Anim. Behav., 1998, **55,** 1387–1396

Heat, safety or solitude? Using habitat selection experiments to identify a lizard's priorities

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*(Received 29 April 1997; initial acceptance 29 July 1997;
final acceptance 25 September 1997; MS. number: 5526)*

Abstract. Laboratory experiments with a rock-dwelling nocturnal gecko, *Oedura lesueurii*, showed that retreat-site selection (and other behaviours) are affected by the interplay between thermal benefits, social advantages and avoidance of predators. Velvet geckos were highly selective in habitat choice: they preferred artificial retreat-sites that mimic the thermal properties of natural rocks in full sun rather than those that mimic rocks in full shade; mature male geckos rarely shared retreat-sites with other adult males; and these lizards strongly avoided retreat-sites covered with the scent of a natural predator (the broadheaded snake, *Hoplocephalus bungaroides*). After documenting these preferences, we carried out additional trials in which two or more of these factors co-occurred, as is often the case in nature. Social dominance interacted with thermal benefits in determining retreat-site selection, with smaller (subordinate) males forced to use cooler retreat-sites when larger (dominant) males were present. Avoidance of predators was a higher priority than thermoregulation: the lizards would forego a warmer retreat-site with predator scent in favour of a cooler, unscented one. There was also an interplay between social dominance and predator scent: smaller males were forced to use either predator-scented retreat-sites or no retreat-site when larger males were present. General activity levels, and the frequencies of specific behavioural acts, also shifted in response to social and predator-scent cues. Our study emphasizes the complexity of habitat-selection behaviour in these lizards, and clarifies the criteria used in retreat-site selection when (as is commonly the case) the animal must choose between conflicting priorities.

Animals usually face a number of important, yet conflicting demands during the course of a day. Among these, predator avoidance is obviously of prime importance but many animals must also seek out habitats with very specific thermal attributes (e.g. Gates 1975; Huey 1982) in order to regulate their body temperatures (e.g. Davies 1978; Huey et al. 1989; Webb 1996). Selection of thermally suitable retreat-sites may be particularly important for ectotherms because the behavioural and physiological processes of these animals depend strongly on temperature (see Huey 1982 for a review). In selecting such habitats, individuals interact socially with conspecifics and other animals that live near their home range (e.g. Kaufmann 1974; Stamps & Tanaka 1981), and often defend this resource (e.g. Buss 1990; Marler et al. 1995).

The importance of these three factors (i.e. thermal preferences, social interactions, predator avoidance) for habitat selection has been amply demonstrated in several studies, but generally only one of these factors has been considered at a time (see below). For example, speckled wood butterflies, *Pararge aegeria*, seek out ground layer woodland habitats that are exposed to direct sunlight rather than those that are shaded (Davies 1978); in an arid woodland habitat, male orb-weaving spiders, *Araneus diadematus*, defend their home range from conspecifics and other animals, and the heavier contestant usually wins (Hammerstein & Riechert 1988); fry of pink salmon, *Oncorhynchus gorbuscha*, reduce their use of profitable open-water feeding areas when they can see potential predators in an adjoining aquarium (Magnhagen 1988). A few studies have

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0003–3472/98/051387+10 $25.00/0/ar970705

investigated the interplay between habitat quality and predation risk (e.g. Kotler 1985; Gilliam & Fraser 1987), but were unable to examine concurrently the influence of social interactions on habitat selection. In practice, all three factors co-occur, so that an animal's choice of a retreat-site reflects a set of decisions that give priority to certain factors (e.g. social advantages, predator avoidance) over others (e.g. thermoregulation).

