The relationship between cranial morphology, bite performance, diet and habitat in a radiation of dwarf chameleon (*Bradypodion*)

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Many animals show unique morphological and behavioural adaptations to specific habitats. In particular, variation in cranial morphology is known to influence feeding performance, which in turn influences dietary habits and, ultimately, fitness. Dietary separation is an important means of partitioning ecological niches and avoiding inter- and intraspecific competition. Consequently, differences in dietary resources may help explain phenotypic divergence in closely-related species occupying different habitats, as well as sexual dimorphism. We test this hypothesis on five phenotypic forms of a recent radiation of dwarf chameleons (*Bradypodion*) that vary extensively in habitat use and cranial morphology. By examining stomach contents, the dietary composition of each phenotypic form is compared to investigate potential differences in feeding strategies. Overall, chameleons in the present study exhibit considerable dietary overlap (at both inter- and intraspecific levels), indicating that diet is not a major driver of variation in cranial morphology within this radiation. However, the stomachs of closed-canopy females were found to contain more prey items than male stomachs, possibly indicating that females require a greater caloric intake than their male counterparts. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **00**, 000–000.

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INTRODUCTION

Morphological and behavioural traits are shown to co-vary with environmental features in a wide array of species (Schluter & D, 2000; Herrel *et al.*, 2008; Dumont *et al.*, 2009; Losos & Mahler, 2010; Alexandre *et al.*, 2014). In lizards, because the head is involved in many ecologically and socially relevant activities (i.e. feeding, mating, and aggressive interactions), morphology and function (i.e. bite

performance) have been widely investigated aiming to better understand the adaptive significance and underlying processes shaping phenotypic variation within and between species (Herrel *et al.*, 1999, 2001a, 2010; Verwaijen, Van Damme & Herrel, 2002; Husak *et al.*, 2006; Huyghe *et al.*, 2006; Lappin, Hamilton & Sullivan, 2006; Herrel, McBrayer & Larson, 2007; Lailvaux & Irschick, 2007; Measey, Hopkins & Tolley, 2009; Vanhooydonck *et al.*, 2010; Kaliontzopoulou *et al.*, 2012).

In particular, variation in cranial morphology has been closely associated with diet, which influences feeding performance, further dietary habits, and, ultimately, fitness (Findley & Black, 1983; Verwaijen *et al.*, 2002; Metzger & Herrel, 2005; Herrel *et al.*, 2008; Timm-Davis, DeWitt & Marshall, 2015). For example, lizards with larger heads (longer, higher, wider) typically benefit from an increased gape and/ or bite force (likely as a result of larger jaw adductor muscles: Herrel *et al.*, 1999; Herrel, De Grauw & Lemos-Espinal, 2001b; Huyghe *et al.*, 2009), which has been associated with the consumption of larger and harder/tougher prey items (Shine, 1989; Herrel *et al.*, 2001a; Verwaijen *et al.*, 2002). This may help broaden the spectrum of potential prey that individuals can consume, thereby alleviating competition for resources. As such, an animal's cranial morphology is expected to show strong adaptations to its dietary niche.

Chameleons consume relatively large prey compared to other lizards (Broadley, 1973; Luiselli & Rugiero, 1996; Pleguezuelos *et al.*, 1999; Herrel *et al.*, 2000; Keren-Rotem, Bouskila & Geffen, 2006; Measey, Raselimanana & Herrel, 2013). This is facilitated by their relatively high bite forces (Vanhooydonck, Herrel & van Damme, 2007) and associated relatively large heads, which are equipped with ballistic tongues with strong tongue retractors muscles (Herrel *et al.*, 2001c, d; Higham & Anderson, 2013). They are considered opportunistic cruise foragers and adopt a foraging mode intermediate between active and sit-and-wait foraging (Butler, 2005). They acquire prey by scanning their environment, slowly moving short distances, and scanning their environment again (Regal, 1978; Butler, 2005; Measey *et al.*, 2013), eventually capturing prey using their ballistic tongues (Zoond, 1933; Wainwright, Kraklau & Bennett, 1991; Wainwright & Bennett, 1992a, b; Herrel *et al.*, 2001d). This strategy enables them to encounter similar proportions of prey types available in their arboreal habitat, which would classify them as generalists (Measey *et al.*, 2011, 2013; Carne & Measey, 2013). Behavioural observations have confirmed this foraging mode in an invasive population of *Trioceros jacksonii* in Hawai'i (Hagey, Losos & Harmon, 2010), as well as in the Cape Dwarf Chameleon,

Bradypodion pumilum (Butler, 2005). However, a recent study analyzing the ingested prey of two ecomorphs of *B. pumilum* found that the 'closed habitat' (woodland) ecomorph consumed more soft items and less sedentary prey than the 'open habitat' ecomorph, which consumed relatively equal proportions of soft and hard, as well as sedentary and evasive prey (Measey *et al.*, 2011). Furthermore, the open habitat ecomorphs possess a greater relative bite force compared to their closed habitat counterparts, which is facilitated by their proportionally wider heads (Measey *et al.*, 2009), thereby enabling them to consume harder prey. Taken together, these results indicate that the degree of cruise foraging (and diet generalism) may be dependent on prey availability and abundance, as well as cranial morphology and function, all of which are dependent on habitat type.

