

Antipredatory behaviour in lizards: interactions between group size and predation risk

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Group size effects on antipredatory behaviour are well documented in numerous animals, but little is known about how the level of predation risk influences this process. We tested the hypothesis that group size and level of risk interact to affect the levels of antipredatory behaviour in the group-living sun skink, *Lampropholis delicata*. We controlled the size of lizard groups ($N = 1, 2, 4, 8$ or 12 females) and altered predation risk by providing either a basking tile covered with chemical cues from a predator (high risk) or one without scent (low risk). The time allocated to individual antipredatory behaviour decreased significantly with increasing group size. The relation between group size and time allocated to individual antipredatory behaviour was nonlinear and asymptotic, and did not change under low and high risks of predation. However, group size and predation risk interacted to affect significantly the time that lizards allocated to antipredatory behaviour. When the overall risk from predators was high, individual responsiveness decreased strongly as group size became larger. In contrast, when the overall risk from predators was low, individual responsiveness decreased weakly as group size became larger. Consequently, the time that lizards allocated to antipredatory behaviour under different risks of predation converged as group size increased.

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Levels of individual responsiveness to predators decrease as a function of group size in many species of birds and mammals (reviewed in Elgar 1989; Quenette 1990; Bednekoff & Lima 1998; but for an exception see Hough et al. 1998). Individuals in larger groups are thought to invest less in antipredatory behaviour because aggregating with others may reduce predation risk by improving detection of predators or diluting risk (Lima 1990, 1995; Roberts 1996; Blumstein et al. 1999; Uetz et al. 2002). In some systems, however, the relation between group size and individual responsiveness may be modified by intraspecific competition for limited resources (see Grand & Dill 1999; Blumstein et al. 2001a).

Theoretical models and studies of how group size affects individual antipredatory behaviour have suggested that both detection and dilution effects should generate nonlinear and asymptotic relations between group size and the time allocated to antipredatory behaviour (e.g. Pulliam 1973; Jarman 1987; Dehn 1990; Blumstein et al. 1999; Grand & Dill 1999). For instance, dilution models assume that a solitary individual's risk of predation decreases by 50% with the addition of one other individual ($N = 2$), by

67% with the addition of two others ($N = 3$), by 75% with the addition of three others ($N = 4$), and so on. Thus, the amount of time devoted to behaviours that are sensitive to predation risk should vary nonlinearly with group size (reviewed in Blumstein et al. 1999). Linear relations between group size and time allocation may reflect the modification of such relations by intraspecific interference competition for limited resources, which would reveal a fundamental cost of sociality (Grand & Dill 1999; Blumstein et al. 2001a, b).

Although there are some noteworthy exceptions (Frid 1997; Grand & Dill 1999; Banks 2001), few empirical data exist about how predation risk influences group size effects. One scenario is that group size and predation risk interact to affect the levels of individual antipredatory behaviour (Frid 1997; see also Banks 2001). In this model, if the overall risk from predators is high, then responsiveness should increase strongly as group size becomes smaller. In contrast, if the overall risk from predators is low, then responsiveness should increase little or not at all as group size becomes smaller. An alternative, but less plausible, scenario is that the antipredatory response to group size has a constant magnitude, regardless of the level of predation risk (Frid 1997). In this model, the response to group size overemphasizes safety at the expense of other activities when the risk from predators is

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low, and overemphasizes other activities at the expense of safety when the risk from predators is high (Frid 1997). We would not expect natural selection to favour such independent relations.

Few studies of group size effects have focused on reptiles, yet numerous species of reptiles live in groups. Heliothermic reptiles are often faced with the conflicting demands of basking and avoiding predation. Thermoregulation is necessary for maximizing performance capacities and hence the rate of energy intake and growth (Pough 1980; Andrews 1982; Huey 1982). However, since the most productive basking sites may be in open areas that are frequented by predators, basking can also significantly increase a reptile's risk of predation (e.g. Formanowicz et al. 1991; Schwarzkopf & Shine 1992). Shuttling between sunlit and shaded areas may also make an individual more conspicuous to predators, and basking may result in a decrease in individual responsiveness, and, therefore, increase the risk of an undetected attack (see Schwarzkopf & Shine 1992 and references within). Therefore, in heliothermic reptiles the effects of group size may be especially important for antipredatory behaviour associated with basking.

