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Diet, morphology and performance in two chameleon morphs: do harder bites equate with harder prey?

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Abstract

Ecologically induced morphological variation has been identified as a mainstay in evolutionary theory. Species that inhabit different habitats are likely to display morphological and functional differences related to the exploitation of different dietary resources available in each habitat within limits imposed by trade-offs. Here, we examine two populations of the Cape Dwarf Chameleon, *Bradypodion pumilum*, from fynbos (heathland) and woodland to investigate whether head morphology and bite performance are related to diet within and between populations. Stomach contents are compared with prey availability to test whether chameleons are selective with respect to prey size, hardness and evasiveness. Our data show that for adult chameleons from the fynbos (Kogelberg; $n = 44$), mean and maximum prey size are tightly correlated with head morphology and performance. In woodland habitat (Stellenbosch; $n = 52$), only maximum prey size is correlated with head morphology and performance. Fynbos chameleons showed no preference with respect to prey hardness, while those from woodland ate less hard and/or sedentary prey than available, thus preferring items that were soft and/or evasive. Finally, fynbos chameleons have a diet of sedentary and/or evasive prey similar in proportions to that available. Our results suggest that diet is not directly related to selection on the head morphology and biting performance of *B. pumilum* in woodland habitat, but that it may be important for selection in fynbos due to a reduction in overall prey availability.

Introduction

Many plants and animals display marked morphological and commensurate functional differences in differing environmental contexts. Indeed, ecologically induced morphological variation through natural selection is a central theme in evolutionary biology (Wainwright & Reilly, 1994; Schluter, 2000; Herrel *et al*., 2005). Consequently, understanding how morphology and function are related to ecology is crucial. Changes in climate are known to result in large-scale habitat shifts such that organisms that find their habitats altered must adapt or move to suitable habitats to survive. In some instances, changes in habitat and morphology may lead to speciation, while in others, gene flow is continuous between populations inhabiting different habitats but specific habitat morphs may still be recognized (Dobzhansky, 1951). In addition to changes in the structural habitat that are likely to affect locomotion, habitat changes may also lead to changes in food resources necessitating adaptations to the feeding system.

Most lizards are generalist predators that include a large variety of prey in their diet (Greene, 1982; Schwenk, 2000). However, in novel habitats, lizards may be faced with different dietary resources and adapt by visible changes in their external head morphology as well as their internal digestive systems in relatively short periods of time (Herrel *et al*., 2008). Bite force is considered to be crucial for expanding the potential dietary scope in lizards, with higher bite forces increasing the availability of larger and harder prey (Herrel *et al*., 1999*a*). Thus, adaptations to more severe environments might be expected to result in changes in head morphology and commensurate bite force increases. However, selection for high bite forces in lizards may also come about through sexual selection, especially where males defend territories or females are in conflict with conspecific males (e.g. Herrel, Meyers & Vanhooydonck, 2001*c*; Irschick *et al*., 2003; Lailvaux *et al*., 2004).

Dietary habits are surprisingly poorly known for chameleons, but it has been shown that, at least occasionally, they eat prey that is large relative to other lizards (see Broadley, 1973;

Luiselli & Ruigiero, 1996; Pleguezuelos *et al*., 1999; Herrel *et al*., 2000; Keren-Rotem, Bouskila & Gefen, 2006). Yet, faecal remains suggest an opportunistic generalist foraging strategy (Hofer, Bauer & Bersier, 2003). Chameleons have excellent visual acuity, which allows the assessment of prey from a distance (Tolley & Burger, 2007). They have large heads and exhibit strong tongue retractors with supercontractile properties used to relay large items into the mouth (Herrel *et al*., 2001*b*; Anderson & Deban, 2010). Chameleons are also known to have a relatively high bite force (Vanhooydonck *et al*., 2007*b*), which may be related to a regular diet of hard or oversized prey items, and/or to intra- and intersexual combat involving fighting and the biting of opponents (Stuart-Fox & Whiting, 2005; Tolley & Burger, 2007; Measey, Hopkins & Tolley, 2009). The limited dietary information available for these lizards restricts our understanding of the relationship between their bite force performance and prey size/intractability (e.g. Herrel *et al*., 2005) and prevents inferences as to the relative importance of bite force for diet versus intraspecific combat.

The Cape Dwarf Chameleon, *Bradypodion pumilum*, has two distinct morphs (Measey *et al*., 2009; Hopkins & Tolley, 2011). Individuals from closed canopy habitats (e.g. woodland) are larger, ornamented with tall casques (parietal crest), large gular scales and brightly coloured flank patches, whereas those from fynbos are small, have a small casque, are dull in coloration and lack colourful flank patches (Measey *et al*., 2009; Hopkins & Tolley, 2011). Although the spatial distribution of these morphs is disjunct and dependent on vegetation (Hopkins & Tolley, 2011), they are not separate mitochondrial lineages (Tolley *et al*., 2006; Measey *et al*., 2009). However, it is known that the fynbos, a type of Mediterranean heathland, is a more recent vegetation type (Cowling & Lombard, 2002; Chase & Meadows, 2007), and that the evolutionary history of the genus *Bradypodion* consists of older woodland clades with at least four radiations into open habitats (grassland, fynbos, strandveld and savannah; Tolley, Chase & Forest, 2008). Populations of the Cape Dwarf Chameleon currently inhabiting fynbos may have undergone ecologically induced morphological adaptations related to a change in their dietary resources available in this habitat.