Extensive variation in head size and shape has been documented in another group of dwarf chameleons: a radiation of dwarf chameleons from Kwa-Zulu-Natal (KZN) Province, South Africa (da Silva & Tolley, 2013; da Silva *et al.*, 2014a). The radiation comprises five phenotypic forms, two of which are described species (*Bradypodion melanocephalum* and *Bradypodion thamnobates*) and the remaining three (Types A, B, and C) are designated as morphotypes (Gray, 1865; Raw, 1976; Tolley & Burger, 2007; Tilbury, 2010; da Silva & Tolley, 2013; da Silva *et al.*, 2014a). All forms are allopatric in distribution and occupy different macro- and microhabitats (da Silva & Tolley, 2013). *Bradypodion melanocephalum* and Type A occupy open-canopy habitats (e.g. grasslands), which contain densely clustered, vertically-oriented vegetation for chameleons to perch upon, whereas *B. thamnobates* and Types B and C occupy closed-canopy habitats (e.g. forests, transformed shrubby landscapes) that contain broader perching substrates arranged both vertically and horizontally. These ecological differences were found to correlate with functional differences in forefoot grip strength, suggesting that the forms are adapted morphologically to their different environments (da Silva *et al.*, 2014b).

Given that variation in head size and shape was found to explain the majority of the morphological differences between forms, variation in bite performance might also be expected (da Silva & Tolley, 2013). However, proportional differences in bite force were only detected between the sexes and to varying degrees, corresponding to the different levels of sexual dimorphism between forms (da Silva *et al.*, 2014a). The lack of proportional differences in bite force between forms could suggest that natural selection is weak or not acting to drive interspecific ('interform') divergence in this performance trait. Instead, sexual selection may be the predominant

selective force influencing intersexual and interform variation in head morphology within this radiation. However, the bite force of each form and sex were found to correlate with overall body size, with larger chameleons (i.e. closed-canopy vs. open-canopy, females vs. males) possessing a stronger bite, as predicted under natural selection (da Silva *et al.*, 2014a). This is noteworthy given that, for many animals, body size is not only highly heritable (Peters, 1983), but also has been shown to be influenced by ecological differences, such as diet (Asplund, 1974; Fleming, 1991; Verwaijen *et al.*, 2002; Herrel & Holanova, 2008). Accordingly, dietary variation may explain at least some of the morphological differences found in head size and shape between these forms and sexes.

To gain a better understanding of the relationship between diet, cranial morphology and function, and habitat in dwarf chameleons, we investigated the dietary differences of chameleons within the *B. melanocephalum–B. thamnobates* radiation. Based on previously published data on head shape and biomechanical models of biting in lizards, we expected to find clear relationships between dwarf chameleon morphology, performance, and diet. First, we predicted that chameleons with wider and/or taller heads, typically associated with a greater jaw closing in-lever and bite force, would consume larger and/or harder prey as part of their diet (Herrel, Aerts & De Vree, 1998a, b; Herrel *et al.*, 1999, 2001b; Metzger & Herrel, 2005; Kohlsdorf *et al.*, 2008). Because the closed-canopy chameleons were found to possess larger heads across all dimensions measured, and *B. thamnobates* and Type B chameleons, in particular, were found to possess harder absolute bite forces (da Silva & Tolley, 2013; da Silva *et al.*, 2014a), we expected them to consume larger and/or harder prey items than the open-canopy forms. Lastly, because absolute differences in body size and bite force were detected between the sexes, with females being larger and typically biting harder than males (da Silva & Tolley, 2013; da Silva *et al.*, 2014a), we expected them to consume larger and/or harder prey compared to males. To investigate these hypotheses, we quantified the stomach contents of dwarf chameleons from each of the five phenotypic forms.