Many studies reporting antipredatory behaviour and group size effects have been criticized because they did not control for potentially influential ecological factors and were conducted in the field on unknown subjects (for more information see Elgar 1989; Blumstein et al. 1999). Manipulating group size experimentally and under controlled conditions to study group size effects is therefore important (Elgar 1989). We describe such an experiment designed to examine how group size and predation risk interact to affect levels of individual antipredatory behaviour. Our study organism was a small group-living heliothermic lizard (sun skink, *Lampropholis delicata*; Cogger 1994). We controlled the size of lizard groups and recorded individual antipredatory behaviour associated with basking at a localized site. We manipulated predation risk by covering the basking area with integumentary chemicals from a common predator (white-lipped snake, *Drysdalia coronoides*; see Downes & Shine 1999). In performing this experiment we not only provided a rigorous test of how predation risk influences group size effects but also conducted one of the first controlled studies in reptiles of how group size affects behaviour.

METHODS

Animals and their Maintenance

Our study animals were sun skinks ($N = 78$, snout-vent length: $\bar{X} \pm \text{SE} = 38.4 \pm 0.92$ mm; mass: 1.89 ± 0.10 g) collected by hand in September and October 2001 from Sydney, NSW, Australia. Lizards were very abundant in our study area. Aggressive encounters in sun skinks are rare especially among females (Torr & Shine 1996). None the less, to reduce the potentially confounding effects of aggressive interactions among our study animals, we used only female lizards (Kaiser & Mushinsky 1985). Only adults were used because hatchlings usually mature in

1 year and therefore juveniles are not present in nature during November and December (the period of our study). These lizards were at various stages of reproduction ranging from nongravid to close to oviposition. Lizards were maintained in small groups of around 10 females in terraria (100×40 cm and 40 cm high) containing bark chips and leaf litter. They had ad libitum access to house crickets, *Acheta domestica*, which were dusted with a calcium supplement. None of the crickets was ever injured and not eaten.

Two adult female white-lipped snakes (360, 300 mm, 16.46, 8.12 g, respectively) were collected in October 2001 from the Brindabella Ranges, ACT, Australia with permission from Environment ACT. This species is known to prey on sun skinks (Shine 1981; Downes & Shine 1999) but is not present at the lizard collection area. However, a pilot study clearly showed that sun skinks perceived scent from the collected snakes as a predator stimulus (see also Downes & Shine 1999). Furthermore, we compared the relative responses of individual lizards in different group sizes towards this predator stimulus, rather than the absolute responses of lizards to scent from white-lipped snakes per se. Thus, it was appropriate to use these chemical stimuli in our experiment. In response to integumentary chemicals from white-lipped snakes, the sun skinks' defence strategy is one typically used during visually mediated encounters with snakes: inactivity and immobility (Downes & Shine 1999).

The snakes were maintained individually in tubs (62×41 cm and 28 cm high), the floor of which was lined with paper. Two layers of sandstone slabs (10×10 cm and 1.5 cm high), separated vertically to form a crevice, were positioned at each end of the tub, for use as shelter sites. We varied the thickness of the crevice to ensure that the snakes made contact with the upper side of the bottom slab and the underside of the top slab. To ensure that the snakes used both retreat sites within their cage, we repositioned the cage several times throughout the day so that one or the other shelter sat on the heat source (see below); the snake would typically follow. We used the slabs as snake-scented basking sites in our experiments. The snakes were not fed while in captivity because they were pregnant females in the last weeks of parturition. During this period the snakes fast and refuse to eat any food offered.

All animals were housed at the Australian National University. They were maintained in a room at 18°C; a strip of heat tape 10 cm wide was positioned under one half of a cage and provided thermoregulatory opportunities from 0800 to 1800 hours. Animals were supplied with water ad libitum which was supplemented with vitamins. The lighting regime mimicked that of the surrounding area.

Lizards were collected with permission of the New South Wales National Parks and Wildlife Service, and the experiments were approved by the Australian National University Animal Experimentation and Ethics Committee. All lizards and snakes were released at the point of capture after the experiments. The period of captivity was up to 16 weeks for lizards and 11 weeks for snakes.

