



Chameleons on the cruise: seasonal differences in prey choice of two dwarf chameleons

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Chameleons exhibit unique foraging behaviour among lizards. They are classified as cruise foragers, an intermediate foraging mode between sit-and-wait and active foraging, but it is not known whether cruise foraging is seasonally adaptive. Seasonal changes in stomach contents and available prey were quantified for two dwarf chameleon species: *Bradypodion ventrale* from coastal thicket habitats and *B. taeniabronchum* from montane fynbos habitat. Around twice the number of invertebrates were available in the fynbos and thicket habitats during summer; moreover the volume of invertebrates available during summer was approximately double. We found that chameleons increased the number of food items in winter to equal summer stomach volumes, and these changes were particularly evident for the montane species *B. taeniabronchum*. Winter austerity was shown for both chameleons as they were more likely to take hard prey in winter, compared to summer when hard prey items were avoided.

Key words: *Bradypodion*, cruise foraging, electivity, fynbos, lizards, predator-prey, thicket

INTRODUCTION

Predators have classically been divided into active foragers, which move through the environment in search of prey, and sit-and-wait foragers, which remain in position for long periods of time and striking when prey comes into reach (Schwenk, 2000). However, most lizards probably forage in a continuum with these strategies at extremes (Huey & Pianka, 1981; Magnusson et al., 1985; Eifler & Eifler, 1999; Perry, 1999; Greeff & Whiting, 2000; Butler, 2005; Hagey et al., 2010). Lizards which forage more actively search for sedentary prey while evasive prey is rarely encountered, and consequently the proportion of sedentary prey in their diet is elevated compared to the potential prey in the environment. Conversely, sit-and-wait foraging lizards rarely encounter sedentary prey and have a higher proportion of active prey in their diet. Changes in the abundance and distribution of prey may then impact on the foraging strategy of some lizards.

As ectotherms, lizards are prone to seasonal changes in climate affecting their foraging performance. In addition, density and size of prey also change seasonally and some lizards have been found to adjust their intake accordingly. In a study of the Jamaican anole (*Anolis opalinus*), Floyd and Jenssen (1983) found that while lizards ate more but smaller prey during the dry season, the total volume did not change compared with wet season prey. Thus they attributed the differences to seasonal fluctuations in prey availability and size. Another study on *A. nebulosus* foraging behaviour showed that feeding rates doubled with prey density in the wet season, and that these

lizards shifted from mainly arboreal to mainly terrestrial foraging in the dry season (Lister & Aguayo, 1992). Seasonal changes are likely to be stronger at higher elevations and may be associated with some habitat types more than others.

Chameleons are Afro-Eurasian, slow moving carnivorous lizards with iconic morphologies linked to their performance as predominantly arboreal foragers (Herrel et al., 2013). Butler (2005) proposed that chameleons should be classified as cruise foragers, a foraging mode intermediate between active and sit-and-wait foraging. Cruise foragers make long, slow movements within their environments, which increases encounters with sedentary prey and evasive prey are consumed when the chameleons pause (Regal, 1983; Butler, 2005; Measey et al., in press). It has been suggested that chameleons developed their foraging mode as a result of their unique morphology (Hagey et al., 2010).

Dwarf chameleons (Genus: *Bradypodion*) are a speciose group endemic to southern Africa, and the foraging behaviour of one species has been studied during summer months (Butler, 2005; Measey et al., 2011), but it is not known what consequences seasonal change will have. For example, prey items may be more or less abundant, but they could also be larger or smaller so that their predators have to consume differing quantities to gain sufficient dietary volume. Chameleons are primarily insectivorous and their prey is highly responsive to seasonal change (Schowalter, 2011; Measey et al., in press). Commensurate with changes in prey type, size and abundance, we predict that foraging behaviour of

insectivorous predators will also change, and as cruise-foragers, we may expect chameleons to become more or less active as prey abundance changes. Further, we suspect that such changes may be exaggerated when seasonal changes are greater, such as at higher elevations.

The aim of this study is therefore to investigate the diets of two cruise foraging lizards: *Bradypodion ventrale* and *B. taeniabronchum* to determine whether the nature of their cruise-foraging is adaptive during an unfavourable season. These species live at different altitudes and in different vegetative biomes. We tested the hypothesis that during unfavourable periods the proportion of sedentary prey in the diet will increase as chameleons are forced to change their cruise foraging behaviour to search for more prey (Measey et al., 2011).