MATERIAL AND METHODS

ANIMALS

A total of 292 dwarf chameleons (147 females; 145 males) (Table 1) representing the five phenotypic forms of the *B. melanocephalum–B. thamnobates* radiation were sampled from 13 localities within southern KZN (Fig. 1) during the summers of 2009 and 2010. Animals were collected at night and geo-referenced using GPS coordinates recorded at the point of capture. Marked flagging tape was placed on the perch of each chameleon to indicate the exact location where each chameleon was found. Each chameleon was then placed in a separate cloth bag and brought back to the field base overnight, where they were stomach-flushed within 3–4 h of capture. Morphological measurements and bite force readings were obtained the subsequent day to minimize stress to the animals (da Silva & Tolley, 2013; da Silva *et al.*, 2014a). Once all data were collected, animals were released at their exact point of capture.

STOMACH CONTENTS

Gastric lavage was carried out in accordance with the protocol described by Herrel *et al.* (2006). Water was gently injected into the animal's stomach using a 500-mL syringe with a modified (30° bend) ball-tipped steel attachment. The size of the tip and the amount of water used (≤ 100 mL) was adjusted to the size of the chameleon. The regurgitated contents were captured in a sieve and forceps were used to transfer the contents into vials with 99% alcohol.

The preserved stomach contents were blotted dry, identified to the lowest possible taxonomic level (mainly Order) *sensu* Picker, Griffiths & Weaving (2002), and measured and weighed. The length and width of all food items was determined using digital callipers (Mitutoyo CD-6″ CPX; precision of 0.01 mm) in accordance with the protocol reported by Carne & Measey (2013). The mass of each item was determined using an electronic balance (SBA31, Scaltec Instruments; precision of 0.1 mg).

In addition to the taxonomic diversity of stomach contents, functional diversity was also assessed by dividing items according to their hardness (soft, intermediate, and hard) (Table 2). Prey items were assigned to hardness categories based on extensive testing of the actual forces needed to crush various prey items (A. Herrel, unpublished data).

We estimated the hardness of each prey item using regression equations (Verwaijen *et al.*, 2002):

$$\text{Hard: } \log_{10}[\text{prey hardness}(N)] = 1.582 \times \log_{10} [\text{prey size (mm)}] - 1.365$$

$$\text{Intermediate: } \log_{10}[\text{prey hardness}(N)] = 1.780 \times \log_{10} [\text{prey size (mm)}] - 1.942$$

$$\text{Soft: } \log_{10}[\text{prey hardness}(N)] = 0.997 \times \log_{10} [\text{prey size (mm)}] - 1.379$$

These equations were determined by the force needed to rupture particular prey (Herrel *et al.*,

Table 1. Summary of morphological and performance data for male (M) and female (F) dwarf chameleons used in the present study, grouped by phenotypic form

	Bradypodion melanocephalum		Type A		*Bradypodion thamnobates*		Type B		Type C	
	M	F	M	F	M	F	M	F	M	F
Morphology										
n	38	26	29	33	42	56	25	18	10	14
Mass (g)	2.11 (0.44)	4.18 (1.19)	2.60 (0.78)	3.08 (1.71)	6.41 (3.62)	9.27 (5.72)	6.84 (3.56)	10.14 (6.60)	2.92 (2.00)	3.83 (3.14)
SVL (mm)	48.81 (4.54)	55.03 (4.66)	48.91 (5.93)	49.13 (8.69)	60.57 (13.28)	68.34 (14.83)	61.74 (15.03)	66.34 (19.21)	46.34 (12.50)	48.92 (13.57)
LJL (mm)	11.31 (1.06)	11.39 (0.91)	12.54 (2.73)	13.51 (2.30)	14.08 (3.51)	14.01 (2.53)	11.31 (2.84)	11.12 (2.58)	11.37 (2.25)	11.03 (2.04)
HL (mm)	11.64 (0.83)	11.72 (0.86)	12.63 (2.08)	13.54 (2.03)	14.01 (2.68)	14.38 (2.59)	10.24 (3.05)	12.08 (2.56)	11.91 (1.74)	11.54 (1.44)
HH (mm)	6.77 (0.70)	6.76 (0.53)	8.04 (1.89)	8.54 (1.64)	8.69 (1.79)	8.80 (1.69)	6.92 (1.86)	7.12 (1.54)	7.07 (1.63)	6.78 (1.42)
HW (mm)	7.42 (0.56)	7.18 (0.88)	8.72 (2.24)	9.24 (2.00)	9.94 (2.51)	9.98 (2.15)	7.63 (1.99)	7.20 (2.07)	7.61 (2.05)	7.37 (1.90)
CT (mm)	8.79 (0.77)	9.04 (0.68)	9.77 (1.96)	10.49 (1.62)	10.77 (2.07)	10.96 (2.05)	8.80 (2.03)	8.39 (2.27)	8.84 (1.43)	8.70 (1.49)
QT (mm)	10.14 (0.84)	10.23 (0.68)	11.28 (2.54)	12.00 (1.97)	12.66 (2.60)	12.75 (2.53)	10.02 (2.72)	9.89 (2.25)	10.23 (2.25)	9.87 (1.92)
InL_Closing	1.35 (0.42)	1.19 (0.44)	1.52 (0.70)	1.50 (0.53)	1.88 (0.70)	1.79 (0.68)	1.22 (0.75)	1.50 (0.98)	1.39 (0.97)	1.17 (0.58)
InL_Opening	1.17 (0.45)	1.16 (0.46)	1.26 (0.52)	1.51 (0.53)	1.37 (0.58)	1.25 (0.42)	1.29 (0.65)	1.23 (0.70)	1.14 (0.59)	1.16 (0.34)
CH (mm)	4.44 (0.86)	4.69 (0.71)	6.27 (2.57)	6.54 (1.90)	7.56 (2.17)	7.88 (2.18)	5.03 (1.75)	5.09 (2.07)	5.10 (1.66)	4.64 (1.05)
CHL (mm)	16.43 (1.38)	16.66 (1.15)	18.75 (4.26)	20.15 (3.86)	21.64 (4.40)	21.82 (4.36)	16.24 (4.37)	16.44 (4.28)	17.05 (3.44)	16.17 (3.09)
CHH (mm)	9.54 (1.34)	10.11 (0.97)	12.08 (4.14)	13.15 (3.10)	14.08 (3.51)	14.66 (3.61)	10.67 (2.94)	10.79 (3.10)	10.59 (2.13)	9.96 (1.69)
Performance										
n	24	12	18	22	19	22	15	12	7	9
Bite force (N)	0.99 (0.12)	1.09 (0.16)	1.01 (0.21)	0.89 (0.26)	1.25 (0.33)	1.27 (0.37)	1.47 (0.88)	1.51 (0.15)	0.71 (0.19)	0.83 (0.36)