Experimental Procedures

We randomly selected 16 nongravid individuals from the total pool of 78 animals ($\bar{X} \pm \text{SE}$; 37.8 ± 0.45 mm, 1.81 ± 0.09 g). These lizards were used as focal individuals for the duration of the experiment, and were distinguished from other animals in the same experiment by a small dot of nontoxic silver paint on their backs. We performed one trial per week with every focal lizard between 2 November 2001 and 14 January 2002. Each focal lizard was tested once in each of 10 treatments: five group sizes under two risks of predation. Therefore, altogether 160 experiments were conducted. The order in which focal animals were tested was preset. Each group size treatment was presented first to approximately one-fifth of the focal lizards and the next treatment followed the order 1, 2, 4, 8, 12. Eight focal lizards were first tested under low risk of predation and eight under high risk of predation. The predation risk treatment experienced by each focal lizard was then alternated.

Our experiments were conducted in nontransparent tubs (62 × 41 cm and 28 cm high) that were lined with sand and contained a basking site at one end and a retreat site at the opposite end. The test room was maintained at 23°C, which is considerably lower than the preferred body temperatures of sun skinks (ca. 28–30°C, Greer 1989). This temperature mimics natural conditions and induces lizards to bask on the heat source to achieve their preferred temperature. Between 0800 and 1700 hours, an unscented sandstone rock (10 × 10 cm and 1.5 cm high) was heated to 40°C by a 100-W globe positioned underneath the tub and provided an optimal area for basking. The sand substrate surrounding the slab (within 3 cm) was heated to 28°C and provided a suboptimal area for basking. The retreat site was plywood (7 × 20 cm) and was not heated. To increase structural complexity, we placed 10 cards (10 × 4 cm) vertically in the sand base throughout the terraria. Water was available in a dish near the retreat site, and we did not provide lizards with food during the acclimation or experimental periods (a total of 48 h). Tubs were positioned side-by-side. A video camera was located directly above, and connected to a time-lapse video cassette recorder (set at 5 frames/s) and monitor. After each trial, the sand on the floor of the cage, the basking rocks and the retreat sites were replaced with fresh material.

We manipulated group size by creating assemblages with 1, 2, 4, 8 or 12 subjects. Sun skinks are regularly observed in groups of up to 12 in nature (unpublished data). A group consisted of a focal individual plus the required number of group members, as randomly selected from the 62 nonfocal individuals. Pilot studies scoring shifts in behaviour of lizards in the range of group sizes over time showed that lizards acclimated to the experimental conditions within 24 h of being introduced into tubs (unpublished data). We therefore placed focal lizards and their group members into experimental tubs late in the afternoon 2 days before the trials, and allowed them to acclimate undisturbed for the following day. At 0600 hours on the following morning, we replaced the basking rock with either a fresh unscented slab (to mimic low

predation risk) or a snake-scented slab (to mimic high predation risk). Snake-scented slabs were used as shelters by snakes for 1 week before the experiment; one snake was housed with the slabs for 3 or 4 days and it was then placed in the cage of the other snake. The slabs were removed from the snake's cage on the morning of the trial.

On the same day that the scent treatments were applied, we used two methods to document behaviour. The first method involved recording behaviour on to videotape. The video camera set above the tubs was activated between 0900 and 1700 hours. The second method involved recording behaviour on to audiotape. From 1000 to 1300 hours we observed the focal lizard in each tub for 20 min. Observations were made from behind a one-way mirror with the aid of an optic binocular (Zeiss Monoskop, 0.3 m near focus), and we recorded behaviour on to audiotape using a dictaphone. One person made all observations and was not aware of the scent treatment experienced by the lizards.

Scoring Behavioural Variables

To categorize behaviours, we used information from a previous study (Downes & Shine 1999) that examined the antipredator behaviour of sun skinks in response to predator chemical cues as well as living predators (see also Downes 2002). We also used Torr and Shine's (1996) interpretations of an ethogram for *Lampropholis guichenoti*, a sister species with ecology and behaviour similar to that of our study animal.