In this study, we explore whether morphological differences in the heads of chameleons from fynbos and woodland habitats are related to their diet. We did this by comparing the types of prey eaten with the head morphology, bite performance and the available prey types (size, hardness and evasiveness). We reason that a difference in the proportion of hard and relatively large prey may explain the difference in relative head size and bite force between chameleons from the two populations reported previously (Measey *et al*., 2009; Hopkins & Tolley, 2011). Similarly, if larger heads are required to eat larger prey, we would expect a correlation between head size and maximum prey size. Furthermore, if prey selection is dependent on head size and bite performance, we might expect a correlation with mean prey size. Lastly, we discuss our results of how chameleons from the two populations exploited prey of differing mobility in relation to potential differences in foraging strategy (Vanhooydonck, Herrel & van Damme, 2007*a*).

Materials and methods

We conducted surveys for chameleons (*B. pumilum*) at two sites: a typical fynbos habitat at Kogelberg and along a woodland river in Stellenbosch, Western Cape, South Africa. The populations at these sites were used in the previous studies of morphology (Hopkins & Tolley, 2011), performance and genetics (Measey *et al*., 2009). Although juveniles were not sampled, we did not otherwise discriminate for a particular size class so that adults represent a cross section of the entire range of sizes in the population. Adult males were identified by eversion of hemipenes. Females were identified as individuals ≥45 mm with no hemipenes (see Hopkins & Tolley, 2011).

We captured 96 adult chameleons on four occasions during the austral summer (in November 2008 and February 2010) from two different sites: fynbos (Kogelberg) (n = 44) and woodland (Stellenbosch; n = 52; see Table 1). All adults sampled conformed to the expected morphs in their respective habitats: large, brightly coloured and highly ornamented chameleons from woodland habitats and small, dull, chameleons with diminutive ornaments in fynbos (see Measey *et al*., 2009; Hopkins & Tolley, 2011). All chameleons captured were tail clipped (≤2 mm) as a batch mark, enabling us to ensure that no animal would be sampled more than once. Animals were brought back to the laboratory, measured, stomach flushed and tested for bite force and subsequently released at the exact site of capture. All stomach flushing and performance measurements were taken within 4 hours of capture.

Morphology and performance measurements

Morphological variables were measured for each individual using digital Mitutoyo callipers (Mitutoyo UK, Andover, UK) (accuracy 0.01 mm): snout-vent length, head height, head length, head width, lower jaw length and the distance from the back of the jugal bone to the tip of the lower jaw (Herrel *et al*., 2006). The in-lever for jaw closing was calculated by subtracting this distance from lower jaw length.

We followed the method of Herrel *et al*. (1999*a*) to measure *in vivo* bite force with a Kistler piezoelectric force transducer (type 9203; ±500 N; Kistler Inc., Winterthur, Switzerland), mounted into a custom-built holder. Gape angle was standardized by varying the distance between plates relative to head size. Performance measurements were repeated five times for each animal and the maximum value obtained was used in analyses.

Diet and prey availability

Each chameleon was stomach flushed using a 500-mL syringe and a modified needle with a 30° bend and a 2-mm diameter ball with aperture at its apex (Herrel *et al*., 2006). Approximately 100 mL of water was used to lavage the stomach, and the contents were captured in a sieve with a mesh size of 0.5 mm. Stomach contents were transferred with forceps into labelled vials with 70% alcohol. Of individuals stomach flushed, six had empty stomachs and three had contents that could not be identified.

Table 1 Prey eaten and potential prey available in the habitat of *Bradypodion pumilum* from two different habitats. Invertebrates (and a single vertebrate) are identified to order and categorized by hardness and speed. Electivity (*E**) is calculated from Vanderploeg and Scavia's (1979) index

			Fynbos (Kogelberg)			Woodland (Stellenbosch)		
Hardness	Speed	Order	Sweep netting (*n* = 10)	Stomachs (*n* = 41)	*E**	Sweep netting (*n* = 10)	Stomachs (*n* = 46)	*E**
Hard	Evasive	Hymenoptera	19	13	0.115	23	24	–0.08
	Sedentary	Coleoptera	39	32	0.025	243	47	–0.727
		Julida				8	4	–0.42
		Stylommatophora	0	1	1	0	2	1
		Squamata				0	1	1
Intermediate	Evasive	Odonata	0	1	1	1	6	0.661
		Orthoptera	17	5	0.491	20	5	–0.661
		Dermaptera				0	2	1
		Hemiptera	38	17	0.317	34	45	0.038
		Isopoda				3	0	–1
		Diptera	9	28	–0.566	24	78	0.452
	Sedentary	Mantodea	1	1	–0.074	3	0	–1
		Mecoptera l.	1	0	–1			
		Neuroptera l.				2	0	–1
		Phasmatodea	2	3	–0.27			
		Collembola	19	16	0.012	0	18	1
Soft	Evasive	Blattodea	2	5	–0.487	0	1	1
		Ephemeroptera	1	1	–0.074	3	0	–1
		Mecoptera				0	1	1
		Acari	5	0	–1	5	0	–1
		Lepidoptera l.	5	14	–0.529	3	27	0.76
	Sedentary	Araneae	55	27	0.274	94	33	–0.555
		Pseudoscorpiones	2	0	–1			
		Psocoptera	42	1	0.946	0	10	1
		Total	**257**	**165**		**466**	**304**	

Sweep netting was conducted in the same vegetation and at the exact same localities in which chameleons were captured using a standard insect sweep net. At each site, five samples were made consisting of 25 sweeps of the vegetation, each sample being 20 m apart. This was repeated after 4 days, making a total of 10 sweep samples per site. After each sweep, the resulting invertebrates captured and preserved in labelled vials of 70% alcohol.