MATERIALS AND METHODS

Study sites & study species

The Nelson Mandela Metropolitan University Nature Reserve (Port Elizabeth, Eastern Cape, South Africa) has vegetation defined as Algoa Dune Strandveld (Mucina & Rutherford, 2006), a type of thicket vegetation dominated by dense bushes around 1.5 m in height. All *Bradypodion ventrale* were located in an area approximately 1 km² immediately to the west of the campus lying at around 50 m a.s.l. Lady's Slipper Mountain (located 32 km north-west of Port Elizabeth) is in a vegetation type defined as Kouga Sandstone Fynbos (Mucina & Rutherford, 2006), and at the time of sampling had dense bushy vegetation around 1 m in height. All *B. taeniabronchum* were found in an area of approximately 0.5 km² on the easternmost side of the mountain at the summit (around 600 m a.s.l.). We hereafter refer to sites by their vegetation type and the allopatrically distributed chameleons within them: thicket with *B. ventrale* and fynbos with *B. taeniabronchum* (see Tolley & Burger, 2007).

Chameleon collection

Twenty individuals from each chameleon species were collected from the thicket and fynbos habitats during austral winter (July to August) and another 20 of each species during summer (December) of 2012. The chameleons were collected at night using flashlights. At night, chameleons perch in prominent positions and their pale colouration contrasts against the dark vegetation, making them easier to find (see Tolley & Measey, 2007). The chameleons were released at the site of capture after stomach flushing and morphological measurements. Sampled chameleons were marked on their stomachs with a permanent marker to prevent re-sampling individuals.

Diet

To determine chameleon diets, their stomachs were flushed after collection as described in Herrel et al. (2006). This was done with 10–20 ml water in a 50 ml syringe, a modified needle with a 30° bend and 2 mm diameter ball with an aperture at its apex. Stomach contents were captured in a sieve (mesh size 0.05 mm) and preserved in 2 ml vials containing 70% ethanol. We

also measured head width, head length, snout-vent length and tail length to the nearest 0.01 mm using a digital calliper (Herrel et al., 2006; Herrel et al., 2011; Measey et al., 2011). Chameleons were sexed by the eversion of hemi-penes in males and the absence of a corresponding bulge in females.

All chameleons sampled were found to have some stomach contents, including all samples from winter. It is important to note however, that our sampling nights were confined to periods following sunny days, and that occasionally this still generated no catches. Catch effort was much greater in the winter to achieve sample sizes. Juveniles, which were abundant in December in the fynbos, were not sampled.

Invertebrate sampling

Sweep netting, pan traps and pitfall traps were used to sample invertebrates potentially available to chameleons in their respective habitats during winter and summer. All insects were captured from within areas where chameleons were found. Sweep nets capture invertebrates on or near the vegetation and are particularly suited for flying insects (Faeth & Kane, 1978). At the beginning of the invertebrate sampling period during winter and summer, the vegetation was swept along a straight line 25 times with a fine mesh net (mesh size 0.05 mm; hoop area 552 cm², Measey et al., 2011). Each sweep was ~2 m wide and an area of ~50 m² was covered at each site. Pan traps are used to capture flying and flower-visiting invertebrates and are filled with a soapy water solution (soap acts as a surfactant and breaks the surface tension of the water, Campbell & Hanula, 2007; Roulston et al., 2007). Different coloured pans attract different types of invertebrates (Campbell & Hanula, 2007; Saunders & Luck, 2012) and therefore yellow, blue and white pan traps (area: 275 cm²; water depth: 1.5 cm) were used. In each habitat, two yellow, two blue and one white pan were filled and placed in relatively open areas to ensure they will be seen by flying insects. Pitfall traps are used to capture invertebrates that are active on the ground (Luff, 1975). The pitfall traps were white cups (area: 42 cm²; water depth: 4.9 cm) that were buried so that their rims were level with the ground and were half filled with soapy water. During winter and summer, the pan and pitfall traps were left out for a total of four days. Captured invertebrates from all traps were preserved in 70 ml of 95% ethanol. Pitfall traps and pan traps were left out continuously during the sampling period and therefore may have trapped nocturnal insects not available to chameleons. Means of invertebrates are presented with all trapping methods combined.

