

## ORIGINAL ARTICLE

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# Size-based predation by kookaburras (*Dacelo novaeguineae*) on lizards (*Eulamprus tympanum*: Scincidae): what determines prey vulnerability?

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**Abstract** Lizards and birds are both popular “model organisms” in behavioural ecology, but the interactions between them have attracted little study. Given the putative importance of birds as predators of diurnal lizards, it is of considerable interest to know which traits (of lizards as well as birds) influence the outcome of a predatory attempt. We studied predation by giant terrestrial kingfishers (kookaburras, *Dacelo novaeguineae*: Alcedinidae) on heliothermic diurnal lizards (highland water skinks, *Eulamprus tympanum*: Scincidae), with particular reference to the role of prey (lizard) size. Our approach was twofold: to gather direct evidence (sizes of lizards consumed in the field, compared to those available) and indirect evidence (size-related shifts in lizard behaviour). We quantified the size structure of a natural population of skinks (determined by an extensive mark-recapture program), and compared it to the sizes of wild lizards taken by kookaburras (determined by analysis of prey remains left at the birds’ nests). Kookaburras showed size-based predation: they preyed mainly on small and medium-sized rather than large lizards in the field. However, the mechanism producing this bias remains elusive. It is not due to any distinctive behavioural attributes (locomotor ability, activity level, habitat usage) of the lizards of the size class disproportionately taken by the kookaburras. The greater vulnerability of subadult lizards may reflect subtle ontogenetic shifts in ecological and behavioural traits, but our data suggest that great caution is needed in inferring patterns of vulnerability to predation from indirect measures based on either the prey or the predator alone. Instead, we need direct observations on the interaction between the two.

**Keywords** Predation · *Eulamprus* lizard · Bird selection

## Introduction

Predation has long been considered a major selective force in the evolution of many aspects of organismal structure and function, as well as an important causal factor in structuring populations and communities (e.g. Lima and Dill 1990 and references therein). Nonetheless, empirical evidence on the operation of predation and the ways in which the outcome of a predatory interaction is determined are meagre or non-existent for most kinds of animals in most kinds of habitats. For example, the two types of terrestrial vertebrates most often identified as “model organisms” in behavioural ecology are birds and lizards (Huey et al. 1983), and birds are major predators of many species of lizard. Moreover, predation has been implicated as a selective force for the evolution of many characteristics of lizards, including life history traits (e.g. Shine 1980), morphology (Stamps 1984; Cooper and Vitt 1991; Fitch and Henderson 1987), sexual dimorphism (Hasegawa 1993), activity times, habitat use (Martin and López 1995) and the maintenance of chromatic polymorphisms within populations (Forsman and Shine 1995). Remarkably, however, there are few quantitative analyses of the predatory interactions between birds and lizards.

The limited data available suggest that one major factor determining a lizard’s vulnerability to bird predation may be body size. For example, American kestrels prey preferentially on large *Anolis* lizard species (McLaughlin and Roughgarden 1989), whereas thrushes feed only on small size classes of the skink *Eumeces okadae* (Hasegawa 1990). Captive greater roadrunners (*Geococcyx californianus*) prey on round-tailed horned lizards (*Phrynosoma modestum*) in preference to larger Texas horned lizards (*P. cornutum*) and death rates due to predation in the field are higher in *P. modestum* than in *P. cornutum* (Munger 1986; Sherbrooke 1990). However, the generality of such size-selectivity, and the mechanisms

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underlying it, remain obscure. Prey of particular sizes might be taken more often either because they are actively preferred by the predator, or because they are easier to capture and/or handle. We investigated the ways in which prey size influences the interaction between a large Australian predatory bird and a medium-sized diurnal lizard. We compared the results obtained using direct methods (quantification of prey availability versus prey taken) and indirect methods (quantification of behavioural attributes of the prey and predator that are likely to affect the intensity of predation on different size classes of prey).

## Methods

The highland water skink (*Eulamprus tympanum*: Scincidae) is a medium-sized [to 96 mm snout-vent length (SVL), 18 g] diurnal heliothermic lizard that is widely distributed across montane regions of south-eastern Australia (Cogger 1992). Adults are found mostly on or near large fallen logs (e.g. Webb 1985; Schwarzkopf and Shine 1991, 1992). Like most similar-sized lizards, *E. tympanum* is potentially preyed upon by a wide diversity of vertebrates and invertebrates (Daniels and Heatwole 1984). However, birds (such as kookaburras, *Dacelo novaehollandiae*) and elapid snakes (such as copperheads, *Austrelaps ramsayi*, and blacksnakes, *Pseudechis porphyriacus*) are likely to be the most significant of these predators (Shea 1987; Barker and Vestjens 1989; Shine 1991 and references therein).