Stomach contents and available prey were identified to taxonomic Order using Picker, Griffiths & Weaving (2002). All invertebrates were classified according to their hardness (soft, intermediate and hard) using prey characteristics based on the actual forces needed to crush various prey items (Herrel, Van Damme & de Vree, 1996; Andrews & Bertram, 1997; Herrel *et al*., 1999*a*, 2001*d*; Herrel, Verstappen & De Vree, 1999*b*; Herrel, De Grauw & Lemos-Espinal, 2001*a*; Aguirre *et al*., 2003). Prey types were further classified in functional groups according to Vanhooydonck *et al*. (2007*a*) into sedentary and evasive food items (see Table 1).

Data analyses

All data were $\log_{10}$ transformed before analysis to fulfil assumptions of normality and homoscedascity, and non-parametric statistics were used where these assumptions were not met. All analyses were conducted in SPSS v.15 (SPSS Inc., Chicago, IL, USA). First, we tested whether chameleons from Stellenbosch had larger heads and a harder absolute bite force than those from fynbos (Kogelberg) using analyses of variance (ANOVAs) with bite force and head dimensions as the dependent variables and habitat, sex and their interaction as factors. Differences in head morphology between sexes and sites were found to be consistent with the results previously reported (Measey *et al*., 2009; Hopkins & Tolley, 2011). Next, we investigated whether the distribution of prey type and size in each habitat was random with respect to that found in the stomach contents of chameleons. We used Mann–Whitney *U*-tests on invertebrate size distributions (width, length and mass of prey eaten and available prey items) within and between each site, and *P*-levels were adjusted for multiple testing. Additionally, we tested for differences in the mean dimensions of prey eaten using univariate ANOVAs with habitat and available or eaten as factors. Differences between groups were tested using Bonferroni *post hoc* tests.

We then investigated how different prey categories based on the functional properties (hardness and evasiveness) were selected using a measure of relative abundance of prey in the diet compared with relative abundance of invertebrates captured in sweep netting using Vanderploeg & Scavia's (1979) relativized electivity index [*E**, see Lechowicz (1982) for justification]. This index gives a value (from +1 to –1) of the over- or under-representation of prey groups in the diet in proportion to their relative abundance in the environment. Values near zero represent neutral selectivity. E^* was only estimated for taxa, which were represented in both stomachs and sweep nets. In addition, E^* was calculated for functional properties (hardness and evasiveness) of prey eaten and prey available by summing invertebrates within each functional property. We then used prey size data to determine whether there was selection on sizes within prey groups.

Prey size (length, width and mass) for the largest prey item per stomach and the mean of all prey items in each stomach were correlated against head measures and bite force using Pearson correlations. We noted which correlations were significant and report only the best correlation.

Results

Prey at the two sites had a similar taxonomic make up with Diptera, Coleoptera, Araneae, Hymenoptera and Hemiptera, collectively making up more than 70% of the prey ingested at each site (Table 1). Quantities of prey in stomachs differed significantly between sites with chameleons from fynbos (Kogelberg) having significantly less prey items in their stomachs (4.05 ± 0.35 prey items per stomach) than animals in woodland (Stellenbosch; 6.63 ± 0.45 prey items per stomach; $F_{1,85} = 19.35$, $P < 0.001$; Table 1). Measures of the prey availability suggest that prey is less abundant in fynbos (Kogelberg: mean number of prey retrieved per sweep sample 14.2 ± 1.4; total biomass 0.79 g) than in woodland (Stellenbosch: mean number of prey retrieved per sweep sample 18.3 ± 1.6; total biomass 6.68 g).

Bite force

Our data show that absolute bite force was less in chameleons from fynbos (Kogelberg) than those from woodland (Stellenbosch), but that the effects of sex and the interaction between sex and habitat were not significant (Fig. 1; ANOVA $F_{1,87} = 40.372$, $P < 0.001$). Previous studies show that given sufficient sample size, the relative bite force of chameleons from fynbos is higher than those from woodland habitats (Measey *et al.*, 2009).

Distribution of available and eaten prey items

Mann–Whitney *U*-tests performed on the size distributions of available versus consumed prey within each site were all significant, demonstrating chameleons selected prey non-randomly from available prey (Table 2a). Moreover, tests on the distributions of available prey width and length at both sites demonstrated significant differences between sites. However, the frequency distribution of available prey mass was not different between fynbos (Kogelberg) and woodland (Stellenbosch) sites after correcting for multiple testing (see Table 2). Mann–Whitney *U*-tests demonstrate that distributions of size (length, width and mass) of prey eaten at the two sites were significantly different (Table 2). Univariate ANOVAs showed significant differences in the length ($F_{3,1200} = 133.7$, $P < 0.001$), width ($F_{3,1200} = 391.6$, $P < 0.001$) and mass ($F_{3,1200} = 15.8$, $P < 0.001$) of the prey available and eaten at both sites.

Post hoc tests showed that prey dimensions differed in complex ways; for example, fynbos (Kogelberg) chameleons ate prey that was wider, longer and heavier than that available. Moreover, these chameleons ate prey that was longer and narrower than that eaten in woodland (Stellenbosch) but equivalent in mass. Prey eaten in woodland was wider and heavier but shorter than that available (Table 2b).

Morphology, performance and diet

Maximum prey size of each chameleon was found to correlate with head size at both sites. The strongest relationships were found between prey width and head length in fynbos (Kogelberg), with prey length and mass having weaker but significant relationships (Fig. 2, Table 3). Interestingly, for animals caught in woodland (Stellenbosch), only maximum prey mass was found to correlate with bite force (Table 3). Mean prey sizes produced weaker but significant relationships in fynbos (Kogelberg), and no relationship with any morphological or performance trait in woodland (Stellenbosch; Table 3).

