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## Diet and habitat use of frillneck lizards in a seasonal tropical environment

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**Abstract** A population of frillneck lizards, *Chlamydosaurus kingii*, was monitored by mark-recapture and telemetry over a 2 year period in Kakadu National Park. The aims of the study were to document changes in diet, growth, condition and habitat use between the wet and dry seasons of northern Australia, in light of recent research examining seasonal variation in the physiology of this species. Frillneck lizards feed on a diverse range of invertebrates in both seasons, even though there is a substantial reduction in food availability in the dry season. Harvester termites from the genus *Drepanotermes* constitute a major component of the diet, and the prevalence of termites in the diet of sedentary foragers in a tropical environment is unusual. Adult male body condition remained relatively stable throughout the year, but females experienced considerable variation. These differences are attributed to different reproductive roles of the sexes. Growth in *C. kingii* was restricted to the wet season, when food availability was high, and growth was minimal in the dry season when food availability was low. The method used in catching lizards was an important factor in determining seasonal habitat use. Telemetered lizards selected a significantly different distribution of tree species than was randomly available, and they selected significantly larger tree species during the dry season. Lizards spotted along roadsides showed little seasonal variation in the selection of tree species or tree sizes. The results suggest a comprehensive change in the ecology of this species, in response to an annual cycle of low food and moisture availability, followed by a period with few resource restrictions.

**Key words** *Chlamydosaurus kingii* · Seasonal ecology · Diet · Food availability · Habitat use

### Introduction

Seasonal variation in temperate and arid habitats has a significant effect on the activity, reproduction, resource acquisition, growth and habitat use of lizards (Huey et al. 1977; Dunham 1978; Ballinger and Congdon 1980; Rose 1981; Andrews 1982; Paulissen 1988). Comparative studies of lizard ecology and life history at the family level (predominantly iguanids) in these habitats have contributed significantly to current theories of life history strategies and general ecology (see Huey et al. 1983; Pianka 1986).

The understanding of the seasonal ecology of reptiles in the tropics is poor. Constant high ambient temperatures and high periodic annual rainfall combine to create a unique environment for reptiles. Studies of tropical lizard ecology have encompassed a variety of habitats (tropical savannas to closed rainforest) in several families, and they have revealed a surprising diversity of responses to seasonal variation (Sexton et al. 1972; Fleming and Hooker 1975; Christian et al. 1983; Floyd and Jenssen 1983; Vitt 1991a,b; Vitt and Blackburn 1991; Bullock et al. 1993; Marken Lichtenbelt 1993). This diversity and the relatively small number of studies limit tests of current ecological theories in tropical habitats.

Previous studies of lizard ecology in the wet-dry tropics of northern Australia are few considering the high species diversity of the region. Seasonal variation in the diet (James et al. 1984; Shine 1986), reproductive strategy (James and Shine 1985, 1988), thermoregulation and energetics (Christian and Green 1994; Christian and Bedford 1995) of lizards have provided a number of hypotheses relating to the evolution of certain life history strategies for lizards in this region.

Frillneck lizards (*Chlamydosaurus kingii*) inhabit open forests and woodlands, and are distributed across

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the northern (wet-dry) and eastern (temperate) parts of Australia (Cogger 1992). The general ecology of this species was studied by Shine and Lambeck (1989), but their field data were exclusively from the wet season. They revealed a diurnal, arboreal, "sit-and-wait" insectivorous lizard that is sexually dimorphic in body size with adult males considerably larger than adult females. Reproduction occurs exclusively during the wet season, and observations suggest they reduce their activity during the dry season. Frillneck lizards exhibit a significant reduction in body temperature, field metabolic rate and water turnover during the dry season (Christian and Green 1994; Christian and Bedford 1995).

The principal aim of this study is to establish how the ecology of the frillneck lizard changes between the wet and dry seasons, in light of the changes in their environment and physiology. The specific aspects of their ecology considered in this study are: diet and food availability, body condition and growth rate, habitat use and seasonal activity. This will allow an assessment of the strategies used by *C. kingii* to survive in a seasonally harsh environment in relation to other lizard species.

## Material and methods

### Site

All field work was done between April 1991 and April 1994 at Kapalga Research Station (CSIRO Division of Wildlife and Ecology) in Kakadu National Park (12° 43' S, 132° 26' E), 250 km east of Darwin, Northern Territory, Australia. This region experiences a distinct seasonal wet-dry climate. The wet season in Kakadu National Park (October to April) is characterised by high maximum (35 °C) and minimum (24 °C) air temperatures, high relative humidity (75% at 0900 hours) and high rainfall (1480 mm; 13 year averages from the Jabiru airport, Bureau of Meteorology). Rainfall is irregular and relatively low during the first months of the wet season (early wet season; October to December), becoming more consistent and higher during the second half (late wet season; January to April). The dry season (May to September) is characterised by high maximum (33 °C) but lower minimum (19 °C) air temperatures, lower relative humidity (57% at 0900 hours), and little or no rainfall (Bureau of Meteorology). The dry season may also be divided into an early dry season (May to July) when the soil and vegetation begin to dry out after the cessation of monsoonal rains, and a late dry season (August to September) when conditions are extremely dry.