Invertebrate identification and measurements

Picker et al. (2004) was used to identify stomach contents and trap invertebrates to Order level. The width and length of each stomach content item and trapped invertebrate was measured (to nearest 0.01 mm) with a digital calliper. Invertebrate Orders were classified as evasive or sedentary and prey characteristics, based on the actual forces required to crush them, were used to classify them according to hardness (Herrel et al., 2006).

Table 1. Potential available prey and prey consumed by *Bradypodion ventrale* in the thicket habitat and *B. taeniabronchum* in the fynbos habitat during winter and summer. Invertebrates are identified to Order level and categorized according to hardness and mobility. a=available, E=eaten, E*=Electivity index.

Hardness	Mobility	Order	<i>B. ventrale</i>						<i>B. taeniabronchum</i>					
			Summer			Winter			Summer			Winter		
			a	E	E*	a	E	E*	a	E	E*	a	E	E*
			n=20			n=20			n=20			n=20		
Hard	Evasive	Hymenoptera	410	21	-0.91	87	17	-0.645	74	13	-0.834	174	18	-0.511
		Myriapoda	0			2			1			1		
	Sedentary	Coleoptera	48	33	-0.228	11	34	0.547	39	12	-0.246	24	76	0.444
		Diplopoda	1	1	-0.044	8			0			0		
		Mollusca	1	5	0.641	4			0			0		
		Acari	1			6			0			4		
Intermediate	Evasive	Orthoptera	84	1	-0.978	4			6	1		8		
	Sedentary	Hemiptera	68	73	-0.009	163	49	-0.502	63	52	-0.094	76	71	0.201
		Isopoda	0			1	2	0.376	0			25		
		Mantodea	1			0	2		0			1		
		Opiliones	1	2	0.293	16	2	-0.757	1			2		
		Dermoptera	2			4			0			1	1	0.143
		Diplura	0	4		0			2			4		
Soft	Evasive	Blattodea	0	4		0	15		0			0	3	
		Collembola	18	3	-0.735	100	17	-0.684	31	9	-0.724	68	6	-0.589
		Diptera	118	35	-0.573	193	80	-0.372	55	24	0.262	17	22	-0.304
	Sedentary	Aranea	36	23	-0.262	42	22	-0.267	14	4	-0.639	22	11	0.023
		Lepidoptera	0	4		3	4	0.191	13	7	0.618	2	5	-0.322
		Thysanura	0			0			0			1		
		Total	789	209		644	244		299	122		430	213	
		Niche Breadth	2.45	5.64		2.45	7.1		4.05	4.8		3.19	4.45	

Data analysis

To test for significance in changes of volume for both available and consumed prey in each season, we constructed a linear model in R (R Development Core Team, 2011) with log invertebrate volume as the explanatory variable and winter/summer and eaten/available as response factors. We then used the step function [step(model)] in R to select the best fitting model according to the Akaike's Information Criterion (AIC), and noted which determinants best fitted the volume calculated. Models were run separately for each species. All means are presented \pm standard error.

An Electivity Index (E^*) (Vanderploeg & Scavia, 1979) was used to determine how prey items (based on mode of mobility – sedentary and evasive) were selected. The same index was used to determine how prey items, based on hardness (hard, intermediate, soft) were selected. For both indices, a measure of relative abundance of prey in the diet compared with the relative abundance of invertebrates captured in combination of the three trapping methods was used to determine this. Only invertebrate Orders encountered in both the traps and stomach samples were considered. This index gives a value (from +1 to -1) for the over- or under-representation of prey groups in the diet in proportion to their relative

abundance in the environment, so that values near zero indicate neutral selectivity (Vanderploeg & Scavia, 1979). Any values between -0.2 and 0.2 were also considered as neutral selectivity.

The inverse of Simpson's Diversity Index was used to determine the dietary niche breadth values for both chameleon species, where the percentage volume of each invertebrate Order in the stomach samples and traps were used in the analysis (Simpson, 1949; Van Der Meer et al., 2010):

$$B = 1 / \sum_{i=1}^n p_i^2$$

In this equation, B represents the niche breadth value, i is the invertebrate Order, the total number of invertebrate Orders is represented by n and p equals the proportion of the Order in the stomach or trap.