Standard deviation is shown in brackets. SVL, snout–vent length; LJL, lower jaw length; HL, head length; HH, head height; HW, head width; CT, snout length; QT, quadrate to snout tip; InL_Closing, in-lever for jaw closing (LJL-QT); InL_Opening, in-lever for jaw opening (QT-CT); CH, casque height; CHL, casque head length; CHH, casque head height.
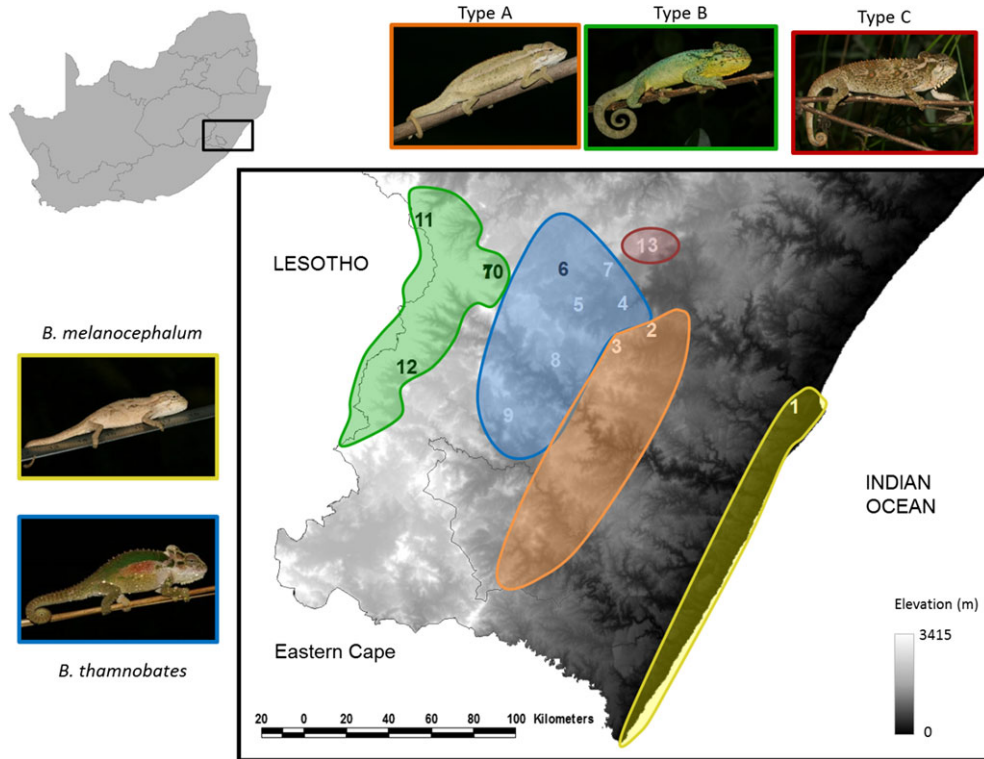
Figure 1. Photographs and general distributions of the five dwarf chameleon forms within the *Bradypodion melanocephalum–Bradypodion thamnobates* radiation from southern KwaZulu–Natal Province, South Africa. Only male forms are shown, although females resemble males in overall coloration (da Silva & Tolley 2013). Numbers indicate sampling localities: 1, Durban; 2, Hilton; 3, Stirling Farm; 4, Howick; 5, Dargle; 6, Nottingham Road; 7, Boschhoek Golf Course; 8, Boston; 9, Bulwer; 10, Kamberg Nature Reserve; 11, Highmoor Nature Reserve; 12, Sani Pass; 13, Karkloof. Modified from da Silva *et al.* (2014b).