Electivity indices

For fynbos (Kogelberg) chameleons, the electivity index was close to zero for each of the prey hardness categories (Fig. 3), indicating that prey selection is random with respect to hardness ($E^* = 0 \pm 0.15$). However, chameleons from woodland (Stellenbosch) displayed a distinct aversion to hard prey ($E^* = -0.50$), near neutral electivity for items with intermediate hardness ($E^* = 0.05$) and positive for soft items ($E^* = 0.22$; Fig. 3).

We found that for chameleons sampled from fynbos (Kogelberg), electivity was close to zero for evasive and sedentary prey items ($E^* = 0 \pm 0.15$; Fig. 3), suggesting that chameleons there rely on a combination of active foraging for passive prey as well as catching active prey. However, for animals caught in woodland (Stellenbosch), there was a positive selection ($E^* = 0.24$) of evasive prey and an aversion to sedentary prey items ($E^* = -0.46$; Fig. 3), suggestive of sit-and-wait foraging.

Discussion

For chameleons from the woodland site in Stellenbosch, our data suggest that prey hardness did not drive the evolution of bite force as these chameleons ate less hard prey than available in the habitat. Moreover, chameleons from woodland had a preference for soft prey. Measey *et al.* (2009) proposed that the larger heads, ornaments and bright coloration of this morph are used for intraspecific communication. These same traits were found to be correlated with the outcome of fighting in male–male combat (Stuart-Fox *et al.*, 2006). In contrast, our data cannot discount selection toward an increase in the relative bite force for fynbos chameleons in relation to their

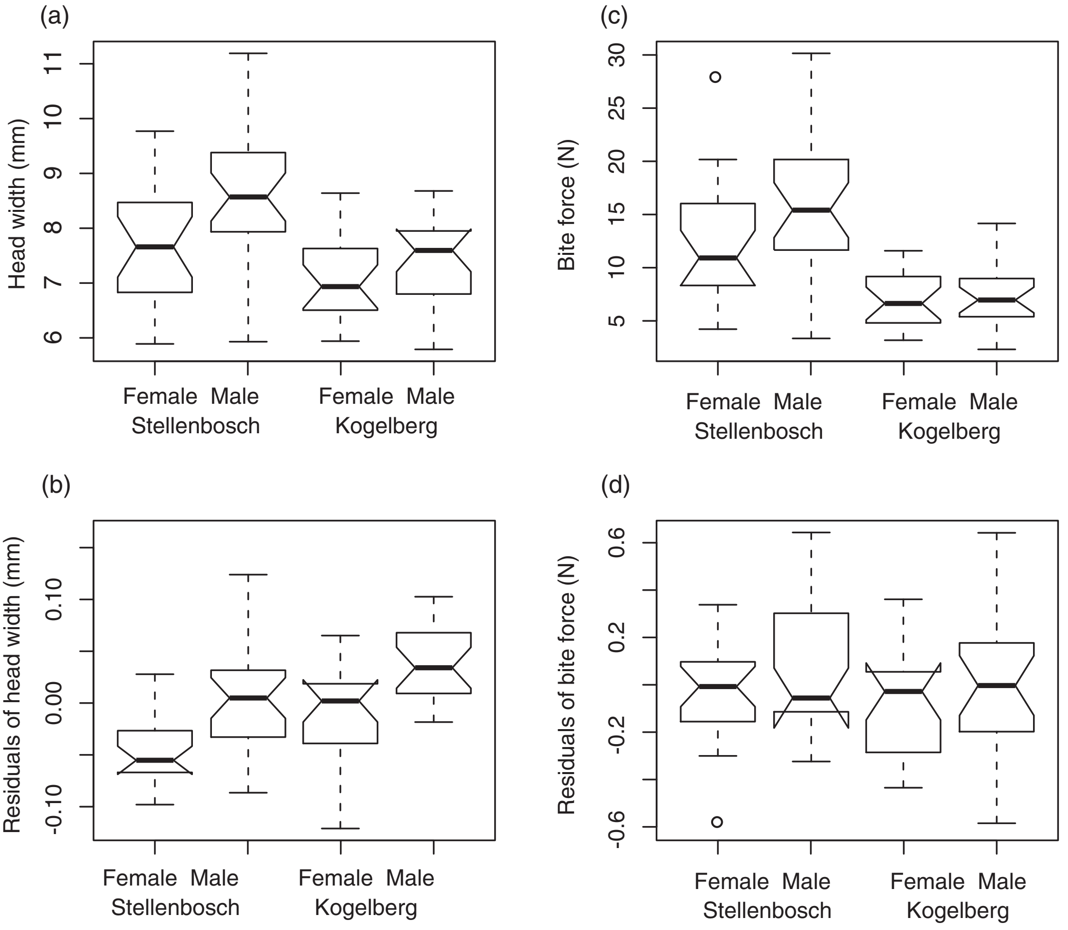

Figure 1 Bite force of *Bradypodion pumilum* morphs collected in fynbos (Kogelberg) and woodland (Stellenbosch) habitats. When notches do not overlap, there is a 'strong evidence' that their medians differ (Chambers *et al.*, 1983: 62). (a) Absolute head width is greatest in Stellenbosch, but (b) residuals of head width on snout-vent length make it clear that Kogelberg have relatively wider heads and males wider than females. (c) There is no absolute sexual difference, although males bite harder than females in Stellenbosch and animals from Kogelberg do not bite as hard as those from Stellenbosch. (d) No difference for relative bite force, although the median bite force of Kogelberg males is the highest.