Nocturnal gekkonid lizards provide an ideal model system in this respect. Thermoregulatory behaviour within diurnal retreat-sites is common (e.g. Dial 1978; Werner & Whitaker 1978; Schlesinger & Shine 1994), and individuals usually select shelter-sites that attain suitable temperature ranges (Huey 1982; see below). In addition, exclusive retreat-site occupancy by males (i.e. only one adult male per shelter site) and aggression between individuals (e.g. Bustard 1968a, b, 1970, 1971; How & Kitchener 1983; Schlesinger & Shine 1994) imply the existence of home-site defence for many gekkonid lizards, and larger individuals are likely to dominate smaller conspecifics (see Stamps 1977; Stamps & Tanaka 1981; see below). Finally, several species of gecko react strongly to the scent of snake predators (e.g. Dial et al. 1989; Downes & Shine 1998), and, for at least one species (velvet gecko, *Oedura lesueurii*), the scent of a predatory snake invokes strong avoidance of otherwise favourable retreat-sites (Downes & Shine 1998). However, although these phenomena have been demonstrated in isolation, the responses of geckos to several conflicting priorities have not been studied previously.

In this paper, we describe the results of a series of laboratory studies on the velvet gecko to investigate how retreat-site selection is affected by the interplay between thermal benefits, social advantages and avoidance of predators. We first confirmed that solitary male lizards consistently prefer retreat-sites that mimic the thermal properties of natural rocks in full sun rather than those that mimic rocks in full shade. Next, we examined shifts in their behaviour when the warm shelter was covered with the scent of a predatory snake, but the cooler shelter was unscented. We then repeated the experiments using two male geckos that differed considerably in body size to investigate the influence on retreat-site selection of the interplay between thermal benefits and social advantages, and how these behaviours vary when the retreat-sites differ in predator scent cues.

MATERIALS AND METHODS

The Study System

The velvet gecko is a small (in our population, up to 60 mm snout–vent length) nocturnal lizard which occurs in rocky outcrops from northeastern Queensland to southeastern New South Wales in Australia (e.g. Cogger 1957; Swan 1990). During the day, these terrestrial geckos remain in diurnal retreat-sites beneath sandstone boulders (Schlesinger & Shine 1994; Webb 1996). They emerge to forage at nightfall, and assess a wide range of thermal, social and chemical aspects of potential shelters before selecting suitable retreat-sites for the following day (Schlesinger & Shine 1994; Downes & Shine 1998; see below). Natural rock crevices vary considerably in thermal properties depending on their size, position and degree of shading (Webb 1996). Mature males rarely (if ever) share the same diurnal retreat-site, although many are found under adjacent rocks in the wild (Schlesinger & Shine 1994). In addition, they assess potential retreat-sites for the presence of a natural predator, the broadheaded snake, *Hoplocephalus bungaroides*. Broadheaded snakes are small (on average, up to 600 mm snout–vent length), saurophagous, rock-dwelling elapids which occur sympatrically with velvet geckos over some of their range. Like the lizards, the snakes are nocturnal, spend the day in rock retreat-sites, and rely heavily on sandstone crevices for shelter during much of the year (Webb 1996; Webb & Shine 1997a). Broadheaded snakes feed heavily on geckos, which they ambush inside crevices at night (Webb 1996; Webb & Shine 1997b), and we have shown previously that velvet geckos distributed sympatrically with broadheaded snakes strongly avoid retreat-sites that are covered with the scent of this snake (Downes & Shine 1998).

Animals and their Maintenance

In August 1996, we captured 30 adult male geckos (mean snout–vent length = 49.9 mm, mass = 3.2 g) and two broadheaded snakes (620.3 mm, 115.2 g) by hand from Sassafras in southern near-coastal New South Wales, Australia (35°04′S, 150°19′E). We verified that the geckos were adult from the gonads; the enlarged testes of adult males are easily discernible through the ventral skin of this species. Sassafras is a sandstone outcrop surrounded by dry sclerophyll forest about 160 km south of Sydney, in Morton National Park, where velvet geckos and broad-headed snakes are locally abundant (Webb 1996). We housed the geckos and snakes at the University of Sydney in separate temperature-controlled rooms maintained at 17°C. The light cycle was the natural cycle of the surrounding area, and all of the animals were provided with a heat source between 0800 and 1600 hours. The lizards were kept in individual plastic cages (22 × 13 × 7 cm), which were covered with a substrate of commercial potting mix (to a depth of 1 cm) and contained a sandstone shelter, and fed mealworms and crickets once a week. The snakes were maintained individually in identical plastic tubs (62 × 41 × 28 cm), the floor of which was lined with paper. A shelter was positioned at each end of the tub, and the constituent portions of this shelter were used in our experiments (see below). Each shelter measured 20 × 20 × 1.5 cm, and was made from two layers of unglazed sandstone slabs (two abutting slabs of 20 × 10 × 1.5 cm slabs), separated vertically by squares of plastic sheet 1 mm thick (20 mm^2). We varied the thickness of the crevice to ensure that each snake made contact with both the upperside of the bottom slab and the underside of the top slab. To ensure that the snake used both retreat-sites within its cage, we moved the heat source (one 75-W bulb) over one or other shelter several times throughout the day; the snake would typically follow. Snakes were fed dead laboratory mice every 10 days, and soiled slabs were not used in the trials. All of the animals were supplied with water ad libitum.