From the videotapes we scored behaviour every 15 min throughout trials beginning at 0900 hours ($N = 33$ observations). Our readings were instantaneous. We assessed whether lizards were moving by watching the 10 s of videotape preceding each observation point. For assemblages with 2, 4, 8 or 12 subjects, we estimated the tendency of lizards to group with conspecifics in the same tub. On the video monitor, each tub was delineated into three sections spaced evenly along its length. At each observation point, we noted the location of the focal lizard and scored the number of conspecifics in the same section of the tub. We used this information to calculate, separately for the three sections of the tub, the proportion of lizards occurring with the focal animal. Values were averaged across the number of observation periods that the focal animal was in that section to obtain an index of grouping behaviour.

We also calculated the following for the focal lizard: activity (the number of periods the lizard was not hidden divided by the total number of observation periods) and mobility (the number of periods the lizard was not stationary divided by the number of periods the lizard was not hidden). We scored proximity to the basking site (basking proximity) by dividing the length of each arena into equal thirds and noting the location of the focal lizard. Each section was assigned a relative value from 1 to 3 that reflected its proximity to the basking site. We calculated an index of basking proximity by multiplying the number of periods that a lizard was in each section of the tub by the value of that section, and dividing by the total number

of periods that a lizard was not hidden. Basking rate was calculated as the number of periods that a lizard was on the basking area (either the rock or the surrounding sand) divided by the number of periods a lizard was not hidden. Lizards with the lowest levels of activity, mobility, basking proximity and basking rate were considered to express the highest levels of antipredatory behaviour (see Downes & Shine 2001; Downes 2002 for further justification).

From the audiotapes we scored detailed behaviours for three broad states (mobile, stationary, basking), and categorized these acts as indicating that lizards expressed high levels of antipredatory behaviour ('responsive') or low levels of antipredatory behaviour ('not responsive'). Mobile lizards were scored as being responsive if they jumped forward or moved in short rapid jerks, and as being not responsive if they moved forward at a normal pace. Stationary lizards that were not basking were considered to be responsive if they were completely still with their eyes open or head tilted towards a stimulus or were vibrating their tail, and to be not responsive if they displayed any of the following behavioural acts: allo-groom, defecate, drink, lie on and eyes closed (see Torr & Shine 1996 for definitions). Basking lizards were scored as being responsive if they had their eyes open or head tilted towards a stimulus, and as being not responsive if they had their eyes closed or one or more limbs raised off the substrate and held against the side of the body.

From the audiotapes we scored the time that focal lizards displayed the various behaviours. We calculated the proportion of time that lizards were responsive in the three broad states, as the sum of the duration of behaviours in the responsive category divided by the total amount of time in that state. We also counted the lizards' tongue extrusions directed towards the basking site.

Data Analyses

We conducted two main analyses on the data: ANOVAs and regressions. The data were checked for all relevant assumptions before statistical analysis (Kleinbaum & Kupper 1978; McCullagh & Nelder 1983; Zar 1984). Some variables were log transformed to normalize variances. Diagnostic tests were used to confirm the success of transformations and to check other assumptions of ANOVA and regression (Kleinbaum & Kupper 1978; Wilkinson 1990).

Since many of the behavioural variables that we measured were interrelated, it is possible to use principal components analysis (PCA) to obtain a smaller number of mutually independent variables. However, we did not use principal components for the ANOVAs because we judged that this method was unlikely to result in a more synthetic analysis. To test whether lizards occurred as groups during trials, we used ANOVA with group size, predation risk and location in test cage as within-subjects factors and grouping behaviour as the dependent variable. To examine the interaction between group size and risk of predation for the different behaviours, we used a repeated measures MANOVA with two within-subjects factors (group size and predation risk) and all eight behaviours measured during the study as dependent variables. Group

size was treated as a random-effects factor, and predation risk and location in the test cage were treated as fixed-effects factors. Wilk's lambda was used as the test statistic. This analysis showed a statistically significant interaction between group size and risk of predation (see Results). We therefore tested for a main effect of predation risk on behaviour using the same MANOVA model on data sets for each group size separately. Our initial model also used order of presentation (predator presence first or second) as a between-subjects factor to determine whether habituation to the test conditions had an impact on the responses of lizards. In all cases this factor did not significantly ($P > 0.2$) explain variation in lizard behaviour and therefore was omitted from the final model.