The study was conducted in open forest dominated by *Eucalyptus tetrodonta*, *E. miniata*, *E. porrecta* and *Erythrophleum chlorostachys*, with an understorey dominated by tall annual grass *Sorghum* spp. The study area was based around a network of roads to facilitate the censuses of lizards. Data were collected from three areas approximately 400–500 ha in area and within 10 km of each other. For this current study, three sites are examined together due to their close proximity.

### Sampling

All frillneck lizards were originally sighted by driving slowly (< 30 km h<sup>-1</sup>) along the roads, and were either caught by hand or by a noose attached to a telescoping pole. At the initial capture, each lizard was given a unique identifying number with a transponder (Destron IDI) implanted subcutaneously under a loose fold of

skin in the neck area. At each capture the following data were recorded: date, time, mass to the nearest gram using an electronic balance (Bonso); and the snout-vent length (SVL) to the nearest millimetre using a clear ruler. Lizards were released at the exact point of capture within 2 h of capture. All field work was carried out between 0700 and 2000 hours.

A sub-sample of adult lizards ( $n = 55$ ) was fitted with small radio-transmitters to assist in data collection. Location transmitters (Biotrack SS-1 and Biotel TX-1) weighing approximately 15 g (2–6% of lizard body mass) were attached to the tail using a small amount of glue and adhesive bandage. After being fitted with transmitters, lizards were released at the exact point of capture within 12 h. Telemetered lizards were relocated a minimum of twice a month, and transmitters were changed every 3 months to replace the batteries.

The mark-recapture and telemetry study provided data on the diet, body condition, seasonal growth, habitat use and activity. Rainfall data were collected every 2 weeks at each site by the CSIRO Division of Wildlife and Ecology.

At initial capture (after April 1992) lizards with a SVL greater than 150 mm were stomach flushed. Stomach contents were stored in 70% ethyl alcohol for later analysis. Lizards recaptured within 6 months of the previous capture were not stomach flushed. Stomach contents were examined under a dissecting microscope and classified to order. Each prey item was assigned to one of five size classes by length (0–5 mm; 6–10 mm; 11–15 mm; 16–20 mm; > 20 mm). The volume for each prey taxa was estimated by the volumetric displacement (in a graduated measuring cylinder  $\pm 0.1$  ml) of a representative sub-samples from each of the five size classes, and then all sizes classes were added together.

Food availability was measured by sweep-netting the foliage (0–2 m above the ground) for invertebrates (Stamps and Tanaka 1981) every 3 months at each site. Ten samples of 30 sweeps were collected for each sampling period at the three sites (total of 900 sweeps per sampling period). Samples were collected along line transects, and no foliage was swept twice. The contents of the net were preserved with 70% ethyl alcohol. Samples were later sorted to the level of order, and into five size classes (as with stomach contents).

Data from the following habitat variables were collected at each capture or sighting of *C. kingii*: tree species, tree height (m) and perch height (m) of the lizard, using a clinometer (Suunto), and trunk diameter (cm) at breast height, using a calibrated tape measure. An estimate of the frequency distribution of tree species in the study area was determined using a random walk sampling method (Goldsmith and Harrison 1976). A minimum distance of 30 m between each sampling point was set to avoid concentration of samples within a confined area.

### Analyses

Seasonal analyses were carried out by either dividing the data into two seasons (dry = May to September; wet = October to April), or, when sample sizes were large and evenly spread across the year, four seasons (late wet = January to March; early dry = April to June; late dry = July to September; early wet = October to December).

Diets were analysed using three measures: (1) the relative abundance (percentage) of total prey items, (2) the relative volume (percentage) of prey taxa; and (3) the occurrence (percentage) of one or more items of a particular prey taxon in the stomach contents. A non-parametric Mann-Whitney *U*-test was used (due to the non-normal distributions) to test for seasonal differences in the number of prey orders and prey size classes. Seasonal differences in the abundance of prey taxa in the stomach contents, and the availability of prey in the field were analysed using contingency tables. The relative volume of prey taxa was analysed using a Kolmogorov-Smirnov non-parametric test. Simpson's diversity index ( $D$ ) was used to determine seasonal changes in dietary diversity:

$$D = 1 - \sum(\phi_i)^2$$

where  $\phi_i$  is either relative abundance or relative volume of each prey taxa in the stomach contents. This index ranges from 0 (low diversity) to a maximum of  $(1 - 1/S)$ , where  $S$  is the number of prey taxa (Krebs 1985).

Body condition was determined by plotting  $\log_{10}$  transformed body mass against  $\log_{10}$  transformed SVL of adult males (SVL > 230 mm) and non-gravid adult females (SVL > 175 mm). This analysis was restricted to the adult population in order to minimise the effect of the high growth rate of juvenile lizards prior to sexual maturity (Griffiths 1994). A linear regression was applied to these data, giving a mean body condition for both adult males and females. The residual deviation from the regression is indicative of an individual's body condition, corrected for different body lengths (James 1991a). Differences in residual deviations between sexes were determined using an unpaired  $t$ -test, and a one-way ANOVA was used to test for seasonal differences.