In contrast to our earlier study (Downes & Shine 1998), we were able to capture mature broadheaded snakes that we could maintain in the laboratory for long-term studies by training them to feed on culled food items (dead mice). This can be difficult to achieve without disturbing the snake. To minimize this, we propped up one end of the rock shelter, held a fresh dead mouse (humanely culled) in front of the crevice using forceps and moved it vigorously until it was taken. It took several weeks of training for the snakes to feed without being disturbed from their site and becoming aggressive, but this avoided the need to feed them live prey items and allowed us to maintain the two snakes in our laboratory for future studies.

Experimental Procedure

Our experiments were conducted in large plastic tubs (62 × 41 × 28 cm), and recorded on videotape. We positioned eight of the tubs side-by side, in two rows of four, inside a temperature-controlled room (maintained at 17°C) devoid of other animals. To prevent overheating (see below), a plastic section (20 × 10 cm) from the end of each tub was replaced with fine wire mesh. A low-light Panasonic video-camera was positioned directly above, and connected to a National AG6010 time-lapse video cassette recorder (set to take one frame per s) and monitor. Four portable lights were taped to the ceiling above the arena: three were fitted with clear 100-W globes and connected to a gradual light dimmer designed to simulate artificial dusk and dawn over a 20-min period (see also Graham & Hutchinson 1977), and the fourth (a 25-W red globe) was used to aid recording.

During mid-afternoon, we constructed a retreat-site (20 × 10 cm) at each end of each tub using two slabs (20 × 10 × 1.5 cm) separated vertically by plastic squares 1 mm thick (20 mm^2). We staged two separate retreat-site selection experiments using solitary and paired geckos, and we hereafter refer to these as: (1) cold versus warm and unscented; and (2) cold versus warm and scented. Both slabs making up a cold or a warm and unscented retreat-site, and the top layer making up a warm and scented retreat-site, had been used previously in a trial but had been thoroughly washed (see below). The bottom slab of a warm and scented retreat-site had been in a broad-headed snake cage for 24 h. Both of the warm retreat-sites were heated with an electric heating board (16 × 60 cm) placed underneath each tub in line with the slabs. Three hours before the start of an experiment, we switched the board on and heated the warm rocks to 37°C (to simulate the operative environmental temperature of retreat-sites preferred by the geckos in their natural environment: see Webb 1996). At 1700 hours, we reduced the rock temperature to 25°C (using a dimmer switch), and then decreased it by 2°C every 2 h thereafter until 2300 hours when we set the temperature to 17°C. The heating board was automatically switched off at midnight, and on at 0630 hours the following morning. Temperatures within the warm retreat-sites (monitored using thermocouples) accurately simulated thermal regimes recorded during spring for similar-sized rocks in full sun in the geckos' natural environment (see Webb 1996). The cold retreat-sites were maintained at room temperature (17°C) which closely mimics those recorded for similar-sized rocks in full shade (see Webb 1996). Thus, we created artificial crevices that were cold (to mimic a natural crevice in full shade), warm and unscented (to mimic a natural crevice in full sun and not occupied by a predatory snake), and warm and scented (to mimic a natural crevice in full sun and occupied by a predatory snake).