2001a). For all prey items, length was used for 'prey size' when calculating hardness.

CRANIAL MORPHOLOGY AND PERFORMANCE

Morphometric and bite force data were taken from previously published studies (da Silva & Tolley, 2013; da Silva *et al.*, 2014a), only incorporating individuals involved in the gastric lavage described above. The morphometric data included snout–vent length (SVL) and nine head measurements (Fig. 2 and Table 1): casque head length, casque head height, casque height, head length, head width, head height, lower jaw length, snout length (measured from the posterior surface of the coronoid process of the mandible to snout tip), and quadrate-tip (measured from the posterior surface of quadrate bone to the snout tip). From the latter three measurements, two additional morphological variables were calculated: (1) in-lever for jaw opening and (2) in-lever for jaw closing. The open in-lever is the distance between the quadrate-tip and the snout length, whereas the close in-lever is the subtraction of the

quadrate-tip length from lower jaw length (Metzger & Herrel, 2005; Kohlsdorf *et al.*, 2008; Barros, Herrel & Kohlsdorf, 2011).

STATISTICAL ANALYSIS

All analyses were carried out using SPSS, version 17.0 (SPSS for Windows 17.0, 2008), and all data (morphological, performance, maximal prey dimensions) were log_{10}-transformed prior to analysis to fulfil assumptions of normality and homoscedascity. After the log_{10}-transformations, all variables displayed a normal distribution. All subsequent analyses used ordinary least squares regressions.

Stomach contents
To investigate possible differences in the diet of these chameleons, the quantity of prey consumed by each phenotypic form and sex was compared using an analysis of covariance. The model was run with 'Phenotypic form' and 'Sex' as the fixed factors, log_{10}-SVL as a covariate to control for the effect of size,

Table 2. Classification of each prey type according to hardness level

Stomach contents	Prey hardness
Invertebrata	
Araneae	Soft
Blattodea	Soft
Chilopoda	Soft
Coleoptera (adults)	Hard
Coleoptera (larva)	Soft
Collembola	Soft
Diplopoda	Intermediate
Diptera	Soft
Gastropoda (snails only)	Hard
Hemiptera	Intermediate
Hymenoptera (excluding Formicidae)	Hard
Hymenoptera (Formicidae)	Hard
Isopoda	Intermediate
Lepidoptera (adult)	Soft
Lepidoptera (larva)	Soft
Mantodea	Soft
Mecoptera	Soft
Opiliones	Soft
Orthoptera	Intermediate
Other	
Vegetation	Hard

and the square root of the 'Number of prey items found in each stomach' as the dependent variable.

Given the presence of sexual dimorphism within this radiation (da Silva & Tolley, 2013; da Silva *et al.*, 2014a, b), all subsequent analyses were carried out separately by sex.

To understand the significance of a particular prey item in the diets of the five phenotypic forms, a relative importance index (IRI) was calculated for each prey type and functional group (Pinkas, Oliphant & Iverson, 1971; Huysentruyt *et al.*, 2004):

$$\text{IRI} = (\%N + \%V).\%Oc.$$

where $\%N$ is the numeric abundance of a particular prey type compared to the total abundance of all prey items, $\%Oc$ is the frequency of occurrence of a prey type (the number of individuals of a species that consumed that prey type), and $\%V$ is the volumetric percentage of the prey type for a given species. In the present study, we replaced $\%V$ with $\%$Mass. Moreover, we calculated $\%$IRI, which is the proportion of IRI of each prey type (or functional group) in relation to the total IRI value for a species.

The overlap in diet among the five phenotypic forms was also calculated using Schoener's D index (Schoener, 1968), which is defined as:

$$\text{DAB} = 1 - 0.5. \sum |\%\text{NA} - \%\text{NB}|$$

where $\%N_A$ and $\%N_B$ are the proportional numeric abundances of a particular prey type for species A and B, respectively. D values range between 0 (when no food is shared) and 1 (when there is the same proportional use of all prey items), with values > 0.6 considered as biologically significant (Wallace, 1981; Wallace & Ramsay, 1982).