We examined the shape of the relation between behaviour and group size by fitting both linear regressions and nonlinear logarithmic regressions to two principal components extracted from the raw data (see Results). We separately examined the data for situations with low and high predation risk, and report the model that had the greater adjusted R^2 . The raw data used in the PCA were the total duration or frequency scores of the behavioural variables measured during the 10 tests for each individual, that is, we performed a single PCA on the whole data set of five group sizes and two predation risks. The PCA was performed on the correlation matrix of the eight behavioural variables; the principal components were varimax rotated. We retained principal components that had eigenvalues greater than one (Norman & Streiner 1994; but see also Jackson 1993).

RESULTS

Grouping Behaviour

The average proportion of lizards occurring with the focal animal during trials was relatively high (mean $\pm$ SE grouping index across all group sizes, both levels of predation risk and all locations in the test cage = 0.76 ± 0.02). Irrespective of group size, level of predation risk and location in the test cage, lizards maintained similar levels of grouping behaviour during trials (ANOVA: group size: $F_{3,360} = 1.12$, $P = 0.34$; predation risk: $F_{1,360} = 0.61$, $P = 0.44$; location in cage: $F_{2,360} = 0.25$, $P = 0.78$).

Interaction Between Group Size and Predation Risk

The level of antipredatory behaviour expressed by sun skinks varied with group size but the magnitude of this effect was always strongly dependent on predation risk (MANOVA: $F_{32,529} = 4.13$, $P < 0.001$; Fig. 1). Analyses performed on separate data sets for each group size showed that the magnitude of the individual antipredatory response to group size was greater during trials with high predation risk than those with low predation risk (Table 1).

Separate analyses performed on data from trials with high and low predation risk showed that individual expression of antipredatory behaviour decreased significantly with increasing group size (MANOVA: low risk:

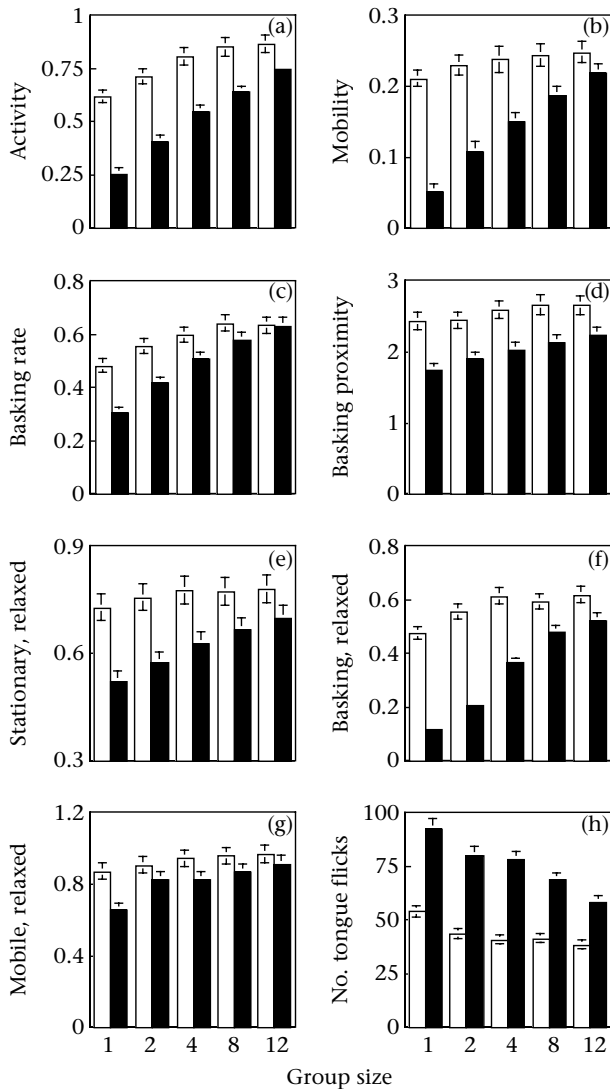


Figure 1. Mean $\pm$ SE scores for all lizard behaviours during trials with 1, 2, 4, 8 or 12 group members and low predation risk ($\square$) or high predation risk ($\blacksquare$). (a) Activity, (b) mobility, (c) basking rate, (d) basking proximity, (e) stationary and relaxed, (f) basking and relaxed, (g) mobile and relaxed and (h) number of tongue flicks. See text for definitions of behaviours and calculations of scores.