Chi-square goodness of fit tests (χ^2) were used to determine if both chameleon species show significant differences between their winter and summer diets. The average volume of the invertebrates consumed for both chameleon species were calculated and significant differences were determined by using one-way ANOVA (assuming unequal variance) and Tukey HSD post-hoc tests. The following formula for a prolate spheroid was

used to calculate the volume of each invertebrate in the stomach contents:

$$\text{Volume} = \frac{4}{3} \pi \left(\frac{\text{length}}{2} \right) \times \left(\frac{\text{width}}{2} \right)^2$$

RESULTS

We found significantly more potential food items in the fynbos during summer than winter (summer mean=86.2; winter mean=59.8; $F_{1,8}=7.594$; $p=0.025$), but in the thicket this difference was not significant (summer mean=161.4; winter mean=128.8; $F_{1,8}=0.690$; $p=0.430$). The volume of invertebrates found in summer was around twice the size of those sampled in winter in both fynbos (summer mean=3.605 mm³; winter mean=1.843 mm³; $F_{1,8}=19.274$; $p=0.002$) and thicket (summer mean=3.530 mm³; winter mean=1.454 mm³; $F_{1,8}=19.065$; $p=0.002$) (Table 1). Thus, the winter sampling would represent a less favourable period for size and abundance of available prey items in both fynbos and thicket.

In total, 16 of the 19 Orders of invertebrates encountered in the sweeps and traps were consumed by our focal chameleon species, and the taxonomic make up of prey was similar for both habitat types. Diptera, Hemiptera and Coleoptera were the principal dietary constituents for *B. ventrale* during winter and summer, but the frequency at which these were consumed, changed from winter Diptera (33%), Hemiptera (20%) and Coleoptera (14%) to summer Hemiptera (35%), Diptera (17%) and Coleoptera (16%). During winter, the predominant invertebrate Orders consumed by sampled *B. taeniabronchum* individuals were Coleoptera (35%), Hemiptera (32%) and Diptera (10%), but in summer this changed dramatically with Hemiptera (43%) and Diptera (20%) dominating while Hymenoptera (11%) and Coleoptera fell (10%; Table 1).

The volume of each prey item eaten by *B. ventrale* in summer was, on average, double the size of those eaten in winter (summer mean=6.2±10.8 mm³; winter mean=3.1±5.6 mm³; Fig. 1B), with the same situation seen for *B. taeniabronchum* (summer mean=7.6±2.3 mm³; winter mean=3.7±1.0 mm³; Fig. 1A). This matches the seasonal change in available prey items (see above). Perhaps unsurprisingly, *B. taeniabronchum* eat nearly twice the number of invertebrates during winter than in summer (mean=10.85±1.22 and 6.15±0.77 items, respectively $F_{1,38}=10.452$; $p=0.002$), so that there is no significant difference in the total relative volume of prey found in the stomachs of individuals sampled in winter and summer ($F_{1,38}=0.833$; $p=0.367$). Likewise, for *B. ventrale* intake of prey items in winter doubled, so that the total relative volumes between seasons was not significantly different ($F_{1,38}=1.496$; $p=0.229$).

We found a significant interaction effect between season and prey selected for *B. taeniabronchum*, where significantly larger invertebrates eaten than those available occurred in winter (Table 2A). This maximization of prey size eaten was not found to be significant for *B. ventrale*, although the p value was close to significance (Table 2B).

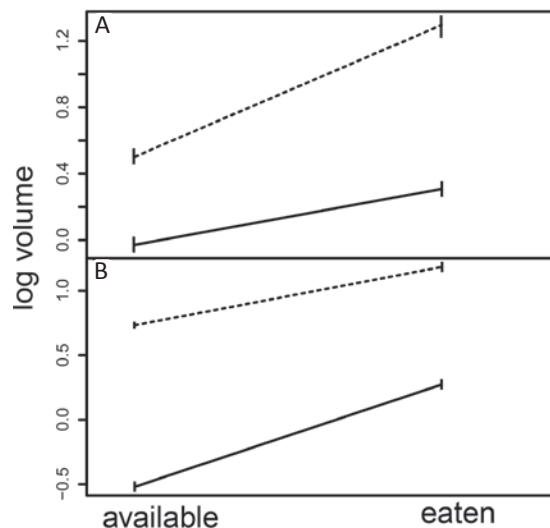


Fig. 1. Changes in mean log volume of invertebrate prey items showing interaction effects between season (summer: dotted and winter: solid) and available/eaten prey (with Standard Error bars) by (A) *Bradypodion taeniabronchum* and (B) *B. ventrale*.