Seasonal growth rates were calculated from lizards caught more than twice within a single dry or a single wet season. Seasonal growth rates (grams per day) were determined by dividing the change in SVL by the number of days between the first and last capture (within a single season). Seasonal difference in growth rate (grams per day) was tested using a Mann-Whitney  $U$ -test. Contingency table analysis tested for differences in the relative frequency of tree species used by frillneck lizards between seasons. Seasonal differences in the habitat use of lizards (tree height, trunk diameter and lizard perch height) were analysed using one-way ANOVA. An index of activity was calculated by dividing the total number of lizards sighted during daily car censuses by the number of kilometres driven during each field census. This index is an indirect measurement of the population's general activity, not an individual animal's activity. Censuses were pooled into four seasons and tested by Kruskal-Wallis one-way ANOVA. All means are presented with 1 SE unless specified.

## Results

### Rainfall

The onset of monsoonal rains occurred in November or December of each year and the highest monthly

rainfall was recorded either in January or February of each year. The cessation of rainfall was similar among the consecutive wet seasons, with minimal rainfall occurring after April in each year. Total rainfall for the 1991–1992, 1992–1993, 1993–1994 wet seasons were 1116 mm, 1410 mm, and 1307 mm, respectively.

### Diet

A total of 226 samples of stomach contents were collected between May 1992 and April 1994. Preliminary analyses revealed no significant differences between sexes in the number of prey taxa, the number of size classes of prey or the taxonomic composition of the diet, therefore the results presented here are for both sexes combined. Table 1 summarises the occurrence, relative abundance and relative volume of prey taxa for stomach contents of *C. kingii* for the dry and wet seasons.

A total of 15 invertebrate orders were recorded from 144 dry season stomach samples. Stomachs contained a mean of  $2.85 \pm 0.12$  invertebrate orders and a mean of  $77.85 \pm 9.15$  items. A total of 15 invertebrate orders were recorded from 82 wet season stomach samples. Stomachs contained a mean of  $3.96 \pm 0.19$  prey taxa and a mean of  $79.62 \pm 11.75$  prey items. The number of prey orders per stomach sample is a broad indicator of the diversity of prey taxa in the *C. kingii* diet, and the wet season diet contained significantly more orders (Mann-Whitney  $U$ -test:  $z = 4.79$ ,  $P < 0.0001$ ). There was no significant difference in the total number of items per stomach between wet and dry season samples ( $t = 0.73$ ,  $df = 226$ ,  $P = 0.43$ ). However, the mean volume of food was significantly greater in the wet season (Christian et al. 1996).

**Table 1** Occurrence, relative abundance and relative volume of prey taxa present in stomach samples of *Chlamydosaurus kingii* during the dry and wet seasons

Prey taxa	Dry season			Wet season		
	Occurrence (%)	Abundance (%)	Volume (%)	Occurrence (%)	Abundance (%)	Volume (%)
Isoptera	36.8	73.3	33.6	57.0	76.8	20.0
Orthoptera	25.7	0.5	15.9	32.9	0.6	9.2
Hemiptera	27.8	0.8	3.8	12.2	1.0	2.3
Coleoptera	18.7	0.6	3.4	51.2	1.7	3.9
Diptera	5.5	0.1	1.4	5.7	0.2	0.4
Lepidoptera	25.0	0.4	3.7	59.7	9.1	40.4
Hymenoptera	66.7	23.4	5.2	68.3	8.9	2.1
Blattodea	4.2	0.1	1.1	6.1	0.2	0.3
Mantodea	1.4	0.01	1.0	1.2	0.01	0.1
Odonata	2.8	0.04	1.9	6.1	0.1	2.7
Phasmatodea	6.9	0.1	3.6	3.7	0.05	0.5
Aranea	9.0	0.1	1.6	13.4	0.4	0.5
Plecoptera	2.8	0.1	1.1	1.2	0.01	0.4
Chilopoda	30.5	0.5	21.8	36.6	0.8	16.1
Gastropoda	2.8	0.03	0.6	7.3	0.1	0.8
Other	1.4	0.02	0.3	2.4	0.03	0.3
Totals	$n = 144$	$n = 11212$	445 (ml)	$n = 82$	$n = 6529$	762 (ml)
Simpson's diversity index		0.635	0.808		0.393	0.759

The relative abundance of prey taxa differed significantly between the wet and dry seasons ( $\chi^2 = 1428.54$ ,  $df = 7$ ,  $P < 0.0001$ ). The relative volume of prey taxa also differed significantly between the wet and dry seasons (Kolmogorov-Smirnov:  $D = 0.23$ ,  $df = 14$ ,  $P = 0.014$ ). Inspection of Table 1 indicates that the variation in relative abundance and relative volume of Hymenoptera, Lepidoptera and Isoptera accounts for much of the difference between the two seasons. Simpson's diversity index of the relative volume suggests a similar diversity of prey taxa present in the dry and wet seasons (Table 1). The diversity index of the relative abundance of prey taxa suggests that stomach samples collected during the dry season contain a higher diversity of prey taxa than wet season samples.

