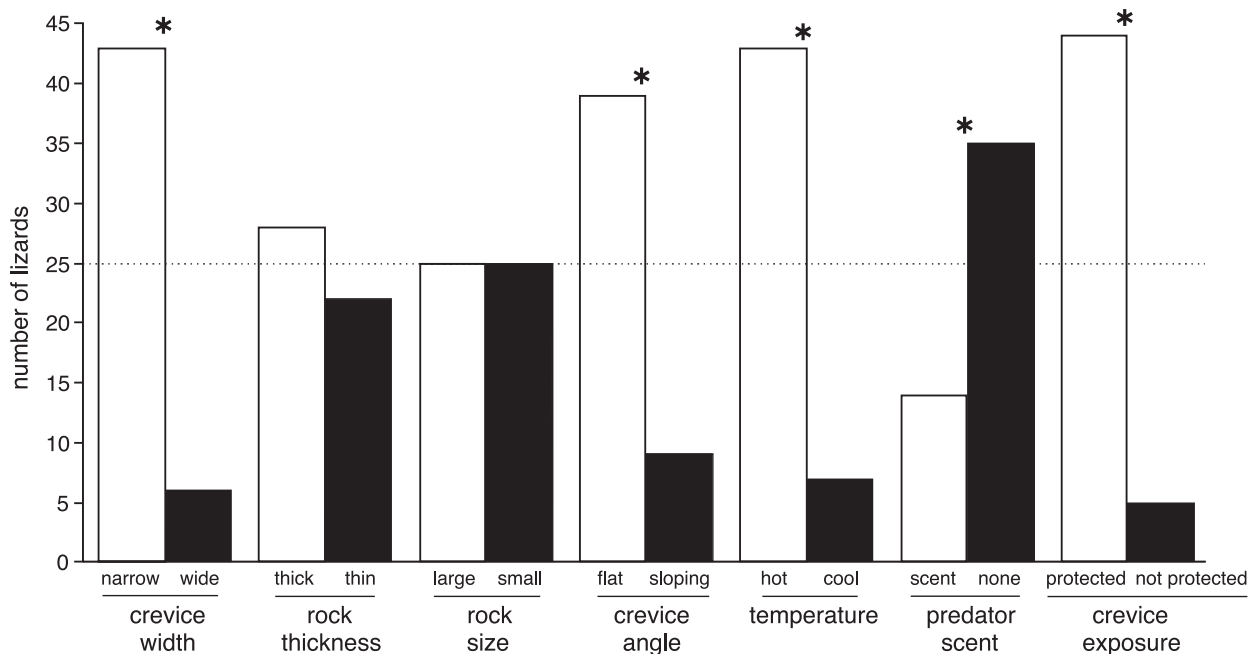


Fig. 1. Shelter-site selection by thick-tailed geckos (*Nephurus miltii*) in laboratory trials. The histograms show the number of lizards (of a total of 50 per trial) selecting each of two types of available crevices. Within each trial, these two crevices differed in a single aspect, such as crevice thickness or temperature. In a few trials, one gecko did not select either retreat, and thus sample size was 49 not 50. The horizontal dotted line at $n = 25$ shows the expected frequencies (equal in the two crevice types) if no selection was apparent. Asterisks show significant results ($P < 0.05$ after sequential Bonferroni corrections across the seven tests, with one per variable).

geckos in southern Australia (Cogger 2000) and consume a wide variety of lizards, including geckos (Shine 1977, 1999). Substrate tiles were exposed to snake scent by placing them inside the cage of a captive snake for seven days. Tiles used as the tops of the shelters were unscented, to mimic field conditions. The alternative shelter-site was unscented.