Table 2a Mann–Whitney tests for differences in distribution of prey size variables within and between sites. Significance of available versus eaten demonstrates non-random selection of prey items. Between sites significance demonstrates a difference in invertebrate availability

Tested prey variables	Width	Length	Mass
Kogelberg available versus eaten	$Z = -6.194$ $P < 0.001$	$Z = -5.202$ $P < 0.001$	$Z = -2.955$ $P = 0.003$
Stellenbosch available versus eaten	$Z = -20.976$ $P < 0.001$	$Z = -12.663$ $P < 0.001$	$Z = -6.018$ $P < 0.001$
Stellenbosch versus Kogelberg available	$Z = -18.305$ $P < 0.001$	$Z = -13.822$ $P < 0.001$	$Z = -2.039$ $P = 0.041$[a]
Stellenbosch versus Kogelberg eaten	$Z = -6.598$ $P < 0.001$	$Z = -7.411$ $P < 0.001$	$Z = -5.939$ $P < 0.001$

[a] Not significant after Bonferroni correction for multiple testing.

Table 2b Results of *post hoc* tests conducted on the dimensions of prey retrieved from the stomachs and available in the habitat at the two sites: woodland (Stellenbosch) and fynbos (Kogelberg)

Width	Stellenbosch eaten > Kogelberg eaten > Kogelberg available = Stellenbosch available
Length	Kogelberg eaten > Stellenbosch available = Kogelberg available > Stellenbosch eaten
Mass	Kogelberg eaten = Stellenbosch eaten = Kogelberg available > Stellenbosch available

diet. This smaller chameleon with diminutive ornaments and dull coloration has a higher relative bite force for its size despite having a small casque (Measey *et al.*, 2009). Their neutral selectivity and the significant correlation of morphology and performance with mean prey size could be interpreted as a requirement for a high bite force to handle prey from the fynbos habitat.

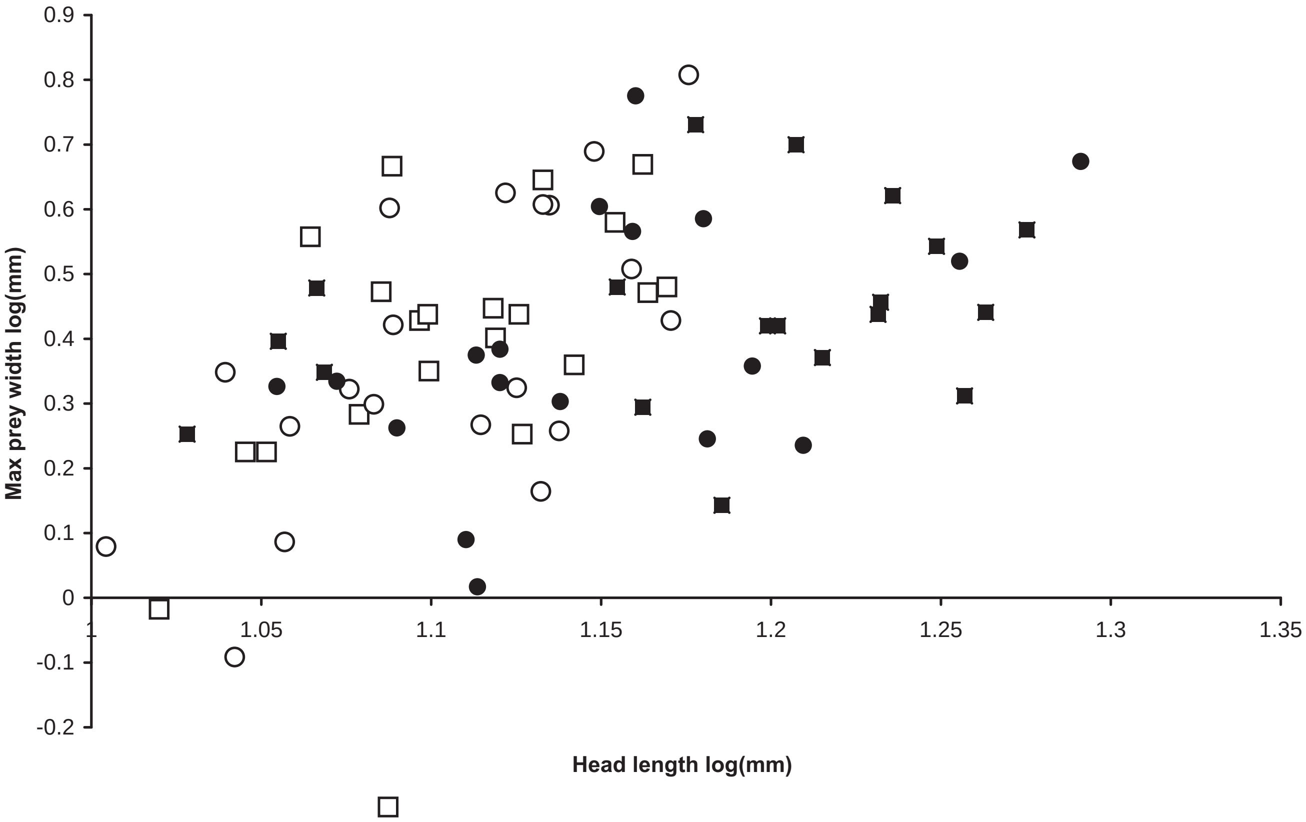

Figure 2 Correlations between the width of the largest prey item with the head length of the chameleon which ate it show that fynbos chameleons are selecting larger prey despite having smaller heads. Open symbols represent animals from the fynbos (Kogelberg); closed symbols those from the woodland (Stellenbosch). Squares represent males; circles represent females.