We measured the snout–vent length (mm) and mass (g) of each lizard 1 week before conducting the experiments. Length and mass were highly correlated (Pearson's correlation coefficient = 0.824), and we divided the lizards into two body size classes (large, $N=15$, $\bar{X} \pm \mathrm{SE} = 57.5 \pm 0.3$ mm; small, $N=15$, $\bar{X} \pm \mathrm{SE} = 42.3 \pm 5.2$ mm), and ranked each lizard according to size. For the experiments using two male geckos, we paired a lizard from the large size class with a lizard from the small class that had the same rank (e.g. the largest lizard from the large size class was paired with the largest lizard from the small size class). On average, lizards from the large body size class were 15% longer (and heavier) than their partner.

Late in the afternoon, we placed a gecko under a small temporary rock in the centre of the tub, and a transparent plastic cage on top of the rock so as to enclose it, thereby preventing the gecko from haphazardly selecting a retreat-site. For the experiments with two geckos, two rocks and two cages were available, and the same procedure was adopted. Ten minutes before the artificial dusk (around 1800 hours), we activated the video camera, removed the cage, and fastened a clear plastic lid to the tub. Once all of the animals were active, we slowly dragged the temporary rock(s) to the side of the tub (by pulling an attached string that had been fed through a hole in the top of the tub) and raised it until vertical. We left the lizards undisturbed until the following morning when we removed them and recorded their retreat-site selection (final retreat).

A previous study (Schlesinger & Shine 1994) and pilot tests (matching geckos of different body sizes under continuous observation) showed that the geckos could be left together safely in our experimental arenas overnight. Our enclosures were large and contained ample shelter. Aggressive encounters typically lasted no longer than a few seconds, and subordinate individuals were always able to escape from conspecifics either by seeking shelter in a sub-optimal retreat-site, or fleeing to the opposite end of the enclosure. Attacks usually occurred within the first hour of the trial, after which time the level of aggressive encounters was significantly reduced. No injuries were sustained and few, if any, repeated attempts to escape were recorded.

After each trial, all of the rocks were soaked for 2 h in hot soapy water, vigorously scrubbed, soaked for a further 30 min in hot water, scrubbed, and then rinsed and air-dried. We have previously confirmed the efficacy of this cleaning method for removing the scent of snake and velvet gecko from the slabs (see Downes & Shine 1998). After this procedure, a slab from the bottom of a warm and scented retreat-site became available for use as a slab for either a cold or warm retreat-site, or the top layer of a warm and scented retreat-site.

We performed the experiments in random order between 26 October and 6 November 1996. Each lizard was tested once in each of the four experiments, with a minimum of 48 h between trials. The order in which animals were tested was always random, as was the selection of the slabs that made up each crevice. From the videotapes, we noted: (1) the initial retreat-site selected by a gecko (first retreat); (2) the number of times a gecko entered each crevice (times entered); (3) the number of lizards displaying the tail-flick behaviour (the arching of the tail from a horizontal to a vertical position, with slow undulation; tail-flick); (4) the number of times the gecko entered one half of the tub (activity); and (5) the amount of time the gecko spent under each retreat-site throughout a trial (timing ceased once the animal had chosen its final retreat-site). For (5), we calculated the proportion of time that an animal spent within the cold retreat-site (time) as a percentage of the total time the gecko spent in either crevice, but timing ceased once the animal had chosen its final retreat. For the experiments with two males, we also recorded the number of times a gecko was: (6) forced by a conspecific to abandon a secured retreat-site (displaced); (7) prevented (usually by chasing) from entering a retreat-site by a conspecific (attempted entry); (8) directly attacked (usually bitten and wrestled) by a conspecific (attacked); and (9) chased for more than half a length of the tub by a conspecific (chased).

For final retreat and variables (1), (2), (6) and (7), we scored the number of geckos with a greater response in one direction versus the other. For variables (3), (8) and (9) we scored the number of lizards that displayed or was subjected to the behaviour during a trial. We separately analysed the data for solitary and paired males using chi-square two-way contingency tables (with experiment and response or number of geckos as factors), and chi-square goodness-of-fit tests (separately for each experiment). We then analysed separately the data from each experimental treatment to examine variation in the retreat-site selection (and other) behaviours of solitary and paired lizards. We used split-plot ANOVA to examine, separately for solitary and paired geckos, the variation in the activity and time behaviours displayed by large and small lizards in the different experiments, and the variation in the activity and time behaviours displayed by solitary and paired lizards in the same experimental treatment. Null hypotheses were rejected at the 95% confidence level for all of the statistical tests.