The relative abundance of prey taxa in the dry season was dominated by the order Isoptera, comprising 73.3% of all items present. Only one species of Isoptera was identified from these stomach samples, *Drepanotermes rubriceps* (A. Anderson, personal communication), and most of these were soldiers. There is some taxonomic confusion within this genus, and these termites will be referred to as *Drepanotermes* spp. *Drepanotermes* spp. occurred in 36.8% of the dry season stomachs samples, representing 33.6% of the relative volume. Another important dry season prey taxon in the stomach samples was the Chilopoda (centipedes). The low relative abundance of Chilopoda (< 1%), is misrepresentative of its importance as a food item for frillneck lizards. Most Chilopoda present in stomach samples (77%) had a large body length (> 20 mm), and therefore the relative volume of 21.8% is more indicative of the importance of centipedes in the dry season diet. Similarly, Orthoptera comprised 14.9% of the relative volume, although relative abundance was low (0.5%). Hymenoptera exhibited a high relative abundance, comprising 23.4% of the total number of prey items taken and was the most common prey taxon in the dry season stomach samples (66.7% occurrence). However, due to the small body length of ants (< 5 mm), they comprised only 5.17% of the relative volume.

Dietary composition during the wet season was dominated by three prey taxa: Lepidoptera, Isoptera and Chilopoda (Table 1). Lepidoptera (larvae) were present in a high proportion of stomachs (59.7%), and contributed substantially to the relative volume (40.4%). The relative volume of Isoptera was lower in the wet season samples compared to the dry season, probably due to the high volume of Lepidoptera. Hymenoptera also occurred in a high proportion of samples in the wet season, but the contribution to the relative volume of the diet remained small.

### Food availability

Table 2 shows the total number and relative abundance of invertebrate orders collected from sweep-netting over

**Table 2** The number and relative abundance (%) of invertebrate orders from sweep-netting during the dry and wet seasons

Invertebrate orders	Dry season		Wet season		June 1993		Dry season		Wet season		
	May 1992	August 1992	December 1992	March 1993	No.	%	August 1993	No.	%	November 1993	February 1994
Orthoptera	32	32	131	142	23	14.8	15	5.5	5.3	221	235
Hemiptera	58	21	40	82	40	8.5	34	9.6	12.1	19	86
Coleoptera	37	20	164	217	78	22.6	22	18.7	7.8	61	211
Diptera	8	18	48	50	40	5.2	43	9.6	15.3	35	71
Lepidoptera	7	3	50	114	7	11.9	1	1.7	0.3	4	24
Hymenoptera	89	71	71	130	191	13.5	125	45.8	44.5	99	183
Blattodea	-	-	5	13	-	1.4	1	-	0.4	2	22
Mantodea	1	1	1	1	-	0.1	-	-	-	-	1
Phasmatodea	6	1	-	20	1	2.1	-	0.2	-	1	107
Araneae	62	29	28	146	29	15.2	49	7.0	17.4	67	16
Plecoptera	-	-	1	7	-	0.8	-	-	-	1	-
Total no. items	303	189	542	961	417	417	281	513	513	1032	1032

2 years. Each sample period is the sum of three permanent sites. A total of 12 invertebrate orders were collected using this method. It should be noted that this method of sampling (sweep-netting) failed to sample some important invertebrate orders that were present in stomach samples of *C. kingii*, namely Isoptera and Chilopoda. There were fewer orders of invertebrates in the dry season samples compared to wet season samples. Dry season samples contained a high relative abundance of Hymenoptera, Orthoptera, Aranea, Hemiptera and Coleoptera (Table 2). Wet season samples contained a high relative abundance of Orthoptera, Coleoptera and Hymenoptera (Table 2). Invertebrates were most abundant in the wet season samples ( $F_{1,18} = 27.19$ ,  $P < 0.0001$ ).

### Body condition

The body mass at a given SVL (body condition) of adult males was significantly larger than adult females ( $t = 3.27$ ,  $df = 372$ ,  $P = 0.001$ ). Therefore, body condition was analysed in separate linear regressions for adult males and females. Male body condition differed significantly among the four seasonal periods ( $F_{3,273} = 3.38$ ,  $P = 0.019$ ). Tukey's comparison of means test indicated that the early wet season sample mean was significantly lower than the other three periods. Female body condition also differed significantly among the four seasonal periods ( $F_{3,110} = 3.14$ ,  $P = 0.028$ ). Tukey's comparison of means test indicated two groups of significantly different mean residuals, one group included the early wet and early dry seasons with relatively high residuals, and the second group included the late wet and late dry seasons with low residuals.

### Seasonal growth rate

Mean dry season growth rates were negligible for both male (mean =  $0.009 \pm 0.004$  mm,  $n = 36$ ) and female (mean =  $0.005 \pm 0.003$  mm,  $n = 9$ ) lizards, and there was no significant difference between the sexes ( $t = 0.58$ ,  $df = 44$ ,  $P = 0.39$ ). Growth rates were calculated over a mean of  $90.2 (\pm 4.3, n = 45)$  days in the dry season sample, and only 27% of the lizards recorded growth. The SVL of lizards did not influence growth; that is, both sub-adults and adults responded similarly to the dry season conditions.

Individuals were recaptured over a mean of  $73.6 (\pm 5.5, n = 24)$  days during the wet season, and exhibited significantly higher seasonal growth rates compared to the dry season ( $t = 3.55$ ,  $df = 23$ ,  $P = 0.001$ ). However, seasonal growth rates of the large adult lizards (males SVL > 240 mm, females SVL > 210 mm) during the wet season were small. These individuals had either reached or were close to their maximum body size, and growth was therefore negligible (Griffiths

1994). Due to the influence of body length in this relationship, ANCOVA was used to test for a difference in seasonal growth rate between the sexes. There was no significant difference (slopes,  $F_{1,20} = 0.076$ ,  $P = 0.78$ ; intercept,  $F_{1,21} = 1.82$ ,  $P = 0.19$ ) in seasonal growth between males (mean =  $0.108 \pm 0.037$ ,  $n = 14$ ) and females (mean =  $0.110 \pm 0.028$ ,  $n = 10$ ).