Table 3 Pearson correlation coefficients between prey size and predator head morphology and performance (bite force). Prey size is tested with the item with maximum size and mean of all items in each stomach. HL, LJL, HH, CT and BF (head length, lower jaw length, head height, caranoid to tip and bite force, respectively)

		Fynbos (Kogelberg)						Woodland (Stellenbosch)				
		d.f. 1, 40						d.f. = 1, 35				
		Max			Mean			Max			Mean	
		r^2	P		r^2	P			r^2	P	r^2	P
Prey width	HL	0.61	<0.001	HL	0.54	<0.001		HH	0.4	0.001	None	
Prey length	LJL	0.41	0.008	HL	0.38	0.02		CT	0.43	0.008	None	
Prey mass	HL	0.46	0.003	HL	0.42	0.007		BF[a]	0.34	0.004	None	

[a]Denotes that bite force alone was correlated.

'None' signifies that no morphological or performance measurements were correlated.

Our data show a strong correlation of maximum prey size with head morphology and bite force in both populations of chameleons, which emphasizes the functional importance of their large head size in prey acquisition. That chameleons occasionally eat very large prey is evident from the literature (see above), and in this study, we found a single rib bone from a lizard in the stomach of a chameleon from woodland (Stellenbosch; Table 1). The finding that bite force alone is correlated with maximum prey mass of woodland (Stellenbosch) chameleons is interesting as it may suggest that the heaviest prey items are restricted to individuals with the highest bite force, which are typically male (Measey *et al.*, 2009).

The reduced numbers of prey items ingested by chameleons in the fynbos habitat and the lower abundance of prey retrieved through sweep netting suggest that prey density in this habitat is lower than that in the woodland habitat. This

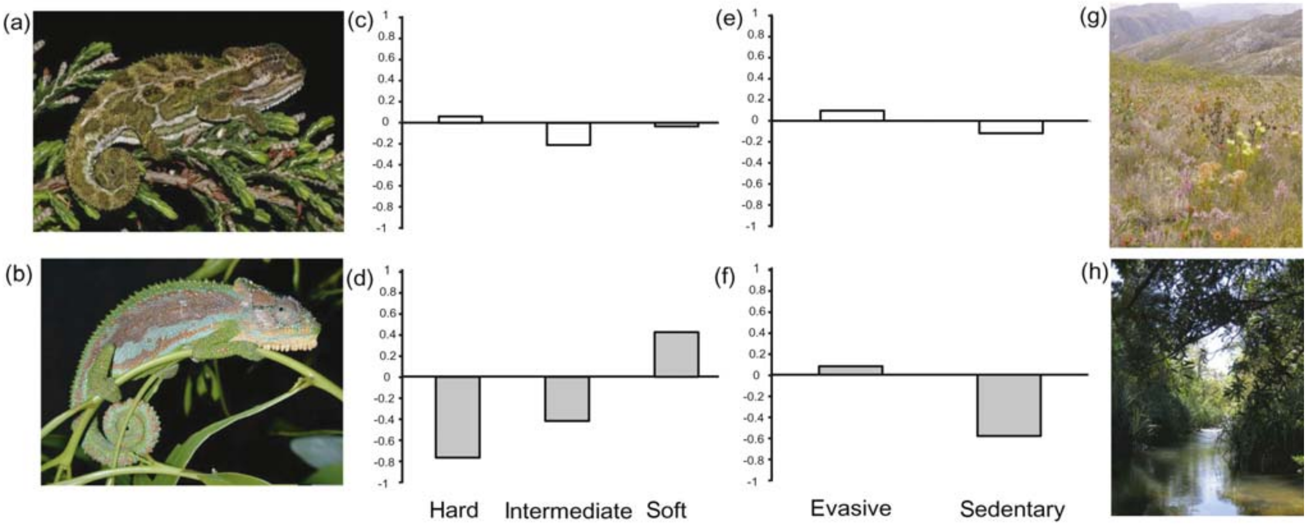

Figure 3 The Cape Dwarf Chameleon, *Bradypodion pumilum*, occurs as two morphs (a, b). Electivity indices for the selection of prey items of Kogelberg chameleons suggest neutral selectivity on hard, intermediate and soft items (c) compared with avoidance of hard and preference for soft in woodland (Stellenbosch) (d). Fynbos (Kogelberg) chameleons had neutral selectivity for evasive and sedentary prey (e), while those from Stellenbosch avoided sedentary prey (f). Each morph is found exclusively in fynbos (g) or woodland habitats (h), respectively.

observation may partially explain the strong correlations between head size and both mean and maximum prey size for fynbos chameleons, in contrast with woodland animals where no correlations were observed between head morphology and mean prey size. Our data suggest that fynbos chameleons spend more time in active pursuit of sedentary prey items and may be more selective in the sizes and types of prey that are eaten. However, chameleons in woodland habitats are likely to occur at greater perch heights, which may explain the increase in proportion of evasive prey in the diet.

Chameleons from the Kogelberg had diets with a mixture of evasive and sedentary prey items with proportions roughly the same in their diet as was available in their fynbos habitat. In contrast, the diet of chameleons from Stellenbosch consists more of evasive prey items, with far more sedentary prey available than eaten. Chameleons are generally considered to be sit-and-wait foragers; their ballistic tongue projection mechanism allows fast capture, while prey handling follows at a more leisurely pace (Herrel *et al*., 2001*b*). A previously published study on activity patterns of the woodland morph of *B. pumilum* from a similar locality established that these animals could be classified as cruise foragers (Butler, 2005). A cruise forager examines the environment for prey, makes short movements and conducts more scans (Regal, 1978). Making short movements would increase the likelihood of encountering sedentary prey items in addition to active prey, such that the proportion of active prey in the diet is reduced. Although not conclusive, our results suggest that chameleons from woodland habitat (Stellenbosch) eat more evasive prey items, including a greater proportion of sit-and-wait foraging behaviour into their repertoire. In contrast, our results on the diet for fynbos (Kogelberg) chameleons are consistent with the cruise foraging hypothesis. Neither prey category was found to be exclusive, and if both morphs are considered cruise foragers, our results suggest that different strategies may exist within cruise foraging. A comparison of activity patterns between woodland and fynbos is needed to further explore differences in foraging behaviour for chameleons from these two sites.