The kookaburra (*D. novaeguineae*) is a large (500 g) terrestrial kingfisher (Coraciiformes: Alcedinidae) that occurs over much of eastern and south-western Australia (Pizzey 1980). Kookaburras are mainly insectivorous, but also take a wide variety of small vertebrate prey (see Parry 1970 for a detailed natural history). These birds are classic ambush predators, waiting on high branches until they detect moving prey, and then sweeping down to seize it. Kookaburras usually nest in tree hollows, and use the same hollow in consecutive years. They are cooperative breeders (*sensu* Lack 1968); young may stay in the parents' home range for up to 4 years and assist in the rearing of successive broods. Thus, as many as six kookaburras in any one year may bring prey items back to the nest to feed the chicks. As a result, the remains of many prey items accumulate in the nest hollow and at the base of the nest tree (personal observation). Kookaburras have previously been used to examine the vulnerability of reproducing water skinks to predation (Schwarzkopf and Shine 1992).

We determined the size structure of a natural population of highland water skinks living adjacent to the Whalania Fire Road in Kanagra-Boyd National Park (33°52'57.6" S, 150°3'6.5" E; 8930-III-S KANANGRA 273431; elevation: 1,285 m). This site has been used for ecological studies of highland water skinks over several years, resulting in extensive information on several aspects of the ecology of *E. tympanum* (e.g. Schwarzkopf 1991, 1992, 1993; Schwarzkopf and Shine 1991, 1992; Blomberg 1994; Doughty and Shine 1997, 1998).

The size-frequency distribution of lizards in the population at the time of year during which kookaburras breed (November–December at our site) was derived from capture-recapture data gathered during a demographic study of these lizards (Blomberg 1994). The lizards were captured in pitfall traps (plastic buckets) and individually marked by toe-clipping. For analysis, we divided the lizards into size classes, the width of each determined using Moloney's (1986) algorithm to identify biologically meaningful units within the population. This procedure generated five size classes, based on SVL: "neonate" (34–45 mm), "juvenile" (46–62 mm), "subadult" (63–81 mm), "adult" (82–87 mm), and "large adult" (88–96 mm). The size classes correspond approximately to yearly age classes (Blomberg 1994); males attain reproductive maturity at 73 mm (in their 2nd year of growth) and females

mature at 80 mm SVL (3rd year of growth; Schwarzkopf 1993). The probability of capture for each size class was obtained using MSSURVIV (Brownie et al. 1993), and abundance estimates for November 1990, December 1990, November 1991 and December 1991 were calculated by dividing the number of lizards caught in each size class by the appropriate capture probability.

During November and December 1990, we observed a family of kookaburras that was foraging close to our water skink capture-recapture site. We followed the birds back to their nest, which we found by listening for a change in the kookaburras' call (Parry 1970; Reyer and Schmidl 1988). The nest tree was approximately 300 m from the capture-recapture study grid, and skeletal remains from prey brought back to the nest were found in the leaf litter beneath the nesting hollow. We removed a 2×2 m quadrat of this leaf litter from the base of the tree, and brought the soil and vertebrate remains back to the laboratory for analysis. In the laboratory, we sieved the leaf litter to remove fine dust (mesh size: 1 mm) and large debris (mesh size: 7 mm). We then sorted the remaining soil sample by hand and collected the vertebrate skeletal remains.

We counted the bones in the sample, and recorded the type of skeletal elements. Lizard dentary bones were examined in detail because we were able to distinguish those from *E. tympanum* from those of other lizard species, based on the dentary size, robustness, and degree of closure of Meckel's groove. The latter character can be used to separate *Sphenomorphus* group species (of which *E. tympanum* is the only representative in our study area) from sympatric lizard taxa belonging to the *Eugongylus* group (e.g. *Pseudemoia* spp.); Meckel's groove is almost completely open along the length of the dentary in *Eulamprus*, but is open only in the most posterior region of the dentary (if at all) in *Eugongylus* group species (Greer 1979). We used Vernier calipers to measure the length of the tooth row, defined as the distance from the mandibular symphysis to the point where the lower, lingual-side margin of the dentary curves up to meet the upper margin posteriorly.