### Habitat use

Two methods were used to acquire data relating to habitat use, and these methods have important implications for the interpretation of these results. The first method involved locating frillneck lizards from a moving vehicle, and the second method involved relocating the lizards fitted with radio transmitters. The first method of locating lizards may be biased in three ways, and the bias is related to the fact that most lizards (90–98%) were perched on vertical tree trunks: (1) different sizes of the tree trunks may alter the probability of sighting an individual, (2) agamid lizards tend to move to the opposite side of a tree trunk when approached or disturbed (Greer 1989), and this may influence the probability of sighting, and (3) lizards perched on vertical trunks may be involved in foraging, social interactions, and predation avoidance (Stamps 1977a; Shine 1990). Relocating lizards using telemetry should not be influenced by these three factors. Therefore, the data have been divided into two groups, data from lizards with radio transmitters (telemetered) and data from lizards without radiotransmitters (non-telemetered).

Preliminary analysis indicated no differences between the sexes in the frequency distributions of tree species used; therefore, males and females were combined in the subsequent analyses. Sightings of lizards located on the ground were not included in the statistical analysis. To determine if the data were biased by repeated observations, the frequency distribution of tree species used by 6 adult males with transmitters (five observations each) was compared to the distribution of trees used by 30 adult males (single observation each). Chi-square analysis revealed no significant difference in the frequency distributions of tree species used by lizards for repeated and single observations ( $\chi^2 = 0.37$ ,  $df = 2$ ,  $P = 0.832$ ).

There was no significant difference in the frequency distributions of tree species occupied by telemetered lizards between the dry and wet seasons ( $\chi^2 = 8.87$ ,  $df = 7$ ,  $P = 0.262$ ). Telemetered lizards frequently occupied *Eucalyptus tetradonta*, with highest use of this species occurring in the dry season (Table 3). During the wet season, telemetered lizards increased their use of the sand palm (*Livistona humilis*) and dead trees, and a higher proportion of lizards were located on the ground. Compared to the random sample of tree

**Table 3** The relative abundance (%) of tree species used by telemetered and non-telemetered frillneck lizards during the wet and dry seasons, and the relative abundance (%) of tree species available in the field as determined by a random walk technique

Tree species	Telemetered		Non-telemetered		Random (%)
	Dry season (%)	Wet season (%)	Dry season (%)	Wet season (%)	
<i>Eucalyptus tetradonta</i>	50.0	43.8	28.7	30.1	29.5
<i>Eucalyptus porrecta</i>	11.2	11.5	12.4	12.0	12.1
<i>Eucalyptus miniata</i>	7.3	6.9	17.1	7.6	18.8
<i>Erythrophleum chlorostachys</i>	11.5	10.0	6.2	6.9	9.2
<i>Terminalia ferdinandiana</i>	3.9	2.3	4.7	1.8	4.6
<i>Livistona humilis</i>	3.9	8.5	5.4	11.2	3.4
<i>Planchonia careya</i>	1.1	1.5	2.3	0.7	0.5
<i>Buchanania obvata</i>	0.6	0.8	–	–	0.5
<i>Petalostigma pubescens</i>	1.1	–	–	0.4	0.7
<i>Xanthostemon paradoxus</i>	0.6	–	–	1.8	0.5
<i>Eucalyptus tectifera</i>	1.1	–	–	0.4	0.2
<i>Eucalyptus bleeseri</i>	0.8	–	–	–	1.4
<i>Eucalyptus clavigera</i>	–	0.8	–	–	0.2
<i>Eucalyptus confertiflora</i>	0.3	–	–	–	–
<i>Owenia vernicosa</i>	0.3	–	–	–	0.2
<i>Acacia mimula</i>	0.3	–	–	–	1.8
<i>Terminalia latipes</i>	–	–	–	0.4	0.2
<i>Terminalia grandiflora</i>	0.3	–	–	–	–
<i>Syzygium suborbiculare</i>	–	1.5	–	–	0.5
<i>Planchonella pohlmaniana</i>	–	0.8	–	–	–
<i>Melaleuca nervosa</i>	0.8	–	–	–	–
<i>Cochlospermum fraseri</i>	0.8	–	–	–	–
<i>Grevillea pteridifolia</i>	0.3	–	–	–	–
Dead tree	2.8	6.2	13.2	15.6	12.1
Ground	1.6	4.6	8.5	10.9	–
Total number of trees (n)	356	130	129	276	437

species in the study area, telemetered lizards used a significantly different distribution of species in both dry and wet seasons (dry season,  $\chi^2 = 63.52$ ,  $df = 7$ ,  $P < 0.0001$ ; wet season,  $\chi^2 = 26.87$ ,  $df = 7$ ,  $P = 0.0004$ ). The telemetered lizards used a much higher proportion of *E. tetradonta* than was randomly available, and they underused *E. miniata* (Table 3).