Correlations between morphology, performance, and diet

To take into account the possible dependences between body size and head shape, performance and prey characteristics, all of these data were regressed against $\log_{10}$-SVL and the unstandardized residuals saved for use in subsequent analyses when these regressions gave significant results. Although studies have shown that the head can develop at a different rate than overall body size (Braña, 1996; Kratochvíl *et al.*, 2003), this was not found to be the case for these chameleons (da Silva & Tolley, 2013; da Silva *et al.*, 2014a). All variables were found to share a common growth axis and follow similar trajectories. Moreover, principal component analyses, carried out separately by sex, revealed that all variables fit within a single principal component, with $\log_{10}$- SVL possessing the highest component score (males: 88.9%; females: 90.4%), validating its use as a suitable covariate (McCoy *et al.*, 2006).

Because extensive morphometric and performance analyses have already been conducted on this dataset (da Silva & Tolley, 2013; da Silva *et al.*, 2014a, b), ontogenetic changes in body size and shape, as well as its influence on bite performance, were not re-examined. Instead, the morphometric and performance variables were solely used to investigate their association with diet among the five phenotypic forms.

To investigate the relationship between morphology, performance, and diet, we first regressed the $\log_{10}$-transformed maximal prey dimensions (width and mass) and hardness variables against $\log_{10}$-SVL. Because of its contribution to the calculation of prey hardness, prey length was not included in this analysis, nor any subsequent analyses involving prey characteristics. For the regressions showing a significant association, the unstandardized residuals were extracted and saved for use in subsequent analyses. Multivariate analyses of variance (MANOVAs) were then conducted on the unstandardized residuals to test for differences between the five phenotypic forms. *P*-values were subjected to Holm's sequential Bonferroni (Holm, 1979) correction to minimize the possibility of Type I errors (Rice, 1989).

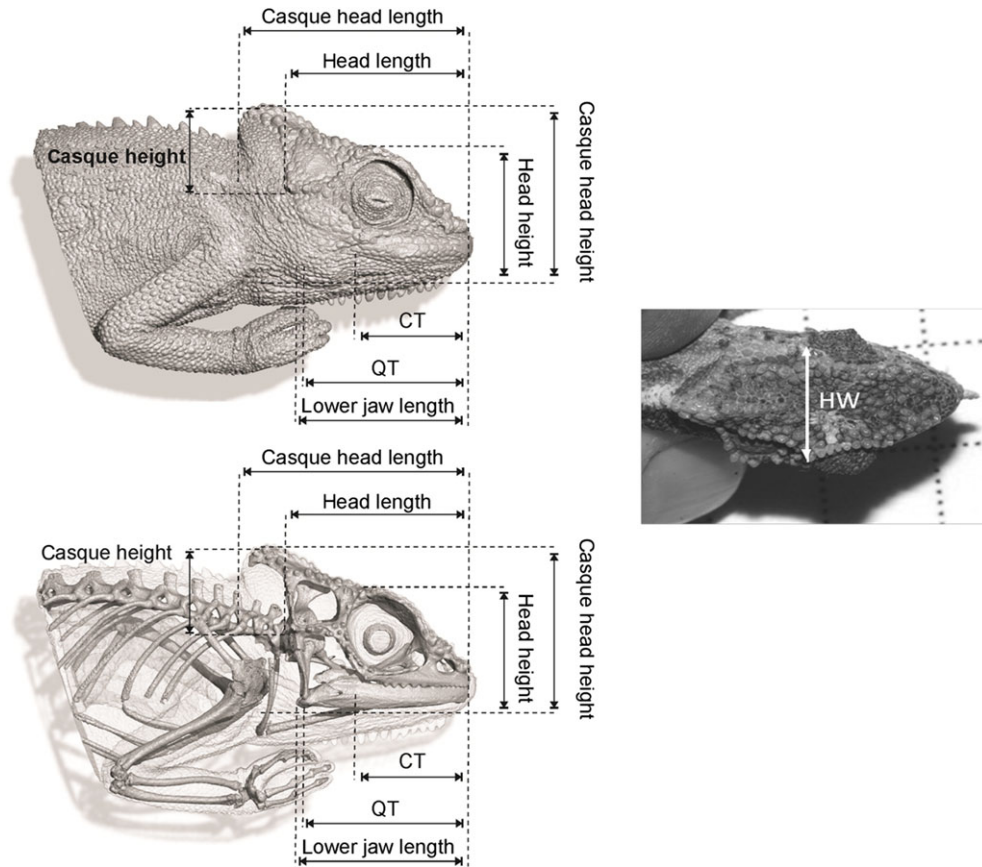Next, we investigated the relationship between head shape and diet to determine whether the same

Figure 2. Nine head measurements recorded for each chameleon. Images on the left are based on a microtomography scan (courtesy of R. Boistel, Université de Poitiers). CT, snout length; QT, quadrate-snout tip; HW, head width. Reproduced with permission from da Silva *et al.* (2014a).

morphological variable or combination of variables best explains the dimensions and hardness of prey consumed by each phenotypic form. To do this, we extracted the residuals of the regressions of head dimensions and introduced them into stepwise multiple regression models, with the maximal prey dimensions (width, mass) and hardness as the dependent variables.