RESULTS

The retreat-site selection and behavioural responses of solitary male geckos differed markedly between the two experiments (Fig. 1). In the absence of both a male conspecific and the scent from a predatory snake, geckos showed strong and consistent preferences for retreat-sites that were heated to mimic natural rocks in full sun (Table I). Indeed, under these circumstances, geckos always chose the warm retreat-site as a diurnal shelter, entered the warm retreat-site more often than the cold retreat-site, and selected the warm retreat-site in the first instance (Table I). When the warm retreat-site was covered with the scent of a broadheaded snake, however, retreat-site selection behaviours were reversed: the solitary males usually preferred the cold retreat-site in both the first and final instance, and usually entered the warm and scented retreat-site less often than the cold retreat-site (Table I). Solitary geckos displayed the tail-flick behaviour only upon approaching warm retreat-sites covered with the scent of broadheaded snake (Table I). The retreat-site selection behaviours of geckos did not vary significantly between large versus small individuals for any of the trials in which these lizards were solitary ($\chi^2_1<1.03$, NS for all possible combinations).

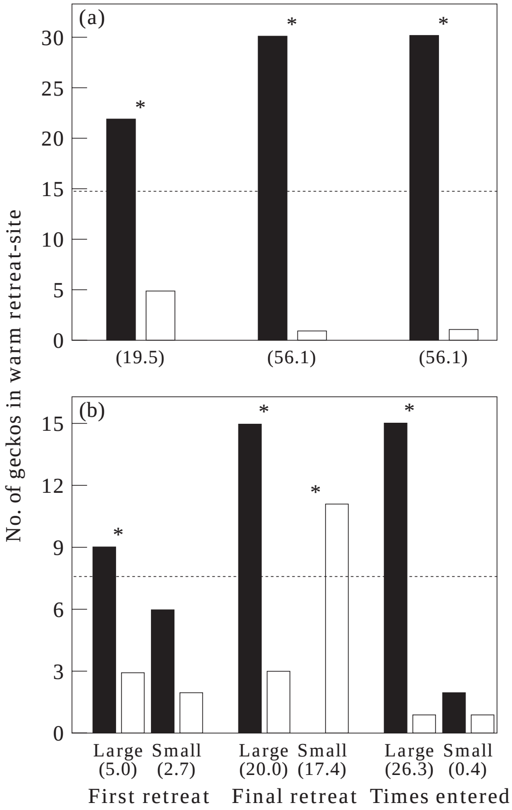

Figure 1. The retreat-site selection behaviours of (a) solitary ($N=30$ males) and (b) paired ($N=15$ pairs of large with small males) velvet geckos in the two experimental situations. ■: Choice between cold, unscented and warm, unscented retreat-sites; □: choice between cold, unscented and warm, predator-scented retreat-sites. The number of lizards showing a bias in response towards the warm retreat-site are shown. The dotted line indicates the number of geckos expected in each retreat-site according to chance. An asterisk above the histograms indicates a significant interaction ($P<0.05$) as indicated by two-way chi-square contingency tables (with experiment and retreat-site as factors), and chi-square values are given in parentheses under each variable. For (a), large and small males did not differ significantly in habitat-selection ($\chi^2_1<2.73$, NS, for all possible combinations).

