Patterns of diet and microhabitat use by four species of sympatric *Ctenotus* lizards: do they reveal foraging specialisation?

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Abstract

The foraging ecology of many *Ctenotus* species is considered to be generalised and opportunistic. If their foraging ecology is generalised, we would predict that *Ctenotus* species in spinifex grasslands of arid Australia will (1) feed largely on the most abundant food source, termites and (2) that any differences in diet will largely reflect differences in microhabitat use. To test these predictions, we examined diets and patterns of microhabitat use by four sympatric *Ctenotus* species in the southern Goldfields of Western Australia. Neither prediction was supported by our results. One species, *C. brooksi*, did not feed on termites and similarity in microhabitat use between species was not related to dietary similarity. Our data suggest that these *Ctenotus* species may have more specialised foraging ecologies than has been previously appreciated. Future research involving detailed observations of *Ctenotus* species foraging in the field is required to determine which species have specialised foraging ecologies and to what extent they are specialised.

Keywords: *Ctenotus*, specialised foraging, diet, microhabitat, Goldfields, Western Australia.

Introduction

Ctenotus is the largest genus of skinks in Australia, with over 90 described species (Wilson & Knowles 1988; Cogger 2000), and is particularly diverse in spinifex (*Triodia* and *Plectrachne* spp.) grasslands of the arid zone where up to 7 species occur in ecological syntopy (Pianka 1969a). *Ctenotus* species are very difficult to observe in spinifex grasslands as they move rapidly and frequently hide in spinifex clumps, so most ecological studies have been based on dead or pit-trapped specimens (Pianka 1969b, James 1991a,b,c; Read 1998). Consequently, very little is known about the foraging strategies of *Ctenotus* species that occur in spinifex grasslands, although most studies have considered them to be generalist, unspecialised foragers (Pianka 1969a; James 1991a; Read 1998). Most ecological studies of *Ctenotus* in spinifex grasslands have reported that they feed primarily on termites (Pianka 1969b, 1986; James 1991a; Twigg *et al.* 1996; Read 1998), and this is interpreted to reflect the abundance of termites in their habitat, rather than specialised foraging strategies for termites (Morton & James 1988; James 1991a). Further, Pianka (1969b) considered the generalised foraging ecology of *Ctenotus* meant that differences in microhabitat use would result in the exposure to different prey items, so dietary differences between species would reflect differences in microhabitat use.

We examined the hypothesis that *Ctenotus* species were generalised foragers by examining microhabitat use and diet of four sympatric *Ctenotus* species in spinifex grasslands in the southern Goldfields of Western Australia. We tested the following predictions: (1) each *Ctenotus* species would feed on the most abundant food source, termites, and (2) that *Ctenotus* species with the greatest similarity in microhabitat use would have the most similar diets.

Methods

Site description

The study area, centred about 18 km NE of Bungalbin Hill (30°17'S, 119°50'E) in the southern Goldfields of Western Australia, was located on a sandplain and soils throughout the study area were deep sands derived from granites. The habitat in the area was predominantly *Eucalyptus leptopoda* Mallee (JK 35), with scattered patches of *Banksia elderiana* Tall Shrubland (JK 39). The predominant ground cover in both habitats was *Triodia scariosa*. The habitat codes (JK) above are from Dell *et al.* (1988), which provides more detailed descriptions of these habitats.

Dietary intake

Individuals were captured in pit-traps in September 1992, killed with a 0.2 ml dose of 300 mg ml^{-1} of Valabarb, and their stomachs removed. Five *C. atlas*, six *C. brooksi*, six *C. schomburgkii* and 12 *C. xenopleura* stomachs were examined. The volume of each stomach was estimated to the nearest 5 μL using volumetric displacement. Stomach contents were identified to order, except for ants, which were identified to family. The number of each prey type was counted and the volumetric proportion of each prey type in the stomach was visually estimated to the nearest percent. Due to the different volume and number of prey items in the stomachs, all data were standardised as a proportion per stomach before analysis.