Niche breadth

Chi-square goodness of fit tests indicate that there were no significant differences in the number of invertebrates consumed per Order by *B. ventrale* during winter and summer ($\chi^2_{0.05,14}=23.68$; $p=0.099$), but there was a significant difference in the number of invertebrates consumed per Order by *B. taeniabronchum* during winter and summer ($\chi^2_{0.05,9}=16.92$; $p=0.023$). Dietary niche breadth indicate a seasonal change for the sampled *B. ventrale*, which were found to be more generalist during winter ($n=11$; $B=7.10$) but more specialized during summer ($n=12$; $B=5.64$; see Table 1). Conversely, *B. taeniabronchum* sampled were found to specialise during winter ($n=10$; $B=4.45$) and summer ($n=8$; $B=3.80$; see Table 1).

Electivity of functional prey groups

Data from *Bradypodion ventrale* showed neutral selection for evasive ($E^*=-0.13$) and sedentary ($E^*=0.10$) prey during winter (Fig. 2A), but selection against evasive ($E^*=-0.67$) and for sedentary prey ($E^*=0.29$) during summer (Fig. 2B). Sampled *B. taeniabronchum* showed a more consistent pattern in terms of prey mobility than *B. ventrale* (Fig. 2C), avoiding evasive prey ($E^*=-0.44$; $E^*=-0.38$) and selecting for sedentary prey ($E^*=0.24$; $E^*=0.22$) during winter and summer, respectively (Fig. 2D).

During winter, *B. ventrale* sampled had neutral selection for all prey hardness categories (hard: $E^*=0.14$; intermediate: $E^*=-0.14$; soft: $E^*=-0.04$) (Fig. 3A), while during summer they selected against hard prey ($E^*=-0.43$), for intermediate prey ($E^*=0.2$) and had neutral selection for soft prey ($E^*=0.05$) (Fig. 3B). *B. taeniabronchum* had neutral selection for hard ($E^*=0.04$) and intermediate ($E^*=0.17$) prey, but selected against soft prey ($E^*=-0.33$) during winter (Fig. 3C). During summer, *B. taeniabronchum* avoided hard prey ($E^*=-0.51$), selected intermediate prey ($E^*=0.24$) and had neutral selection for soft prey ($E^*=0.02$) (Fig. 3D).

Table 2. Results of a linear model for with log invertebrate volume as the explanatory variable and winter/summer and eaten/available as response factors (A) *Bradypodion taeniabronchum* ($F_{3,1062}=18.36; p<0.001$) and (B) *Bradypodion ventrale* ($F_{3,1898}=85.84; p<0.001$)

(A) Coefficients	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	0.457	0.081	5.625	< 0.001
Time Winter	-0.485	0.127	-3.829	< 0.001
Eat/Avail eaten	0.838	0.173	4.859	< 0.001
Time Winter : Eat/Avail eaten	-0.502	0.228	-2.198	0.028
(B) Coefficients	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	0.733	0.060	12.233	< 0.001
Time Winter	-1.253	0.090	-13.928	< 0.001
Eat/Avail eaten	0.451	0.133	3.404	<0.001
Time Winter : Eat/Avail eaten	0.341	0.184	1.849	0.065

DISCUSSION

In both thicket and fynbos habitats, there is a clear reduction in the availability and volume of prey for each species of chameleon during winter. Winter is clearly a less favourable season as available prey is less abundant and smaller, and each chameleon species responds by eating more prey so that the total mean volume eaten in each season is not significantly different. However, our data also suggests that the chameleons change their foraging behaviour to respond to this difference in prey type between seasons. Prey hardness type selection shifts from avoiding hard prey in summer (for both species), while in winter there is more neutral prey selection. This result might be expected as when prey is abundant in summer, the less digestible (and perhaps therefore less valuable) hard prey items can be avoided while in winter, a general reduction in the availability of prey means that there is less choice available. Hard prey items are energetically more expensive to digest