$F_{32,252} = 4.71$, $P < 0.001$; high risk: $F_{32,252} = 10.47$, $P < 0.001$). Under both predation risk treatments, lizards in larger groups were more active and more mobile, and spent more time on the warmest section of the arena and basking, than when they were in smaller groups (Fig. 1). Our analysis of detailed behaviour showed that in larger groups stationary, mobile and basking lizards were significantly less likely to express high levels of antipredatory behaviour, and extruded their tongues at much lower rates, than when they were in smaller groups (Fig. 1).

Relation Between Group Size and Behaviour

We extracted two principal axes that were significant and accounted for 60.7 and 11.5% of the total variation in

Table 1. Summary statistics describing the main effect of predation risk on the behaviour of focal lizards in groups of different size

Group size	$F_{8,23}$	P
1	73.31	<0.001
2	48.21	<0.001
4	24.99	<0.001
8	20.01	<0.001
12	10.60	<0.001

We first conducted MANOVA including all eight behaviours recorded during the study as dependent variables and group size and predation risk as factors, then tested for a main effect of predation risk on behaviour using the same MANOVA model on data sets for each group size separately.

our data (total explained variation = 72.2%; Table 2). The alignment of the experiments along the component axes was studied by considering the projections (i.e. scores) of the individual tests on these axes. The r values indicated are the factor loading of the original (raw) variables on the extracted principal components.

The first principal component represents a behavioural gradient characterized by a transition of frequent tongue flicking ($r = -0.75$) towards spending long periods being active ($r = 0.74$), mobile ($r = 0.78$), basking ($r = 0.81$) and in a relaxed mode while mobile and basking ($r = 0.85$ in both cases). The second principal component was negatively correlated with basking proximity ($r = -0.92$) and positively correlated with the duration of remaining stationary and relaxed ($r = 0.88$). Hence, it represents a behavioural shift from frequenting areas of the arena that were close to the basking resource to remaining stationary for long periods in a relaxed mode.

Under both risks of predation and with both principal components, nonlinear regression models explained group size effects better than linear models did (Table 2 lists values for nonlinear logarithmic regression models).

DISCUSSION

Sun skinks detected chemical cues deposited by a predatory snake. This is evident from an increased tongue-flick rate, decreased activity, mobility and basking rates, and the use of behaviours typically associated with stress situations (tail vibrations, fast starts, strobe motion). These responses are qualitatively highly similar to those of other species of lizard in analogous experimental conditions (reviewed in Downes & Bauwens 2002). Furthermore, they have been shown experimentally to increase an animal's chances of evading capture by snake predators (Downes 2002; see also Sih 1992; Skelly 1994; Rodd & Reznick 1997). We are therefore confident that (1) our experiment effectively simulated different predation risk situations, and (2) we correctly interpreted the responsiveness of lizards as indicating different levels of antipredatory behaviour.

Our results show that the time allocated to expressing high levels of antipredatory behaviour decreased significantly with increasing group size in female sun skinks. The relation between group size and time allocated to

Table 2. Mean principal component factor scores $\pm$ SE for the behaviour of adult female *Lampropholis delicata* ($N = 16$) at different levels of predation risk and group sizes

Group size	Component 1		Component 2	
	Low risk	High risk	Low risk	High risk
1	-1.24 ± 0.07	-2.12 ± 0.07	-1.62 ± 0.10	-0.54 ± 0.11
2	0.56 ± 0.07	-1.07 ± 0.09	-1.23 ± 0.18	0.74 ± 0.29
4	0.84 ± 0.08	-0.52 ± 0.07	-0.05 ± 0.14	0.63 ± 0.28
8	0.96 ± 0.08	0.01 ± 0.06	0.08 ± 0.15	0.47 ± 0.18
12	0.99 ± 0.17	0.46 ± 0.08	-0.25 ± 0.18	0.41 ± 0.91
R^2	0.75	0.94	0.47	0.55
P	<0.001	<0.001	<0.001	<0.001

Also shown are adjusted R^2 and P values for nonlinear logarithmic regression models examining the relation between group size and each principal component. Separate analyses were performed on data from trials with low predation risk and high predation risk.

expressing high levels of antipredatory behaviour was nonlinear and asymptotic (see also Pulliam 1973; Jarman 1987; Dehn 1990; Blumstein et al. 1999), and did not change under low and high risks of predation. However, group size and predation risk interacted to affect significantly the time that lizards spent expressing high levels of antipredatory behaviour (see also Risenhoover & Bailey 1985; Frid 1997).