We estimated the SVL of ingested (prey) lizards from their tooth row length using the geometric mean regression equation relating known SVL to known tooth row length, derived from dissection and measurement of 89 *E. tympanum*. SVL in dissected specimens was measured to the nearest millimetre using a steel rule, and tooth row length was determined using Vernier calipers. The individuals used to construct this curve were captured at least 200 m from the Whalania Fire Road site, and were also used for dietary analyses (Blomberg 1994). Only the right-hand dentary was used, as this was the most common element in the nest-site sample (see Results). Geometric mean regression, also known as central trend or functional regression, was chosen because it was not clear which variable (SVL, tooth row length) should be treated as the dependent variable, and which should be treated as independent. In addition, geometric mean regression allows for variance in both variables whereas ordinary, predictive regression only allows variance in the dependent variable.

## Comparison of prey size distributions: availability versus use

The capture probabilities for each size class during each of the four critical sampling periods (those periods in which kookaburras bring prey back to the nest) were not without error. These errors decrease the precision of the estimate of the pooled size-frequency distribution of the wild lizard population because population size was calculated as the observed (raw) number of captures divided by the capture probability. However, MSSURVIV produces maximum-likelihood estimates of the standard deviations of the capture probabilities, and we used these estimates to bootstrap the estimate of the size distribution of the field population using the following procedure (Manly 1991). For each size class at each of the four sampled time periods, we chose a capture probability at random from a truncated normal distribution, the mean of which was equal to the maximum likelihood of the capture probability, and the standard deviation equal to the maximum-likelihood standard deviation from MSSURVIV. The population size estimates for each size class at each time were then calculated and

pooled across all four sampling periods. A log-linear model was then used to test for significant size-related prey selection by the kookaburras (Manly et al. 1993; Heisey 1985). This procedure was repeated 2,000 times, and the mean *P*-value was used as the test for significant prey selection. Mean parameter values and standard errors for the log-linear model were also calculated and used to calculate Manly's  $\alpha$  statistics for the post hoc comparison of relative selection among size classes (Heisey 1985; Chesson 1978; Manly et al. 1972). Confidence limits for multiple comparisons were computed using the Dunn-Sidak correction (Sokal and Rohlf 1995). Programming and calculation of the bootstrap and log-linear modelling procedures were done in XLISP-STAT (Tierney 1990) on a Silicon Graphics Origin 2000 supercomputer.

### Influences on predation vulnerability

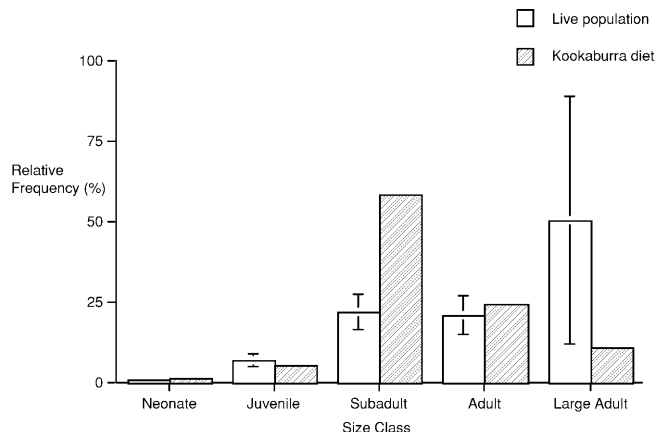
The size classes of lizards most vulnerable to kookaburras might depend upon other attributes of the lizards. For example, smaller lizards might be more vulnerable than larger conspecifics if they have larger home ranges, or are more often found away from shelter. To evaluate these possibilities, we used data obtained during a 3-year mark-recapture study of the skinks at the Whalanian Fire Road site. Our aim was to identify correlates of lizard activity that may be associated with sex- or size-specific variation in predation risk.

Skinks were captured in 121 10-l buckets spread systematically at 10-m intervals over a 1 ha (100×100 m) study grid. Each bucket was sunk into the ground so that the lip was flush with the surface. Holes were drilled in the bottom for drainage, and a small amount of leaf litter was placed in the bottom to provide shelter for lizards. Finally, a square of chicken-wire (1×1 m) was placed over the top of the trap to prevent predation of trapped lizards by birds. Because *E. tympanum* uses logs as basking sites and runways, traps were placed beside logs whenever possible. However, a few traps were not located near logs, allowing us to test whether some lizards strayed further from cover than others. The mark-recapture study began in November 1989 and ceased in November 1992, and consisted of 15 surveys, each of approximately 12-days duration. Surveys were only conducted during months when lizards were active (October–March). This resulted in 3,942 captures of 1,334 individuals over 22,748 trap-days.