(Crovetto et al., 2012) and the presence of hard, biting mouth parts may make it more risky to consume hard prey items. In summer, *B. ventrale* favours sedentary prey, while evasive prey is not favoured, but in winter neither prey category is favoured and the niche breadth was found to broaden to a more generalist predator. For *B. taeniabronchum*, the change in season does not appear to make an impact on prey categories consumed, as in both seasons sedentary prey is preferred over evasive prey items and they have a relatively narrow niche breadth. Our results do not support our hypothesis that the proportion of sedentary prey increases in winter for either of the chameleon species we studied.

The apparent aversion and/or neutral selection of soft prey was not expected (Measey et al., 2011). We note that two of the four Orders classified as soft prey were also evasive. The evasive prey items also occurred at the highest frequency. For example, mosquitoes were highly abundant in the thicket habitat during winter, but relatively few were selected. The small number of soft

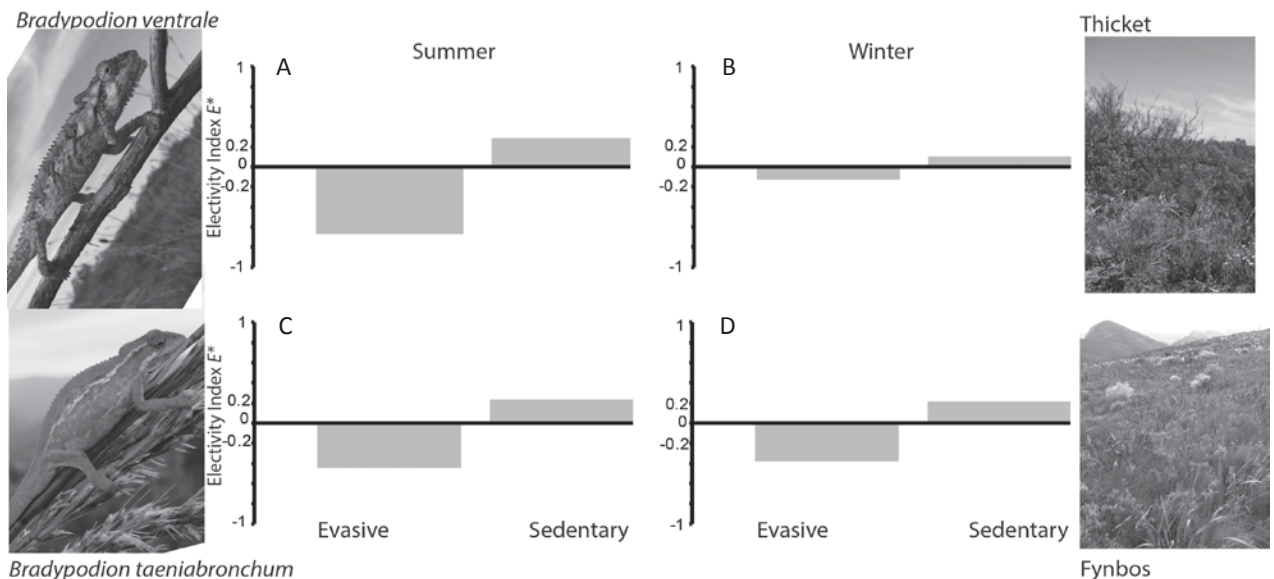


Fig. 2. Electivity indices for evasive and sedentary prey items for two species of dwarf chameleon, each inhabiting a different biome.