Experiments using two geckos per trial gave very different results. All of the retreat-site selection behaviours of larger lizards varied markedly between the experiments with and without snake scent, whereas only the final retreat behaviour of

Table I. The behaviours displayed by solitary ($N=30$) and paired ($N=15$) male velvet geckos in the two experimental retreat-site selection situations

Behaviours	Cold versus warm and unscented			Cold versus warm and scented		
	Solitary male	Large male and small male		Solitary male	Large male and small male	
Initial retreat-site*	**8–22** (6.53, 0.01)	6–9 (0.60, 0.47)	9–6 (0.60, 0.47)	**25–5** (13.3, <0.01)	**12–3** (5.40, 0.02)	**13–2** (5.40, 0.02)
Diurnal retreat-site*	**0–30** (30.0, <0.01)	**1–14** (11.3, <0.01)	**14–1** (11.3, <0.01)	**29–1** (26.1, <0.01)	**12–3** (5.40, 0.02)	**3–12** (5.4, 0.02)
Entry into retreat-site*	**0–30** (30.0, <0.01)	**0–15** (15.0, <0.01)	**13–2** (8.1, <0.01)	**29–1** (26.1, <0.01)	**14–1** (11.3, <0.01)	**14–1** (11.3, <0.01)
Displacement from retreat-site*	—	0	4–11 (3.3, 0.08)	—	0	**14–1** (11.3, <0.01)
Attempted retreat-site entry*	—	0	**0–15** (15.0, <0.01)	—	0	**14–1** (11.3, <0.01)
Attacked by male conspecific	—	0	11–4 (3.3, 0.08)	—	0	**2–13** (5.4, 0.02)
Chased by male conspecific	—	0	**15–0** (15.0, <0.01)	—	0	10–5 (0.67, 0.44)
Tail-flick	0	**0–15** (15.0, <0.01)	**0–15** (15.0, <0.01)	12–18 (1.2, 0.24)	**12–3** (5.4, 0.02)	11–4 (3.3, 0.08)

For the retreat-site selection behaviours (*), the first line for each variable shows the number of lizards with a greater response in one direction or the other. For the remaining variables, the first line shows the number of lizards that displayed that behaviour versus the number that did not. Significant results ($P<0.05$) from goodness-of-fit tests are in bold, and chi-square and P-values are given in parentheses under each value ($df=1$).

the smaller males differed significantly (Fig. 1). Larger geckos were apparently dominant over the smaller geckos during both experiments. In the absence of snake scent, the larger lizards preferred to enter and seek shelter in the warm retreat-site rather than the cold retreat-site, resulting in the smaller lizards being restricted to the latter site (Table I). During the same experiment, lizards from both size classes usually chose their initial retreat-site at random, and never displayed the tail-flick behaviour (Table I). In contrast, geckos from both size classes consistently selected the cold retreat-site in the first instance during the trials incorporating the scent of snake; and larger lizards usually selected the cold retreat-site as a diurnal shelter, whereas the smaller lizards either did not select a diurnal shelter or used the warm and scented retreat-site (Table I). During both experiments, the smaller geckos rarely entered the warm retreat-site (Table I), and lizards from both size classes displayed the tail-flick behaviour only upon approaching scented rocks (Table I). The size class of the gecko had little influence on whether a lizard entered the warm retreat-site before its conspecific ($\chi^2_1<0.60$, NS).

Aggressive behaviours between males were evident during the experiments with two conspecifics (Table I). Aggression was always directed towards the smaller males, and the frequency of these behaviours during a trial varied significantly between the two experiments (see below). In the experiments with two males and no snake scent, smaller geckos attempted to enter, and were displaced from, the warm retreat-site more often than the cold retreat-site, and were always chased and usually attacked by the larger male (Table I). In the experiments with the scent of snake, the larger lizards attacked and chased their smaller conspecifics less often ($\chi^2_1>8.9$, $P<0.03$, for both behaviours), and smaller lizards attempted to enter and were displaced from cold retreat-sites more often than warm and scented retreat-sites ($\chi^2_1>13.9$, $P<0.01$, for both behaviours; Table I). Solitary geckos both reduced their level of activity and spent more time in the cold retreat-site during trials with the scent of snake (ANOVA: $F_{1,28}<64.25$, $P<0.01$), whereas only dominant geckos were less active and spent more time in the cold retreat-site during the paired trials with the scent of snake ($F_{1,28}=10.40$, $P<0.01$; Fig. 2). Geckos never shared retreat-sites during the paired encounters.