There was no significant difference in the frequency distribution of tree species used by non-telemetered lizards between the dry and wet seasons ( $\chi^2 = 13.45$ ,  $df = 7$ ,  $P = 0.062$ ). The frequency distribution of tree species used by these lizards during the dry season closely reflected the distribution of randomly available trees ( $\chi^2 = 6.55$ ,  $df = 7$ ,  $P = 0.477$ ). However, during the wet season, they did not select trees according to availability ( $\chi^2 = 44.55$ ,  $df = 7$ ,  $P < 0.0001$ ). Inspection of Table 3 reveals an underusage of *E. miniata*, and a higher than random use of the sand palm, *L. humilis*, during this season. A within-season comparison of the tree species used by telemetered and non-telemetered lizards revealed a highly significant difference in the dry season between the two groups, but this was not evident in the wet season (dry season,  $\chi^2 = 44.88$ ,  $df = 7$ ,  $P < 0.0001$ ; wet season,  $\chi^2 = 13.75$ ,  $df = 7$ ,  $P = 0.056$ ) (Table 3).

The sampling bias described in the previous paragraphs was also evident with respect to the structural habitat in which the lizards were found. Telemetered lizards were located on significantly larger trees than non-telemetered lizards (tree height,

$t = 11.06$ ,  $df = 737$ ,  $P < 0.0001$ ; trunk diameter,  $t = 14.69$ ,  $df = 737$ ,  $P < 0.0001$ ). Therefore, it was necessary to analyse the two groups separately. Telemetered lizards used larger trees and were perched higher in the early and late dry seasons (Fig. 1). However, trunk diameter was the only variable that was significantly different over the four seasons (ANOVA:  $F_{3,441} = 8.71$ ,  $P < 0.0001$ ). Tukey's comparison of means test indicated that the mean trunk diameter of the trees used in the early dry season was significantly larger than the other three periods.

The height and trunk diameter of trees used by non-telemetered lizards remained extremely constant throughout the four seasons (Fig. 1). However, the perch heights used by these lizards were significantly different (ANOVA:  $F_{3,308} = 9.09$ ,  $P < 0.0001$ ) over the four seasons. Tukey's comparison of means test indicated that the mean of the early dry season period was significantly lower than the late dry and early wet season periods, but not significantly different from the late wet season period.

#### Seasonal activity index

The number of lizards captured or sighted per kilometre from a vehicle during censuses changed substantially throughout the year (Fig. 2). This index showed that the largest number of lizards was sighted between November and February, and the lowest

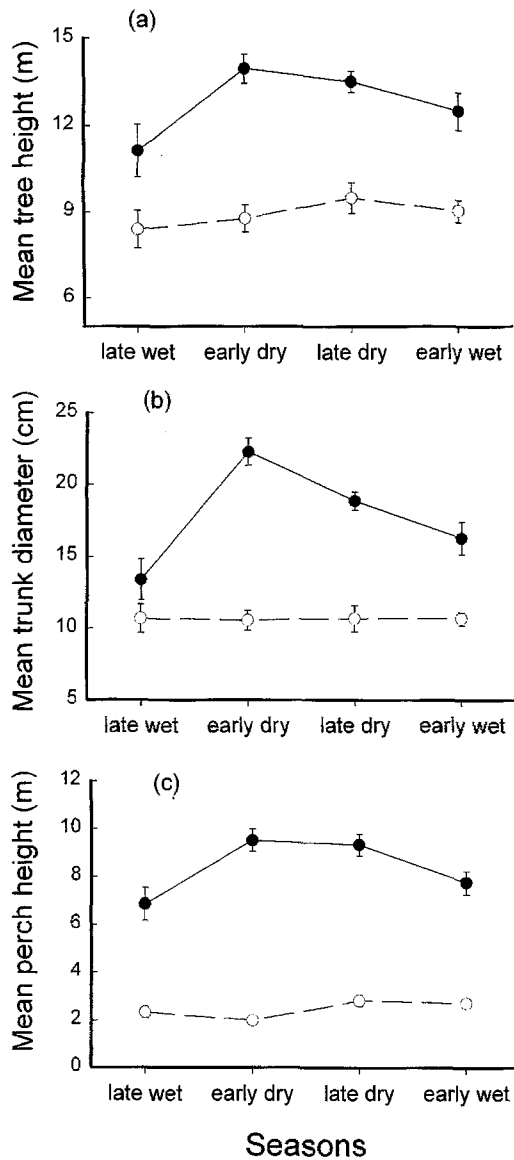


Fig. 1a-c The seasonal habitat use of telemetered (closed circles) and non-telemetered (open circles) frillneck lizards. The three graphs are: a mean height of trees, b the mean trunk diameter, and c mean perch height of lizards. Error bars are 1SE

number of lizards from June through to August. A large increase occurred in the index between October and November, the period coinciding with the beginning of the frillneck lizard reproductive season (Shine and Lambeck 1989). The pooling of monthly data into four seasonal periods produced unequal variances between the four sample periods, therefore a Kruskal-Wallis one-way ANOVA was used to test for differences among seasons. There was a significant difference among the four seasons ( $z = 31.73, P < 0.0001$ ). Inspection of the activity index means indicated that the two wet season periods were higher than the two dry season periods.