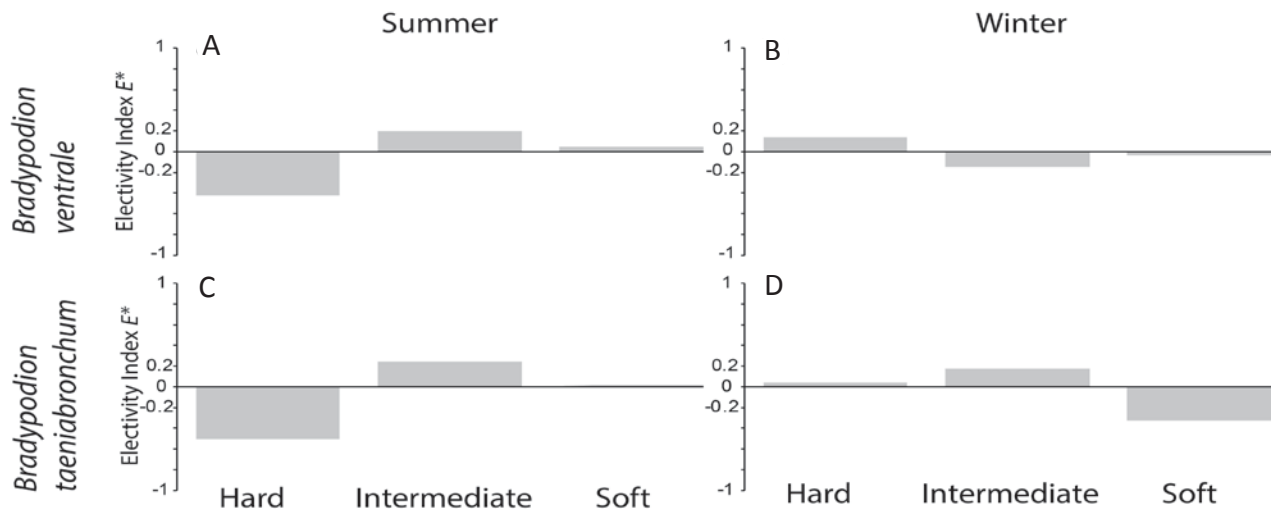


Fig. 3. Electivity indices for relative hardness of invertebrates show that both dwarf chameleons studied avoid hard prey items in summer when more food items are available.

prey items consumed versus the number of soft prey items available and the mobility of the soft prey items are possible explanations for this unexpected result.

Winter is not only less favourable for potential prey, but the chameleons must also thermoregulate in shorter day lengths (approximately 10 hour days in June compared to 14 hour days in December). Thus, our finding that more prey is eaten is significant as it is done in less time, and compliments our finding that both sets of chameleons are prepared to take most prey hardness types in the same proportion that they were found. However, we predicted that with reduced prey availability, chameleons would be forced to change their cruise foraging strategy and spend more time searching for sedentary prey items (Measey et al., 2011). *Bradypodion taeniabronchum* were found to prefer sedentary and avoid evasive items with equal difference in both winter and summer. Conversely, *B. ventrale* changed from no discernable preference in winter, to an aversion of evasive prey items in summer. Our (unpublished) observations of *B. ventrale* behaviour in summer suggest that they spend the majority of their time moving within their thicket vegetation. We interpret this as a predator avoidance strategy. Chameleons are generally regarded as being vulnerable to avian predators (Wager, 1986; Branch, 1998; Jenkins et al., 2009; Measey et al., in press), and are known to modify their behaviour and hide from avian models (Stuart-Fox et al. 2006). A possible interpretation of our results in winter is that the option of hiding from predators by consuming mostly sedentary prey items is not available. An alternative explanation is that *B. ventrale* move less in the winter as it is colder, but this would be expected to affect the higher altitude *B. taeniabronchum* more. Further investigations would be required to test these hypotheses.

Previous studies have shown that, in general, lizards show seasonal differences in their diets and changes in prey availability and selection are the drivers of seasonal dietary changes (Gadsden & Palacios-Orona, 1997; Van Wyk, 2000; Mella et al., 2010). Our study demonstrates that not only do availability and composition of prey change, but that a dramatic reduction in prey size can co-occur with a reduction in prey availability. We found that

for the montane population of *B. taeniabronchum*, they significantly shifted to selecting much larger prey items, and thereby maintained the volume of their stomach contents, as was found previously in *Anolis* lizards (Lister & Aguayo, 1992). While our analysis does not suggest that there was a commensurate shift in foraging tactics, we presume that given the shorter day length, a much greater portion of the day was given over to prey acquisition. We also noted that for *B. taeniabronchum* there was a distinctly seasonal distribution of juveniles, with an abundance of very small individuals found in December and only adults (including gravid females) found in June. Breeding aseasonality has been suggested to be a means of avoiding the risks of living in a fire prone environment (Jackson et al., in press), but it may be that this option is not open to *B. taeniabronchum*.

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