Minimum convex polygon (MCP) "home range sizes" and "home range spans" were calculated using Ranges V (Kenward and Hodder 1995) on an IBM-compatible PC under MS-DOS. Statistical analyses were performed using SAS (SAS/STAT 1989) on a Power Macintosh. ANOVA assumptions were tested by examining plots of the data, and using the Wilk-Shapiro test for normality and the Brown-Forsythe test for equality of variances (SAS/STAT 1989). Although we calculated "home range" sizes and spans and we use the terminology of "home ranges" for convenience, we wish to make clear that our measurements are not of the true "home range" of the skinks. This is because the geometry of our measurements is entirely dependent on the layout of the mark-recapture trapping grid. Similarly, measurements through time depend on when lizards were trapped, and we could not control the date of capture for individual lizards. Some lizards were caught across several seasons and several years, further complicating the interpretation of the data as the "home range". Instead, we use the MCP data as an index of relative space use by water skinks without the connotations of the "home range" terminology.

## Results

Vertebrae (20.39%) and limb bones (29.81%) were the most common skeletal elements in the remains from the kookaburra nest site. Four mammalian elements were found: a bat (microchiropteran) jawbone and three mammalian limb elements. All other vertebrate material



**Fig. 1** Size-frequency distribution of water skinks (*Eulamprus tympanum*) at the Whalanian Fire Road site, and in the sample derived from the kookaburra nest remains. The distribution for the Whalanian Fire Road site is derived from 200 bootstrap estimates of the pooled population size for November and December 1990 and 1991. Error bars are SEs of the bootstrap estimates

was of saurian origin. Of all elements, 9.91% were dentaries, and of these, 74 were right-hand dentaries from *E. tympanum*. Seven dentaries belonged to *Eugongylus* group species, and one was too eroded to determine its specific affinities. Examination of freshly killed lizards showed that the relationship between SVL and the length of the tooth row was approximately linear, explaining 94% of the variance in the data (reduced major axis regression:  $SVL = (\text{tooth row length} \times 12.825) - 21.613$ ). The length of the tooth row was shorter in mature females than in mature males at a given SVL, reflecting sexual dimorphism in head size in this species. Only one *E. tympanum* right-hand dentary was unusable in constructing the distribution because of its eroded condition.

Kookaburras did not take a random sample of the size classes of lizards available to them (log-linear model to test the hypothesis of "no selection":  $\chi^2 = 6.12$ , 1 *df*,  $P < 0.015$ ). Closer inspection showed that the birds took relatively few "large adult" and relatively more of the "subadult" size class (Fig. 1). Manly's  $\alpha$  for "large adult" lizards was significantly different from and less than that for "subadults" as indicated by the lack of overlap of the 95% confidence intervals. There were no significant differences in selection among the other size classes which appeared to be chosen according to their availability in the population, as none were significantly different from 0.2, the random expectation (Table 1).

Home range data were obtained for 363 lizards. There was no relationship between the home range area and number of fixes when we used at least four fixes to calculate the MCP home range size ( $r_{\text{Spearman}} = 0.049$ ,  $P = 0.44$ ). Therefore, we discarded from the data set individuals for which we had only three fixes, leaving a sample of 248 lizard home ranges for further analysis.

There was a significant interaction between sex and size class in the analysis of MCP home range area (two factor ANOVA on log-transformed data,  $F_{3,240} = 3.33$ ,