Microhabitat use

Microhabitat use was determined by locating individuals foraging in the study area in September 1992 and following them for up to an hour (mean = 21.2 ± 2.3 min). Five *C. atlas*, six *C. brooksi*, six *C. schomburgkii* and 15 *C. xenopleura* were followed and the average period of observation for each individual (mean ± s.e.) was: *C. atlas* (30.1 ± 10.1 min), *C. brooksi* (20.3 ± 5.0 min), *C. schomburgkii* (11.1 ± 3.3 min) and *C. xenopleura* (22.8 ± 2.3 min). Microhabitat use was divided among four categories: Spinifex (within clumps of *Triodia scariosa* or underneath overhanging foliage), Grass (within clumps of other Poaceae, Cyperaceae and Restionaceae or underneath overhanging foliage), Bush (within two cm of trunk of other plants or underneath overhanging foliage if it was within five cm of the ground) and Open (areas other than the above). The amount of time spent in each microhabitat was rounded to the nearest five sec and standardised to a proportion per lizard before analysis. The order in which each species was observed was randomised with respect to time of day (Table 1) and there was no significant difference between the species in the mean air temperature during observations ($F_{3,21}$ = 1.01, P = 0.408) (Table 1).

Statistical analysis

To determine if there were significant differences in the overall diet and microhabitat use of the four species, we analysed all variables from each class using MANOVA. For individual variables, we analysed species differences using a one-way ANOVA and conducted post-hoc analyses using a Tukey-Kramer HSD as recommended by Day & Quinn (1989). These analyses were conducted using SuperANOVA Version 1.11 (Abacus Concepts 1993). To determine whether there was a relationship between diet and microhabitat use of the four species, we calculated the similarity in each between all pairs of species using Pianka's Index (Pianka 1973). We compared similarity values for each species pair by correlation using JMP 3.2.1 (SAS 1997).

Table 1

Range of time of day and range and mean ± s.e. air shade temperatures during microhabitat observations for each *Ctenotus* species.

Species	Time of day Range	Air temperature Range	Mean ± s.e.
C. atlas	1043 –1527	21.5 – 30.5	25.3 ± 1.6
C. brooksi	1145 –1437	24.0 – 28.0	25.8 ± 1.4
C. schomburgkii	1044 – 1557	24.0 – 29.5	26.3 ± 1.4
C. xenopleura	1032 – 1634	16.0 – 28.0[a]	23.3 ± 1.3[a]

[a]n = 8

Results

Dietary intake

The proportional volume of prey consumed differed significantly between the four species (MANOVA: $F_{27,57}$ = 2.97, P = 0.001) (Table 2). The main dietary difference was in the volume of Isoptera consumed by the four species. *C. xenopleura* consumed a significantly greater volume of Isoptera than the other three species, which did not consume significantly different volumes from each other. There were also significant differences in the volume of Araneae consumed, with *C. brooksi* consuming more than *C. schomburgkii* (P < 0.05) and *C. xenopleura* (P < 0.05). *C. brooksi* also consumed more Neuroptera than *C. xenopleura* (P < 0.05). The volume of the other prey items consumed did not differ significantly between the four species (Table 2).

The differences in diet were similar when the proportional number of prey items was analysed (MANOVA: $F_{27,57}$ = 2.37, P = 0.003) (Table 3). The number of Isoptera consumed differed between all four species (P < 0.05). In addition, *C. brooksi* ate significantly more Araneae and Neuroptera than the other three species (P < 0.05). No other means were significantly different (Table 3).

Microhabitat use

Microhabitat use differed significantly between the four species (MANOVA: $F_{9,84}$ = 2.25, P = 0.026). Univariate analyses revealed that there were significant differences between species in the proportion of time spent in the Open ($F_{3,28}$ = 6.75, P = 0.001) and Spinifex ($F_{3,28}$ = 5.35, P = 0.005), but not in Grass ($F_{3,28}$ = 1.16, P = 0.343) or Bush ($F_{3,28}$ = 0.83, P = 0.487) (Fig. 1). Both *C. brooksi* and *C.*

Table 2

Proportional dietary intake, by volume, for the four *Ctenotus* species. P-values are for univariate ANOVAs on individual prey groups. Volumes of prey items that are not significantly different are signified by the same superscript letter.

	Species				
Prey taxa	*C. atlas*	*C. brooksi*	*C. schomburgkii*	*C. xenopleura*	P of $F_{3,25}$
Isoptera	0.124[a]	0[a]	0.378[a]	0.788[b]	<0.001
Formicidae	0	0.008	0.005	0.060	0.382
Coleoptera	0.126	0.073	0.258	0.011	0.145
Araneae	0.160[ab]	0.452[a]	0.03[b]	0.001[b]	0.001
Hymenoptera	0.420	0	0.325	0.067	0.089
Orthoptera	0.110	0.033	0	0	0.253
Lepidoptera	0	0.167	0	0.073	0.511
Blattodea	0.060	0	0	0	0.188
Neuroptera	0[ab]	0.267[a]	0[ab]	0[b]	0.035

Table 3

Proportional dietary intake, by number of individuals, for the four *Ctenotus* species. *P*-values are for univariate ANOVAs on individual prey groups. The numbers of Isoptera, Araneae and Neuroptera consumed differed significantly between the four species. Numbers of prey items that are not significantly different are signified by the same superscript letter.