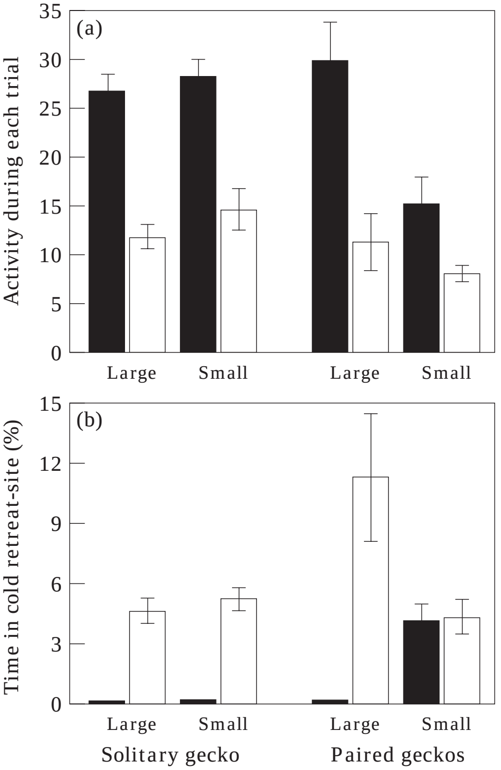

Figure 2. The mean ± SE (a) number of times that large and small male geckos moved into one half of the experimental arena and (b) the percentage of time they spent in the cold retreat-site. ■: Choice between cold, unscented and warm, unscented retreat-sites; ☐: choice between cold, unscented and warm, scented retreat-sites.

DISCUSSION

Our results clearly demonstrate that retreat-site selection (and other behaviours) of velvet geckos are affected by the interplay between thermal benefits, social advantages and avoidance of predators. Social dominance interacted with thermal benefits in determining retreat-site selection, with smaller (subordinate) male geckos forced to use cooler retreat-sites when larger (dominant) males were present. Avoidance of predators was a higher priority than thermoregulation for the lizards: they would forego a warmer retreat-site with predator scent in favour of a cooler, unscented one. There was also an interplay between social dominance and predator scent: smaller males were forced to use either predator-scented retreat-sites or no retreat-site when larger males were present.

General activity levels, and the frequencies of specific behavioural acts, also shifted in response to social and predator-scent cues (see below).

Our results are consistent with previous investigations that have examined separately the effects of thermal benefits, social interactions and predator avoidance on habitat selection by velvet geckos. For example, in two laboratory experiments, Schlesinger & Shine (1994) found that velvet geckos displayed thermoregulatory behaviours within retreat-sites, and adult males never shared retreats. In the same paper, they reported no preference by the geckos for warm versus cold retreat-sites; however this result probably reflects the low variation in thermal properties between the retreat-sites offered (Schlesinger & Shine 1994). In a similar study, we demonstrated (Downes & Shine 1998) that velvet geckos strongly avoid retreat-sites covered with the scent of the broadheaded snake, and we observed similar behaviours in the present study (see below).

Our results also accord with intuition, in that the criteria used by geckos to select retreat-sites and modify behavioural acts have a plausible linkage to fitness.

(1) Selection of warm (rather than cool) retreat-sites presumably raises metabolic costs (i.e. expenditure of energy and water), but simultaneously enhances the lizard's locomotor and sensory abilities (and hence, its ability to capture food and evade predation), facilitates processes such as digestion and gonadal maturation, and increases opportunities to monitor and defend territories (e.g. Schoener 1974; Congdon et al. 1979; see Huey 1982 for a review).

(2) Avoidance of retreat-sites containing the scent of predatory snakes confers obvious survival advantages. Broadheaded snakes are a major predator of velvet geckos, and sit and wait for up to 4 weeks at a time for prey to enter their retreat-site (Webb 1996). In the field, even a brief penetration into such a crevice is likely to have dire consequences for a gecko (see also Downes & Shine 1998).

(3) Agonistically enforced relegation of subdominant males to lower quality (cooler or more dangerous) retreat-sites may decrease a subordinate male's chances of surviving and mating. Physical competition for limited thermoregulatory sites is common in other systems, and may be a significant influence on an individual's reproductive success. For example, male speckled wood butterflies engage in spiral flights when competing for thermally optimal, ground layer, woodland habitats that offer high mating opportunities, and the winners invariably have a higher reproductive success (Davies 1978). However, we are not aware of any previous studies that have examined the three-way interplay between thermal benefits, social interactions and predator avoidance.