Many organisms benefit by forming temporary or permanent aggregations for a variety of reasons. When snake predators attack groups of skinks, usually only one individual is captured and killed (e.g. Skelly 1994; Downes 2002). Therefore, in our study system (and numerous others), one benefit of aggregating with conspecifics may be a decrease in the probability that a predator will kill a given individual (e.g. Mooring & Hart 1995). Sun skinks spent less time inactive and immobile as group size increased. For instance, under low predation, skinks in groups of 12 spent 40% more time active than solitary lizards did (Fig. 1). By remaining hidden for longer, lizards may decrease their chances of encountering predators (Sih 1992; Rodd & Reznick 1997; but see Banks et al. 2000). Reduced mobility may lessen rates of detection and attack by visually oriented predators (Skelly 1994; Downes & Shine 2001). Therefore, these shifts in behaviour are probably a function of a decline in perceived risk of predation. However, we cannot discount other possibilities. For instance, an alternative explanation for our results is that animals in larger groups attained different body temperatures through aggregation and therefore showed different antipredatory behaviour from animals in smaller groups (Van Damme et al. 1990; see also the discussion of this topic below).

We did not test whether this per capita reduction in predation risk results from the presence of alternative prey (the dilution effect), or from having more individuals to locate predators (the detection effect). However, models and studies of how group size affects antipredatory behaviour suggest that both detection and dilution effects should generate nonlinear and asymptotic relations between group size and the time allocated to antipredatory behaviour (see Introduction). In this study, nonlinear logarithmic regression models explained significantly more variation than linear regression models (Table 2).

Since basking sites are abundant in a sun skink's natural environment (Torr & Shine 1993; S. Downes, personal observation), we did not limit the basking area available to lizards. Thus, increased competition for limited resources is unlikely to explain the positive relation between risk-taking behaviour and group size in this system.

More responsive individuals may be safer, but excessive responsiveness may conflict with other activities, such as sleeping, feeding, grooming and fighting (reviewed in Treves 2000). Thus, the optimal level of antipredatory behaviour should be sensitive to predation risk (reviewed in Elgar 1989; Lima & Dill 1990; Dukas 1998; Hunter & Skinner 1998). When the overall risk from predators was high, the time that lizards devoted to high levels of antipredatory behaviour decreased strongly as group size became larger. In contrast, when the overall risk from predators was low, the time devoted to high levels of antipredatory behaviour decreased weakly as group size became larger (see also Frid 1997).

Lizards in larger groups under high predation risk adopted a similar level of antipredatory behaviour as lizards in smaller groups under low risk from predators. Accordingly, we might expect that in nature, lizards would form larger groups when the risk from predators is high, and smaller groups when the risk from predators is low. However, reducing predation risk may not be the only benefit of increasing group size in this system. For instance, basking skinks often lie on conspecifics and this behaviour may enhance heat uptake rates and transfer information about the position of quality basking sites (Torr & Shine 1993). Furthermore, skinks frequently groom each other (Torr & Shine 1994), although the function of this behaviour is unknown. Thus, unless there are significant costs involved with group living, skinks may benefit from remaining in large groups for most of the time in the wild. Our anecdotal observations of field populations and experimental data on grouping behaviour suggest that this may be the case.

Our study shows that female sun skinks may perceive a significant and substantial new antipredator benefit from living with others, and that the magnitude of this benefit depends on the prevailing level of predation risk. This result should stimulate further investigation of the functional significance of group living and the

mechanisms underlying group effects. For instance, it suggests that the probability of being killed by a predator decreases with increasing group size (Treves 2000). If so, this result may be caused by the presence of alternative prey, or having more individuals to locate potential predators (Uetz et al. 2002). The challenge is to design rigorous experiments involving direct encounters between actual predators and lizards to test these questions.

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