Finally, we tested whether bite force also explained variation in prey characteristics by conducting regression analyses using both $\log_{10}$-transformed (absolute) and residual (relative) bite force as the independent variables and prey width, mass, and hardness as the dependent variables. For analyses involving relative bite force, all variables (dependent and independent) were size-corrected against $\log_{10}$-SVL.

RESULTS

STOMACH CONTENTS

Of the 292 chameleon stomachs examined, five (1.71%) were empty. Of the remaining 287 stomachs,

no differences were found in the quantity of prey consumed by each form ($F_{4,272} = 0.950$; $P = 0.436$); however, differences were detected between the sexes ($F_{1,285} = 4.691$; $P = 0.031$), with Bonferroni post-hoc tests revealing that closed-canopy females consume more prey items than closed-canopy males (Fig. 3). No differences were detected between the sexes within the open canopy forms.

These chameleons were found to prey on an assortment of 20 different invertebrate Orders (Table 1; see Supporting Information, Table S1); however, four Orders predominated (Table 3): Hemiptera, Dipetra, Isopoda, and Araneae. Hemiptera and Diptera were amongst the top two prey types within four forms (*B. thamnobates* and Types A, B, and C). For *B. melanocephalum*, Hemiptera and either Isopoda or Araneae were amongst the most important prey items for females and males, respectively.

An analysis of prey types according to their hardness (Table 2) showed that females consumed prey of equal or lower hardness than males, and that all forms predominantly ate soft or intermediately hard prey (Table 4).
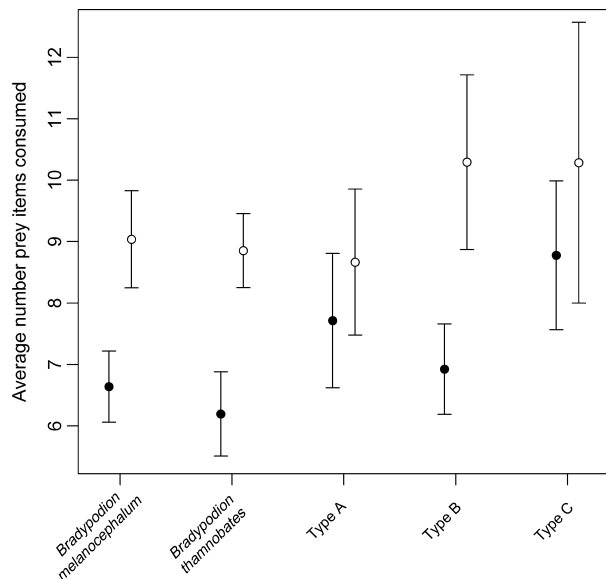
Figure 3. Error plot depicting differences in mean prey abundance across each phenotypic form and sex within the *Bradypodion melanocephalum–Bradypodion thamnobates* radiation. Filled circles: males; open circles: females.

Comparing the dietary overlap between the five forms revealed that the diets of Type B chameleons are most dissimilar to those of the other phenotypic forms, except for *B. thamnobates* (Table 5), likely as a result of the vast predominance of Diptera in their diets (Table 3). The diets of *B. thamnobates* showed significant overlap with all other forms (Table 5), as a result of the presence of all but two prey types in its diet: Chilopoda (centipedes) and Diplopoda (millipedes) (Table 3). The diets of *B. melanocephalum* and Type A males showed complete overlap (Table 5).

CORRELATIONS BETWEEN MORPHOLOGY, PERFORMANCE, AND DIET

For both males and females, prey width and hardness were found to correlate positively and significantly with SVL (Table 6). Accordingly, the residuals of these characteristics against SVL were used in the MANOVAs to test for differences in prey characteristics between forms: no differences were detected in either sex (males: Wilks' $\lambda = 0.861$; $F_{4,138} = 1.275$; $P = 0.222$; females: Wilks' $\lambda = 0.856$; $F_{4,145} = 1.383$; $P = 0.146$).