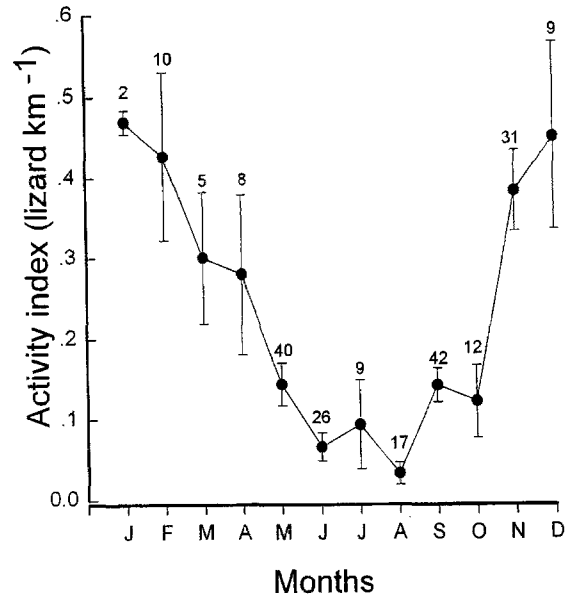


Fig. 2 Monthly variation in the number of lizards sighted or captured per kilometre driven during routine censuses of sites. Numbers are sample sizes, and error bars are 1 SE. The graph represents 2 years of data combined

### Discussion

Frillneck lizards undergo seasonal changes with respect to diet, condition, growth, habitat use and activity. The dry season is characterised by a decrease in the activity of frillneck lizards, and selection of large trees and canopy perches. The reduction in food is reflected in reduced growth rates, although general body condition remains relatively stable. The lizards continue to feed on a diverse array of invertebrates despite the low abundance of invertebrates. Termites, centipedes and ants are common prey items. The wet season is characterised by an increase in activity, and the selection of shorter trees with small diameters. This increase in activity and associated changes in this species coincides with four ecologically significant events: (1) an increase in ambient temperature and relative humidity, (2) the onset of rainfall, (3) an increase in food availability, and (4) the onset of the reproductive period. The relative importance of these four factors is unclear, but they are probably all important.

One of the most interesting aspects of the prey taken by *C. kingii* is the high incidence of the harvester termite, *Drepanotermes* spp., in the diet throughout the year. Termites are an important food source for many species of lizards in arid environments (Pianka 1986; Morton and James 1988; James 1991b; Abensperg-Traun 1994). The presence of termites in the diet of lizards has been related to the foraging mode of both predator and prey in arid habitats (Huey and Pianka 1981). Lizards that are primarily sedentary in locating prey or "sit-and-wait" foragers (in arid habitats) tend

**Table 4** A summary of tropical lizards' foraging strategy, habitat, and the relative abundance of ants and termites in their diets (*SW* sit-and-wait, *WF* widely foraging)

Species	Climate	Foraging mode <sup>a</sup>	Habitat type	Diurnal?	Ants (%)	Termites (%)	Reference
<i>Chlamydosaurus kingii</i>	Wet-dry	SW	Open forest	Yes	18.1	74.6	This study
<i>C. kingii</i>	Wet-dry	SW	Open forest	Yes	26.5	56.2	Shine and Lambeck 1989
<i>Anolis auratus</i>	Wet-dry	SW	Open forest	Yes	75.0	0	Magnusson et al. 1985
<i>A. opalinus</i>	Wet-dry	SW	Open forest	Yes	69.4	0	Floyd and Jenssen 1983
<i>A. cupreus</i>	Wet-dry	SW	Open forest	Yes	34.3	0	Fleming and Hooker 1975
<i>A. aeneus</i>	Wet-dry	SW	Closed forest	Yes	31.5	0	Stamps et al. 1981
<i>A. ocellatus</i>	Wet	SW	Closed forest	Yes	46.8	5.2	Bullock et al. 1993
<i>Corytophanes cristatus</i>	Wet	SW	Closed forest	Yes	0	0	Andrews 1979
<i>Plica plica</i>	Wet-dry	SW	Closed forest	Yes	61.1	0	Vitt 1991b
<i>Uranoscodon superciliosum</i>	Wet-dry	SW	Closed forest	Both	24.3	0	Howland et al. 1990
<i>Tropidurus</i> spp (4 species)	Wet-dry	?	Open forest	Yes	42.3	44.7	Vitt 1993
<i>Kentropyx calcarata</i>	Wet-dry	WF	Open forest	Yes	2.8	3.1	Vitt 1991a
<i>K. striatus</i>	Wet-dry	WF	Open forest	Yes	45.0	20.0	Magnusson et al. 1985
<i>Ameiva ameiva</i>	Wet-dry	WF	Open forest	Yes	5.0	75.0	Magnusson et al. 1985
<i>Cnemidophorus lemniscatus</i>	Wet-dry	WF	Open forest	Yes	25.0	60.0	Magnusson et al. 1985
<i>C. deppii</i>	Wet-dry	WF	Coastal	Yes	2.3	86.6	Vitt et al. 1993
<i>Mabuya bistriata</i>	Wet-dry	WF	Closed forest	Yes	9.0	45.1	Vitt and Blackburn 1991