Although our data demonstrate some clear trends in the dietary preferences of Cape Dwarf Chameleons, our sampling (in austral spring/summer) does not provide a full picture of variation of diet in this species. It is known that this species of chameleon continues to forage throughout the year, although probably at a reduced rate in winter (Measey & Tolley, pers. obs.), and periods when food is less abundant may provoke a change in foraging strategy. A simple extrapolation of our own data suggests that where food is less abundant (fynbos habitat), chameleons ingest more sedentary prey items, which should involve an increase in movement. In addition, we do not know how the different sites vary with respect to prey abundance throughout the year, or whether the differences in prey assemblages across vegetation types (Proches & Cowling, 2006) are meaningful for these predators. Such hypotheses are testable with additional sampling.

In conclusion, our results suggest that the exaggerated head morphology and high absolute bite force in chameleons from the woodland habitat likely did not evolve to cope with larger or harder prey items, but may be related to sexual selection through communication and/or territory defence. However, for both sexes of the morph from the open fynbos habitat, individuals with higher bite forces eat larger prey. Furthermore, classification of dietary items suggest a shift to more active foraging in open habitats despite a potential increase in predation risk (Anderson, 2007), reinforcing the need for crypsis in this morph. Chameleons in the genus *Bradypodion* are known to have radiated from closed to open habitats in multiple events (Tolley *et al.*, 2006, 2008), and the associated morphological, functional and niche shifts are yet to be investigated. However, our study provides the first insight into the potential evolutionary mechanisms that this model group provides and underlines the interest in research of this unusual group of lizards.

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References

Aguirre, L.F., Herrel, A., Damme, R.V. & Matthysen, E. (2003). The implications of food hardness for diet in bats. *Funct. Ecol.* **17**, 201–212.

Anderson, C.V. & Deban, S.M. (2010). Ballistic tongue projection in chameleons maintains high performance at low temperature. *Proc. Natl. Acad. Sci. USA* **107**, 5495–5499.

Anderson, R.A. (2007). Food acquisition modes and habitat use in lizards: questions from an integrative perspective. In *Lizard ecology: the evolutionary consequences of foraging mode*: 450–490. Reilly, S.B., McBrayer, L.B. & Miles, D.B. (Eds). Cambridge: Cambridge University Press.

Andrews, C. & Bertram, J.E.A. (1997). Mechanical work as a determinant of prey-handling behavior in the Tokay Gecko (*Gekko gecko*). *Physiol. Zool.* **70**, 193–201.

Broadley, D.G. (1973). Predation on birds by reptiles and amphibians in south-eastern Africa. *Honeyguide* **76**, 19–21.

Butler, M.A. (2005). Foraging mode of the chameleon, *Bradypodion pumilum*: a challenge to the sit-and-wait versus active forager paradigm? *Biol. J. Linn. Soc.* **84**, 797–808.

Chambers, J.M., Cleveland, W.S., Kleiner, B. & Tukey, P.A. (1983). *Graphical methods for data analysis*. Pacific Grove: Wadsworth & Brooks/Cole.

Chase, B.M. & Meadows, M.E. (2007). Late quaternary dynamics of southern Africa's winter-rainfall zone. *Earth-Sci. Rev.* **84**, 103–138.

Cowling, R.M. & Lombard, A.T. (2002). Heterogeneity, speciation/extinction history and climate: explaining regional plant diversity patterns in the Cape Floristic Region. *Divers. Distrib.* **8**, 163–179.

Dobzhansky, T. (1951). *Genetics and the origin of species*. 3rd edn. New York, NY: Columbia University Press.

Greene, H.W. (1982). Dietary and phenotypic diversity in lizards: why are some organisms specialized? In *Environmental adaptation and evolution*: 107–128. Mossakowski, D. & Roth, G. (Eds). Stuttgart: Gustav Fischer.

Herrel, A., Van Damme, R. & de Vree, F. (1996). Sexual dimorphism of head size in *Podarcis hispanica atrata*: testing the dietary divergence hypothesis by bite force analysis. *Neth. J. Zool.* **46**, 253–262.

Herrel, A., Spithoven, L., Van Damme, R. & De Vree, F. (1999a). Sexual dimorphism of head size in *Gallotia galloti*; testing the niche divergence hypothesis by functional analyses. *Funct. Ecol.* **13**, 289–297.

Herrel, A., Verstappen, M. & De Vree, F. (1999b). Modulatory complexity of the feeding repertoire in scincid lizards. *J. Comp. Physiol. A* **184**, 501–518.

Herrel, A., Meyers, J.J., Aerts, P. & Nishikawa, K.C. (2000). The mechanics of prey prehension in chameleons. *J. Exp. Biol.* **203**, 3255–3263.

Herrel, A., De Grauw, E. & Lemos-Espinal, J.A. (2001a). Head shape and bite performance in xenosaurid lizards. *J. Exp. Zool.* **290**, 101–107.

Herrel, A., Meyers, J.J., Aerts, P. & Nishikawa, K.C. (2001b). Functional implications of supercontracting muscle in the chameleon tongue retractors. *J. Exp. Biol.* **204**, 3621–3627.

Herrel, A., Meyers, J.J. & Vanhooydonck, B. (2001c). Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis. *Biol. J. Linn. Soc.* **74**, 305–314.

Herrel, A., Van Damme, R., Vanhooydonck, B. & De Vree, F. (2001d). The implications of bite performance for diet in two species of lacertid lizards. *Can. J. Zool.* **79**, 662–670.