	Species				
Prey taxa	***C. atlas***	***C. brooksi***	***C. schomburgkii***	***C. xenopleura***	***P* of $F_{3,25}$**
Isoptera	0.401[a]	0[b]	0.708[c]	0.888[d]	<0.001
Formicidae	0	0.042	0.027	0.038	0.773
Coleoptera	0.135	0.098	0.071	0.018	0.166
Araneae	0.080[a]	0.390[b]	0.030[a]	0.001[a]	0.001
Hymenoptera	0.307	0	0.167	0.042	0.208
Orthoptera	0.029	0.042	0	0	0.361
Lepidoptera	0	0.167	0	0.012	0.119
Blattodea	0.100	0	0	0	0.188
Neuroptera	0[a]	0.260[b]	0[a]	0[a]	0.010

Table 4

Similarity between the volume of prey taxa consumed and microhabitat use for each species pair of *Ctenotus*, calculated using Pianka's Index. The rank of the similarities between each species pair is shown in brackets to the right of the value.

Species pair	**Diet**	**Microhabitat**
C. atlas vs *C. brooksi*	0.307 (4)	0.535 (6)
C. atlas vs *C. schomburgkii*	0.788 (1)	0.679 (4)
C. atlas vs *C. xenopleura*	0.459 (3)	0.991 (1)
C. brooksi vs *C. schomburgkii*	0.109 (5)	0.981 (2)
C. brooksi vs *C. xenopleura*	0.033 (6)	0.575 (5)
C. schomburgkii vs *C. xenopleura*	0.721 (2)	0.713 (3)

schomburgkii spent significantly more time in the Open than either *C. atlas* or *C. xenopleura* ($P < 0.05$). *C. brooksi* spent significantly less time in Spinifex than *C. atlas* and *C. xenopleura* ($P < 0.05$). *C. schomburgkii* spent significantly less time in Spinifex than *C. xenopleura* ($P < 0.05$). No other means were significantly different.

Relationships between diet and microhabitat use

There were differences in both diet and microhabitat use between the species. *C. brooksi* was different from *C. atlas* and *C. xenopleura* in both diet and microhabitat use, while the last two were similar to each other (Table 4). There was no significant relationship between similarity in diet and similarity in microhabitat use ($r_4 = -0.03$, $P = 0.960$).

Discussion

Despite differences between the four *Ctenotus* species in diet and microhabitat use, there was no obvious pattern to these differences between the species. Our prediction that *Ctenotus* species, being generalist foragers, would feed primarily on termites was only partially supported. *C. schomburgkii* and *C. xenopleura* did feed primarily on termites, but they were only one of the wide variety of items consumed by *C. atlas* for which they were ranked only fourth in terms of volume, although they were the most important taxa in terms of