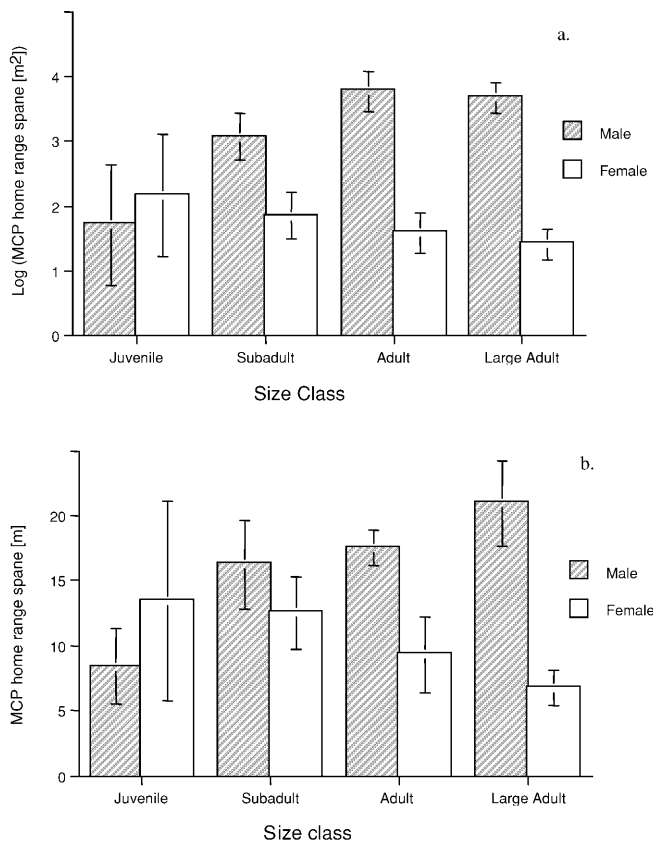


**Table 1** Manly's  $\alpha$  selection indices for five size classes of skinks (*Eulamprus tympanum*) preyed on by kookaburras (*Dacelo novaeguineae*) (\*significantly different from random expectation and from each other)

Size class	Manly's $\alpha$	SE ( $\alpha$ )	Lower 95% confidence limit	Upper 95% confidence limit
Neonate	0.283	0.283	0	1.00
Juvenile	0.123	0.061	0	0.294
Subadult*	0.352	0.054	0.201	0.502
Adult	0.144	0.034	0.049	0.239
Large adult*	0.099	0.035	0.001	0.198

**Table 2** Results of regression analyses on minimum convex polygon (MCP) home range areas and spans of highland water skinks

Sex	Log(MCP home range size)				Home range span			
	Intercept	P	Gradient	P	Intercept	P	Gradient	P
Male	0.1768	0.8413	0.040167	0.0003	-1.1708	0.8907	0.2328	0.0270
Female	3.0497	0.0085	-0.0174	0.2067	24.6900	0.0052	-0.1865	0.0774



**Fig. 2** Relationship between sex, size class and home range characteristics for water skinks (*E. tympanum*): minimum convex polygon home range size (log scale) (a), home range span (b). Size classes were based on snout-vent length and were defined as: juvenile, 46–62 mm; subadult, 63–81 mm; adult, 82–87 mm; large adult, 88–96 mm

$P=0.02$ ; Fig. 2a). Analysis of the MCP home range span showed similar patterns, except that the interaction between sex and size class was not significant (two-factor ANOVA,  $F_{3,240}=2.41$ ,  $P=0.07$ ; Fig. 2b). To further describe these patterns, we repeated the analysis using

analysis of covariance (ANCOVA; with SVL as the covariate) and calculated lines of best fit for each sex/size class group, assuming that each animal was at the median size for each size class. The sex $\times$ SVL interaction term was significant for both home range area and span (log MCP home range area:  $F_{1,247}=10.89$ ,  $P=0.001$ ; MCP range span:  $F_{1,247}=7.42$ ,  $P=0.007$ ). We conclude that the sexes have different relationships between home range characteristics and SVL. Both home range area and home range span increased with SVL for males, whereas home range area and span tended to decrease for females, over the range of possible body sizes (Table 2, Fig. 2).

We used data from the capture of 175 females and 146 males to analyse the relationships among sex, body size and distance from the nearest log ( $d_{\log}$ ). We took  $d_{\log}$  as a measure of exposure to predation risk, as skinks readily flee to logs if they are away from cover when disturbed by humans. There were differences between the sexes in  $d_{\log}$ , but there was no effect of SVL on  $d_{\log}$  (ANCOVA with SVL as a covariate: sex:  $F_{1,318}=4.10$ ,  $P=0.04$ ; SVL:  $F_{1,318}=0.12$ ,  $P=0.74$ ). The mean value of  $d_{\log}$  for males ( $\pm$ SD) was  $0.33\pm0.811$  cm, whereas for females it was  $0.23\pm0.343$  cm.

## Discussion

Our study provides a cautionary tale in terms of interpreting size-selective predation. The field data from prey remains compared to population size structure provide unambiguous evidence that the birds prey disproportionately on small rather than large skinks. However, detailed analyses of behaviour and habitat use by the prey species provided no obvious mechanisms for such size-associated shifts in vulnerability. Home range sizes and patterns of habitat use of the “more vulnerable” size group did not differ substantially from the same attributes of “less vulnerable” size classes (Fig. 2). Similarly, although locomotor ability (running speed) in this species increases with body size, even major differences in locomotor

speed do not modify the lizards' vulnerability to kookaburras, because the bird is much faster than even the fastest lizard (Schwarzkopf and Shine 1992).