to encounter and eat fairly mobile prey (e.g. ants, centipedes), whereas more actively foraging lizards consume less active prey (e.g. termites, caterpillars) (Huey and Pianka 1981). Table 4 summarises studies of tropical lizards with respect to foraging mode and termite prey. The proportion of termites in the diets of six species of tropical "sit-and-wait" lizards (excluding *C. kingii*) in open and closed forests was negligible, whereas the proportion of ants was generally high. In contrast, the diets of active foraging lizards in tropical habitats included a substantial proportion of termite prey, and relatively fewer ant prey. This relationship supports the foraging strategy hypothesis of Huey and Pianka (1981). The saxicoline *Tropidurus* group consume a high numbers of both social insect prey groups. Comparisons of this genus are problematic as they may use a range of foraging strategies, and they also consume some plant material. The presence of a large proportion of both termites and ants in the diet of *C. kingii* is clearly distinct. Considering the almost exclusive "sit-and-wait" foraging strategy used by this species (Shine and Lambeck 1989), the presence of high proportion of termites appears to be an exception to the generalisation of Huey and Pianka (1981) regarding other tropical lizards. However, the presence of other mobile prey (Orthoptera and Chilopoda) in the diet of *C. kingii*, broadly supports the pattern of a sedentary predator consuming mobile prey.

Much of the discussion of the prevalence of termites in the diet of lizards is based on the assumption that the spatial distribution of termites is unpredictable (Wilson and Clark 1977, as cited in Huey and Pianka 1981). There are two possible explanations why this relationship does not hold for frillneck lizards and harvester termites. Firstly, *Drepanotermes* spp. may have a more even spatial distribution or higher density than is generally considered to be the case for termites. The

density and spatial distribution of *Drepanotermes* spp. in tropical open forests of Australia is unknown, but density estimates of *Drepanotermes* spp. in arid habitats may be as high as 200 mounds ha<sup>-1</sup> (Watson and Perry 1981). A high density of termites would increase their predictability and availability to both "active" and "sit-and-wait" foragers. Secondly, the above-ground activity during the day throughout the year by harvester termites allows *C. kingii* access to a seemingly large, and relatively constant food resource. This suggests that these termites are active throughout the year at Kapalga and contrasts with previous statements that foraging in *Drepanotermes* spp. is restricted to summer months in arid and temperate habitats (Watson 1974; Watson and Perry 1981; Park et al. 1993). This may be an important factor in the diet of *C. kingii*, especially during the dry season when other food sources are relatively low. This food supply may also be available to other "sit-and-wait" insectivorous lizards, as well as actively foraging insectivorous lizards in the seasonal tropics of Australia, and warrants further investigation.

Reduced growth during periods of low food and water availability has been well documented in lizards from arid environments (Stamps 1977b; Dunham 1978; Ballinger and Congdon 1980; Stamps and Tanaka 1981; Andrews 1982), and *C. kingii* in the seasonal tropics follow this pattern. Feeding continues throughout the dry season (Christian et al. 1996), but the volume of food taken in this season is apparently not sufficient to support growth in either juvenile or adult frillneck lizards.

The body condition of male *C. kingii* decreased during the early wet season, but they were able to maintain a relatively constant level of body condition throughout the dry season, even though there is a marked reduction in food availability during this season (Table 2; Churchill 1994). Males actively defend



their home range during the reproductive season (October to April) by using spectacular displays and combat (Shine and Lambeck 1989; Shine 1990), and it is likely that these and other activities associated with sexual activity are responsible for the drop in male body condition. This decrease in body condition during the reproductive season is consistent with males of other tropical lizard species (Fleming and Hooker 1975; Floyd and Jenssen 1983; Howland et al. 1990). Female *C. kingii* exhibit a more variable pattern of body condition across the seasons, with low body condition in the late wet season and the late dry season. Again, expenditure of energy for reproduction may explain the drop in body condition.

Trees are an important component of the habitat used by *C. kingii*. Over 95% of all lizards in this study were located in trees of a large number of species, and this concurs with previous observations (Shine and Lambeck 1989). The way habitat data were collected should be considered for the interpretation of the data presented here. If only non-telemetered lizards were used in this study of seasonal habitat use, then the conclusion would have been that frillneck lizards perch close to the ground on small trees from randomly available tree species throughout the year. However, telemetered lizards revealed that in the dry season frillneck lizards select significantly larger trees and a significantly different distribution of trees species than available (with a strong preference for *E. tetradonta*).

Lizards perched on vertical tree trunks may be engaged in foraging or social behaviour (Stamps 1977a), and this behaviour may change seasonally because of social (Zucker 1986) and resource factors (Scott et al. 1976). It is suggested here that frillneck lizards perched close to the ground on smaller trees are probably engaged in foraging or social behaviour, and the selection of this perch remains constant regardless of seasonal changes in reproductive condition and food availability. Lizards perched higher in the canopy are considered to be relatively inactive and use this perch as a refuge (Christian and Green 1994). This perch position does change seasonally and is part of an overall strategy of reduced energy expenditure in the dry season. The lizards perched lower in the trees are more visible than those perched high in the canopy, and thus the data from non-telemetered lizards are biased towards the individual engaged in foraging and social behaviour.

The seasonal ecology of the frillneck lizard is a unique combination of both behavioural and physiological change, which enables it to successfully inhabit an environment that is subject to extremes. Many of these strategies have been observed in other lizard species from both arid and tropical environments. However, aspects of the frillneck lizards' ecology indicates that differences between other lizard species from other continents and climatic regions do exist. The importance of these differences

will be further understood with continued research in this region of Australia, and other tropical regions of the world.

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