RESULTS

Our thick-tailed geckos were highly selective for five of the seven shelter item traits that we examined (Fig. 1). Geckos exhibited statistically significant preferences for narrow rather than wide crevices ($\chi^2 = 26.47$, degrees of freedom (d.f.) = 1, $P < 0.0001$ prior to Bonferroni correction); horizontal rather than sloping shelters ($\chi^2 = 18.75$, d.f. = 1, $P < 0.0001$); warmer rather than cooler shelters ($\chi^2 = 25.92$, d.f. = 1, $P < 0.0001$); and 'protected' rather than 'unprotected' shelters ($\chi^2 = 31.04$, d.f. = 1, $P < 0.0001$). The lizards also showed significant avoidance of predator scent ($\chi^2 = 9.00$, d.f. = 1, $P < 0.0005$). No preference was evident for the other two aspects of shelter-sites that we manipulated (thicker rather than thinner roofs, $\chi^2 = 0.72$, d.f. = 1, $P > 0.30$; larger rather than smaller shelters, $\chi^2 = 0.00$, d.f. = 1, $P > 0.99$; Fig. 1). Application of sequential Bonferroni corrections did not modify any of the above conclusions (all significant P -values remain < 0.05).

DISCUSSION

Previous studies on two other species of gekkonid lizards concluded that these animals are highly selective with respect to the attributes of their diurnal retreat-sites (Schlesinger & Shine 1994; Downes & Shine 1998b; Stow 1998). Our study further supports the notion that saxicolous nocturnal gekkonid lizards can evaluate a range of physical characteristics of potential retreat-sites, including crevice height, presence of predator scent, gradient of substrate, temperature within shelter and degree of cover or protection around the shelter. Most of the attributes that thick-tailed geckos selected in the present experimental trials might be related to (i) the degree of protection from predators available in alternative crevices; or (ii) opportunities for behavioural thermoregulation within crevices (Schlesinger & Shine 1994; Downes & Shine 1998b; Kearney 2001). This explanation is consistent with the following results.

Crevice height

Thick-tailed geckos showed a strong preference for narrow shelters (just large enough for them to fit into)

rather than wider crevices. Other saxicolous gecko species (southern leaf-tailed geckos, *Phyllurus platurus*, and the velvet gecko *Oedura lesueurii*) also select narrow rather than wide crevices (Schlesinger & Shine 1994; Doughty & Shine 1995; Stow 1998). Narrower crevices might reduce access by predators.

Thickness of overlying rock

Geckos did not show any preference for a thick-roofed rather than a thin-roofed shelter. Field studies at Mount Korong similarly revealed no selection of thicker- or thinner-roofed crevices by marbled geckos in spring or summer (Kearney 2002). In contrast, biophysical models and empirical studies of the thermal properties of rocky retreat-sites show that thickness is the most influential linear dimension of a rock in terms of heat transfer (Huey *et al.* 1989; Webb & Shine 1998; Kearney 2002). Variance in thermal conditions among rocks of different thickness at Mount Korong might be too low compared with the thermal variation within a large rocky crevice for retreat-site selection to be an effective thermoregulatory mechanism in spring (Kearney & Predavec 2000; Kearney 2002). In addition, during summer, most rocks are too thin to provide protection from overheating (Kearney 2002). At this time of year, some marbled geckos shelter under larger or shadier rocks, but most lizards move into crevices (Kearney 2002). Similarly, most thick-tailed geckos spend summer in deep crevices or rabbit burrows rather than under rocks (M. Kearney, unpubl. data).

Crevice size

Geckos did not show any preference for large over small shelters. This result is contrary to shelter-site usage by these geckos in the field, where they select larger rocks than those used in our trials (Shah 2002). Similarly, a previous laboratory study documented a significant preference for larger shelters in *O. lesueurii* (Schlesinger & Shine 1994). However, the shelters offered in that study were larger than in the current experiment. Once rocks reached a certain size, velvet geckos showed no preference for those that were larger still (Schlesinger & Shine 1994). These results suggest a threshold in rock size preference by geckos.

Slope of crevice

The geckos in the present study preferred horizontal shelters rather than sloping shelters. In the field, thick-tailed geckos are frequently found sheltering under rocks in areas that are sloping, often steeply (pers.

obs.). This slope could provide enhanced drainage or microclimatic conditions. However, our results suggest that the geckos' use of such rocks might be a secondary consequence of the availability of suitable rocks in sloping areas. By contrast, *O. lesueurii* are found in both horizontal and vertical crevices in the field and showed no preference for either in the laboratory (Schlesinger & Shine 1994). This lack of preference by velvet geckos could reflect their greater ability to cling to vertical surfaces as a result of their adhesive toe-pads (lacking in thick-tailed geckos).