Herrel, A., Podos, J., Huber, S.K. & Hendry, A.P. (2005). Bite performance and morphology in a population of Darwin's finches: implications for the evolution of beak shape. *Funct. Ecol.* **19**, 43–48.

Herrel, A., Joachim, R., Vanhooydonck, B. & Irschick, D.J. (2006). Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard *Anolis lineatopus*. *Biol. J. Linn. Soc.* **89**, 443–454.

Herrel, A., Huyghe, K., Vanhooydonck, B., Backeljau, T., Breugelmans, I., Grbac, R., Van Damme, R. & Irschick, D.J. (2008). Rapid large scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource. *Proc. Natl. Acad. Sci. USA* **105**, 4792–4795.

Hofer, U., Bauer, H. & Bersier, L.-F. (2003). Three sympatric species of the genus *Chamaeleo* in a tropical upland forest in Cameroon. *J. Herpetol.* **37**, 203–207.

Hopkins, K.P. & Tolley, K.A. (2011). Morphological variation in the Cape Dwarf Chameleon (*Bradypodion pumilum*) as a consequence of spatially explicit habitat structure differences. *Biol. J. Linn. Soc.* **102**, 878–888.

Irschick, D.J., Carlisle, E., Elstrott, J., Ramos, M., Buckley, C., Vanhooydonck, B., Meyers, J. & Herrel, A. (2003).

Comparing habitat use, morphology, and performance in two divergent anolis lizard populations. *Integr. Comp. Biol.* **43**, 921–921.

Keren-Rotem, T., Bouskila, A. & Gefen, E. (2006). Ontogenetic habitat shift and risk of cannibalism in the common chameleon (*Chamaeleo chamaeleon*). *Behav. Ecol. Sociobiol.* **59**, 723–731.

Lailvaux, S.P., Herrel, A., VanHooydonck, B., Meyers, J.J. & Irschick, D.J. (2004). Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proc. Roy. Soc. Lond. Ser. B-Biol. Sci.* **271**, 2501–2508.

Lechowicz, M.J. (1982). The sampling characteristics of electivity indices. *Oecologia* **52**, 22–30.

Luiselli, L. & Ruigiero, L. (1996). *Chamaeleo chamaeleon* diet. *Herpetol. Rev.* **27**, 78–79.

Measey, G.J., Hopkins, K. & Tolley, K.A. (2009). Morphology, ornaments and performance in two chameleon ecomorphs: is the casque bigger than the bite? *Zoology* **112**, 217–226.

Picker, M.D., Griffiths, C. & Weaving, A. (2002). *Field guide to insects of South Africa*. Cape Town: Struik Publishers.

Pleguezuelos, J.M., Poveda, J.C., Monterrubio, R. & Ontiveros, D. (1999). Feeding habits of the common chameleon *Chamneleo chamneleon* (Linnaeus, 1758) in the southeastern Iberian Peninsula. *Isr. J. Zool.* **45**, 267–276.

Proches, S. & Cowling, R.M. (2006). Insect diversity in Cape fynbos and neighbouring South African vegetation. *Glob. Ecol. Biogeogr.* **15**, 445–541.

Regal, P.J. (1978). Behavioral differences between reptiles and mammals: an analysis of activity and mental capabilities. In *Behavior and neurobiology of lizards*: 183–202. Greenberg, N. & Maclean, P.D. (Eds). Washington, DC: Department of Health, Education and Welfare.

Schluter, D. (2000). *The ecology of adaptive radiation*. Oxford: Oxford University Press.

Schwenk, K. (2000). Feeding in lepidosaurs. In *Feeding. Form, function, and evolution in tetrapod vertebrates*: 175–291. Schwenk, K. (Ed.). San Diego, USA: Academic Press.

Stuart-Fox, D. & Whiting, M.J. (2005). Male dwarf chameleons assess risk of courting large, aggressive females. *Biol. Lett.* **1**, 231–234.

Stuart-Fox, D., Firth, D., Moussalli, A. & Whiting, M.J. (2006). Multiple signals in chameleon contests: designing and analysing animal contests as a tournament. *Anim. Behav.* **71**, 1263–1271.

Tolley, K.A. & Burger, M. (2007). *Chameleons of southern Africa*. Cape Town: Struik.

Tolley, K.A., Burger, M., Turner, A.A. & Matthee, C.A. (2006). Biogeographic patterns and phylogeography of dwarf chameleons (*Bradypodion*) in an African biodiversity hotspot. *Mol. Ecol.* **15**, 781–793.

Tolley, K.A., Chase, B. & Forest, F. (2008). Speciation and radiations track climate transitions since the Miocene Climatic Optimum: a case study of southern African chameleons. *J. Biogeogr.* **35**, 1402–1414.

Vanderploeg, H.A. & Scavia, D. (1979). Calculation and use of selectivity coefficients of feeding: zooplankton grazing. *Ecol. Modell.* **7**, 135–149.

Vanhooydonck, B., Herrel, A. & van Damme, R. (2007a). Interactions between habitat use, behavior and the trophic niche of lacertid lizards. In *Lizard ecology: the evolutionary consequences of foraging mode*: 427–449. Reilly, S.M., McBrayer, L.B. & Miles, D.B. (Eds). Cambridge: Cambridge University Press.

Vanhooydonck, B., Van Damme, R., Herrel, A. & Irschick, D.J. (2007b). A performance based approach to distinguish indices from handicaps in sexual selection studies. *Funct. Ecol.* **21**, 645–652.

Wainwright, P.C. & Reilly, S.M. (1994). *Ecological morphology: integrative organismal biology*. Chicago, IL: The University of Chicago Press.