(4) The tail-flick behaviour (arching of the tail from a horizontal to a vertical position, with slow undulation) displayed by the majority of the geckos in response to the scent of broadheaded snake is likely to reduce a lizard's vulnerability to predation. Similar predator-specific displays have been reported in other species of lizard (e.g. *Lacerta vivipara*: Thoen et al. 1986; *Coleonyx variegatus* and *C. brevis*: Dial et al. 1989; *Eumeces laticeps*: Cooper 1990), and may function to redirect the predator's attack from the body to the tail (see Dial 1978; Vitt & Cooper 1986). Alternatively, tail waving may act as a stimulus for predators: it may be advantageous for the lizard to maintain movement, which would keep the predator in motion, while maintaining the head motionless so that it can detect movement (Magnusson 1996).

Most interesting, however, is the hierarchy among these potentially conflicting habitat-choice criteria. The clear result from our study is that predator avoidance takes precedence over thermoregulatory benefits, and that the form and intensity of intraspecific interactions between males is sensitive to both the physical environment (thermal heterogeneity between adjacent retreat-sites) and the lizard's perception of its relative vulnerability to predation in alternative retreat-sites. Again, this result accords well with intuition.

(1) The benefits of thermoregulation (in terms of performance, etc.) are unlikely to outweigh the costs (such as death) associated with using a retreat-site that is thermally optimal but contains a predator (see also Huey & Slatkin 1976).

(2) Reducing activity levels by remaining inactive within a thermally sub-optimal retreat-site is likely to lessen the chance of a gecko encountering a sit-and-wait predator such as the broadheaded snake. However, there is obviously a point beyond which such a tactic is disadvantageous; for example, hatchling Galapogos iguanas, *Conolophus pallidus*, that do not regulate their body

temperatures (and are therefore cold) are highly susceptible to predation by hawks (Christian & Tracy 1981).

(3) In particular, overt displays of social dominance between velvet geckos may be lessened in environments where the risk of predation is high. This reduction probably reflects the fact that aggressive behaviours increase the conspicuousness of a lizard to potential predators, and hence, its vulnerability to predation (see also Endler 1987; Ryer & Olla 1996).

We infer that these processes are also likely to be at work in the field also, and to substantially affect the retreat-site selection (and hence, spatial dispersion and survival rates) of different segments of the gecko population. The inference is clearest from the experiment in which we examined the simultaneous effects of all three factors (thermal, social and predator scent). Geckos maintained exclusive retreat-site occupancy during these trials, with dominant (larger) males forcing subordinates to select either a retreat-site covered with the scent of a predator, or no shelter-site at all. In the real world, both of these alternatives would undoubtedly increase the vulnerability of the subordinate geckos to predation: in the first instance, to broadheaded snakes, and in the second, to actively foraging predators (e.g. some birds of prey, centipedes, etc.). Consequently, the hierarchy of retreat-site selection criteria used by the lizards, combined with significant variation between retreat-sites in relevant traits (thermal opportunities, predation risk) is likely to impact directly on the survival rates of lizards of different body sizes. This kind of interplay between environmental characteristics (i.e. retreat-site availability), predator densities and social systems may well be both widespread and important in many natural populations.

ACKNOWLEDGMENTS

We thank V. Barclay, P. Borges and P. German for their field assistance, and J. Suckau for constructing the gradual light dimmer. D. Bauwens, M. Elgar, K. Handasyde, B. Kins, M. Lee, C. Midnight, E. Miller, J. Webb and P. Whitaker provided inspiration, and/or useful comments on this manuscript. J. Webb's elegant radiotelemetric studies provided the initial stimulus for our work. This project was approved by the Sydney University Animal Care and Ethics Committee; conducted under Research Permit B1646 issued by the NSW National Parks and Wildlife Service; and funded by an Australian Postgraduate Research Award (to S.D.) and the Australian Research Council (grant to R.S.).

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