One possible resolution to this paradox in our results is that the data are somehow in error. However, we doubt that this is the case. Our estimates of prey availability (i.e. relative numbers of potential prey of different sizes) are robust. This variable was measured very accurately for the field population because the predation work was only a small component of a long-term intensive population study that focussed on size-associated ecological traits of skinks (Blomberg 1994). Another possibility is that kookaburras actively select small prey. We have no evidence from kookaburras in the field, but semi-tame kookaburras exhibit no preference among different-sized prey items (R. Shine and S. Blomberg, unpublished data).

Similarly, our sample of prey remains may be biased if (1) skeletal elements from prey of one size group weather away faster than those of larger or smaller individuals, and hence their numbers are underestimated, or (2) kookaburras are selective in terms of which prey items they carry back to the nest to feed the nestlings. Both processes are likely to occur, but would yield a bias in the opposite direction to the one we detected. That is, the remains of smaller prey may be more likely to weather rapidly, and the birds are likely to carry large rather than small prey back to the nest rather than eating it at the point of capture. Great grey shrikes (*Lanius excubitor*) and kestrels (*Falco tinnunculus*) both consume small prey at the site of capture, while large prey are transported back to the nest (Sonerud 1989). Hence, if either of these biases occurred during our study, we will have underestimated rather than overestimated the magnitude of the prey size selectivity of the kookaburras.

Similarly, we can dismiss the possibility that kookaburras are less capable of capturing and overpowering larger skinks. This effect may be important when a relatively small predator attempts to consume relatively large prey (e.g. Hasegawa and Nikishata 1991). However, kookaburras are very large and powerful predators, and easily capable of overpowering even the largest skink. Indeed, these birds have been recorded to kill and eat venomous snakes that weigh an order of magnitude more than the largest *Eulamprus* (e.g. Parry 1970; V. Parry, personal communication).

Why, then, were subadult lizards taken more frequently than other size classes under field conditions? We suspect that this difference reflects subtle ontogenetic shifts in lizard behaviour, not apparent from simple measures of home range size or proximity to cover. Adult water skinks occupy fixed home ranges, and vigorously attack intruders; success in these territorial contests is determined by body size, with small lizards remaining cryptic in the presence of adults (Blomberg 1994). Thus, subadults may be forced to occupy suboptimal habitat. Such sites may well provide less protection from predator attack than the home ranges defended by larger conspecifics.

The other plausible determinant of the greater vulnerability of subadult lizards involves learning. Larger skinks are older, and hence may have learned behaviours that

reduce their vulnerability to predation. Many lizards are capable of conditioned learning, and can learn to avoid predators in the field (Brattstrom 1978). Water skinks that have been caught using a noosing gun (sensu Bertram and Cogger 1971) are more difficult to noose a second time (personal observation), which suggests that learned predator avoidance may be possible for *E. tympanum* also.

How general are these results? Inevitably, the vulnerability of a lizard to a predator depends upon many factors that are specific to the study system. For example, habitat features, social influences on habitat use and the way in which habitat features modify predation vulnerability are all system specific. Nonetheless, at least one feature of our study system may apply fairly generally to the interaction between lizards and their predators. Ontogenetic shifts in the pattern of temporal activity, foraging mode or micro-habitat preference have been described for several species of lizard (Bradshaw 1971; Jenssen 1973; Huey et al. 1974; Stamps 1983a, 1983b; Taylor 1986; Paulissen 1988), including the congeneric *Eulamprus quoyii*. Such shifts are likely to influence the times, places and frequencies at which a lizard is exposed to predators. Given that escape tactics and locomotor ability in lizards depend on the animal's body temperature (e.g. Christian and Tracy 1981), even minor ecological shifts during ontogeny may substantially affect the relationship between a lizard and its potential predators. However, given that we have only been able to examine prey selection by one family of kookaburras, we are unable to apply our results to kookaburras in general.

In summary, our study suggests that the determinants of vulnerability to predation may often be very complex, and involve an interaction between predator preferences (or lack of them) on the one hand, and prey attributes (e.g. behaviour, habitat selection) on the other. These latter attributes are in turn likely to be substantially influenced by an equally complex set of processes, including (but not restricted to) size-dependent social interactions.

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