Crevice thermal regime

Thick-tailed geckos actively selected warm rather than cold retreat-sites. This behaviour allows the geckos to attain the high body temperatures they require for physiological processes such as digestion. Such temperatures are normally unattainable during nocturnal foraging (Autumn & DeNardo 1995). Higher temperatures could also enhance the lizards' ability to avoid predators (Downes & Shine 1998b). Field studies at Mount Korong showed that geckos were found in rock crevices with relatively stable thermal regimes, but that average temperatures were no higher in occupied than in unoccupied crevices (Shah 2002). However, complex covariation among traits such as rock sizes and thermal regimes confound any straightforward interpretation of such patterns in terms of cues for habitat selection. By minimizing confounding factors of variation, the present laboratory study confirms that hotter crevices are more attractive to lizards.

In the field, the thermal conditions beneath rocks of different size and shape within the range used by thick-tailed geckos during spring generally converge well before dawn (Kearney 2002). Nonetheless, thermal variation among retreat-sites extends through the first few hours after dusk, which is the peak period of activity for many geckos (Bustard 1967, 1968; Schlesinger & Shine 1994), including thick-tailed geckos (pers. obs.). At this time, large thick rocks experiencing full sun during the day would provide warmer environments than small thin rocks because of the greater thermal mass and thus slower rate of heat gain and heat loss (Huey *et al.* 1989; Kearney 2002). In this sense, the thermal conditions beneath rocks early in the evening could provide important information about the thermal properties of a retreat-site in addition to the physical dimensions of the rock, because shading by vegetation and boulders also strongly influences the thermal regime of a retreat-site. We predict the use of temperature as a cue for retreat-site selection by these geckos would depend on (i) the physical characteristics of the retreat, because a rock that is cool at night could have been very warm or very cool during the day

depending on whether it was a small rock in full sun or a large rock in full shade; and (b) the time of year, because under the extremely seasonal environment of Mount Korong a lizard might seek rocks that reach relatively low daytime temperatures in summer or relatively high daytime temperatures in winter (Kearney & Predavec 2000).

'Protected' shelter

Thick-tailed geckos showed a strong preference for retreat-sites where the lizards were more effectively concealed. Forty-four of 49 individuals chose these protected shelters over less protected ones. Such a choice could have survival advantages to the lizard. If the opening to the retreat-site is small, then a predator might be less likely to encounter it, or to be able to enter. Additionally, less light penetrates such a shelter and the lizard might therefore be less likely to be detected visually by diurnal predators. For example, in one study, garden skinks (*Lampropholis guichenoti*) exposed to predator scent (small-eyed snake, *Cryptophis nigrescens*) remained in open areas for shorter periods, preferring 'safer' covered microhabitats (Downes 2001). Such a shelter might also provide additional benefits, including protection from wind and rain.

Predator-scented crevice

Oedura lesueurii and western banded geckos (*Coleonyx variegatus*) are both able to detect predators using chemical cues (Dial *et al.* 1989; Downes & Shine 1998a). Avoidance of predators is a higher priority than thermoregulation or social cues for retreat-site selection by velvet geckos (Downes & Shine 1998a,b). Similarly, the presence of predator scent under a shelter resulted in avoidance of that shelter by thick-tailed geckos in the present study. Avoiding areas used by predators confers obvious survival advantages to the geckos.

CONCLUSIONS

Our results show that thick-tailed geckos are highly selective with respect to their shelter-sites. These lizards exhibited a strong preference for warm, narrow, horizontal, protected shelters that did not contain the scent of a predator, but the lizards did not select shelters on the basis of size or thickness of overlying rocks. Our data add to the expanding evidence that small ectotherms base their retreat-site selection on complex abiotic and biotic cues in ways that plausibly enhance fitness.

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