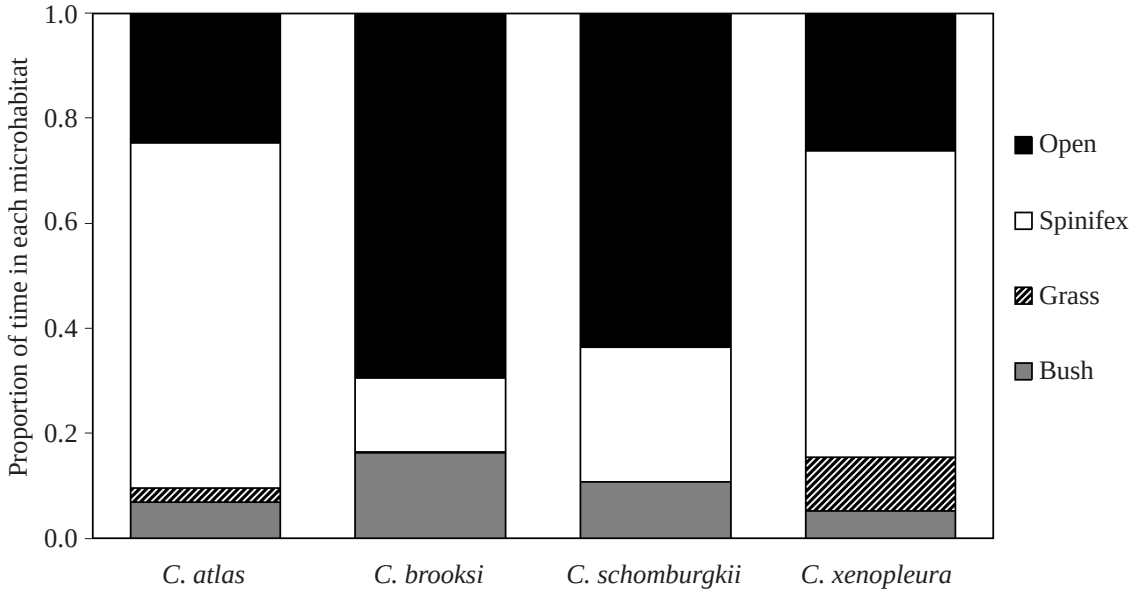

Figure 1. The proportion of time spent by each species of *Ctenotus* in the four microhabitats. *C. brooksi* and *C. schomburgkii* spent most of their time in the open while *C. atlas* and *C. xenopleura* spent most of their time in spinifex.

number of individuals. *C. brooksi* consumed no termites at all. These data need to be interpreted with caution as they were collected from one site at one time period, and lizards' diets are known to vary both spatially and temporally (James 1991a; Vitt & Colli 1994; Gadsden-Esparza and Palacios-Orona 1997; Vitt *et al.* 1998). The low volume of termites in the diet of *C. atlas* and the absence of termites in the diet of *C. brooksi* might be a reflection of when the study was conducted (cf. James 1991a), as the winter of 1992 was very wet. However, the dietary information for both these species is very similar to other studies conducted on these species at other sites over a range of wet and dry periods (Pianka 1969b, 1986), suggesting that the low volume of termites consumed by these species is not an artefact of the sampling period.

Microhabitat use appeared to reflect taxonomic relatedness, being most similar between the two species in the *C. schomburgkii* group (*C. brooksi* and *C. schomburgkii*) and the two species in the *C. atlas* group (*C. atlas* and *C. xenopleura*). The prediction that species with the greatest similarity in microhabitat use would show the greatest similarity in diet was not supported by our data. The main difference in diet was between *C. brooksi* and the other three species, with smaller differences recorded between *C. atlas*, *C. schomburgkii* and *C. xenopleura*. *C. schomburgkii* and *C. brooksi* had similar microhabitat preferences but consumed very different prey items, even though they are of similar size (Pianka 1969b; MDC, unpublished data). *C. atlas* and *C. xenopleura* also had very similar microhabitat preferences but had different diets. One possibility for the lack of concordance between diet and microhabitat use maybe that animals ingested prey items from pit-traps. However, our dietary information for *C. atlas*, *C. brooksi* and *C. schomburgkii* are similar to data from Pianka (1986), who collected his data from free-ranging animals. In addition, if animals were eating invertebrates from pit traps then we would expect the diet of all four species to be similar, which they are not suggesting that the dietary information collected was from free-ranging individuals. Therefore, we concluded that the lack of concordance between the dietary and microhabitat data indicates that the four *Ctenotus* species are not generalists, foraging opportunistically on whatever invertebrates they encounter, but may instead be using particular foraging strategies to locate specific prey items within their preferred microhabitats.

Neither prediction, based on the assumption that *Ctenotus* species are generalist foragers, was supported by this study. Our results need to be interpreted with caution, as the descriptions of both diet and microhabitat use were based on small sample sizes. Ten is typically considered to be a sufficient sample size to accurately describe diets (Winemiller *et al.* 2001), which is greater than our sample sizes for all species except *C. xenopleura*. However, both our microhabitat and dietary data for *C. atlas*, *C. brooksi* and *C. schomburgkii* are similar to data for these species in Pianka (1986), suggesting our data are an accurate description of diet and microhabitat in the four species studied. Different *Ctenotus* species may encounter similar prey items, preferentially feeding on certain prey items and avoiding others. This is unlikely, though, as captive *C. brooksi* fed freely on termites (MDC, personal observation), so they probably eat termites when encountering them in the field. Therefore, we concur with previous studies (Pianka 1969b; Archer *et al.* 1990; James 1991a; Read 1998) that *Ctenotus* species are not dietary specialists, but our results suggest that dietary differences between *Ctenotus* species studied here are likely to reflect different foraging strategies that result in them encountering different suites of invertebrates. Exactly how the foraging strategies might differ between species is not clear, as many *Ctenotus* species are very difficult to observe foraging in the field. Future research should concentrate on obtaining detailed information on *Ctenotus* species foraging in the field to determine to what extent species are specialised for specific prey items.

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