Stepwise multiple regression models using residual head dimensions as the independent variables and prey width, mass, and hardness as the dependent variables identified significant correlations for each phenotypic form. However, no single morphological variable was found to best predict all prey

characteristics within and across forms (Table 7). Snout length was the only variable found to explain prey hardness among *B. melanocephalum* males, showing a direct relationship, whereas a combination of variables was typically found to explain prey characteristics within the other forms. Only Type B males showed significant morphological correlations for all three prey characteristics. No correlations were detected for open-canopy females (*B. melanocephalum* and Type A) and *B. thamnobates* males.

Regression analyses showed no relationship between relative bite force and prey characteristics ($0.099 \geq P \leq 0.699$); however, relationships were detected when absolute bite force was used as the independent variable, with the bite of both males and females showing positive and significant associations with all three prey characteristics, indicating that body size strongly relates to prey choice of these chameleons (Table 8). The subsequent MANOVA and Bonferroni post-hoc test used to determine which forms were contributing to these results revealed fewer significant associations (Females – mass, hardness; Males – mass) (Table 8). These were attributed to Type A chameleons generally consuming smaller (in mass) and softer prey for a given bite force compared to all other phenotypic forms (Fig. 4).

DISCUSSION

Although we predicted that differences in head size and shape within the *B. melanocephalum–B. thamnobates* radiation would result in dietary differences between the morphological forms, our analyses did not detect significant differences between them. The closed-canopy chameleons, *B. thamnobates* and Type B, which possess larger heads across all dimensions measured, as well as harder absolute bite forces (da Silva & Tolley, 2013; da Silva *et al.*, 2014b), did not consume larger or harder prey than the open-canopy forms. We also predicted that females would consume larger and harder prey than males as a result of them being larger and biting harder; however, no differences were detected between the sexes within the open-canopy forms, and closed-canopy females typically consumed softer prey or prey of equal hardness.

Overall, the phenotypic forms within this radiation exhibited dietary overlap, which, initially, appears to suggest that natural selection is not driving differences in head morphology and function between phenotypic forms. However, closed-canopy females were found to consume more prey items than males. Considering that females tend to possess a greater absolute body size, overall (da Silva & Tolley, 2013), this

Table 3. Proportional significance of each dietary item (%IRI) found within the stomachs of chameleons within the *Bradypodion melanocephalum–Bradypodion thamnobates* radiation, separated by sex and phenotypic form

Prey item	*Bradypodion melanocephalum* F (N = 26)	*Bradypodion melanocephalum* M (N = 39)	Type A F (N = 33)	Type A M (N = 29)	*Bradypodion thamnobates* F (N = 56)	*Bradypodion thamnobates* M (N = 39)	Type B F (N = 17)	Type B M (N = 24)	Type C F (N = 14)	Type C M (N = 10)
Invertebrata										
Araneae	4.88	**14.23**	7.67	6.08	3.46	6.51	0.03	6.50	3.88	3.91
Blattodea	0.00	0.05	0.00	0.00	0.08	0.01	0.00	0.00	0.00	0.00
Chilopoda	0.00	0.00	0.00	0.00	< 0.01	0.00	0.00	0.00	0.00	0.00
Coleoptera (adults)	3.72	5.58	2.95	5.32	3.39	2.21	4.98	1.69	1.66	8.20
Coleoptera (larva)	0.00	0.01	0.00	0.02	0.05	0.06	0.15	0.00	0.00	0.00
Collembola	0.06	0.00	1.50	0.05	0.08	0.42	0.00	7.14	0.70	3.55
Diplopoda	0.09	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Diptera	6.15	13.15	**23.80**	**26.53**	**57.91**	**56.96**	**79.08**	**75.45**	**53.49**	**25.79**
Gastropoda (snails only)	0.01	0.01	0.00	0.10	0.67	0.68	0.00	0.06	0.72	1.11
Hemiptera	**26.49**	**54.80**	**52.16**	**52.14**	**25.94**	**29.91**	**11.45**	**10.66**	**35.44**	**31.14**
Hymenoptera (excluding Formicidae)	2.84	1.33	4.30	1.43	5.54	1.69	2.30	3.93	3.75	9.27
Hymenoptera (Formicidae)	0.71	0.06	0.49	0.59	0.77	0.03	0.00	0.00	0.00	0.00
Isopoda	**46.45**	7.73	1.41	2.26	0.20	0.90	0.03	0.02	1.94	15.79
Lepidoptera (adult)	0.02	0.00	0.44	0.22	0.31	0.01	0.00	0.00	1.33	0.00
Lepidoptera (larva)	0.27	0.48	4.98	3.86	1.43	0.43	1.53	1.39	0.20	0.47
Mantodea	0.08	0.03	0.04	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Mecoptera	0.00	0.00	0.08	0.00	0.07	0.11	0.07	0.03	0.06	0.27
Opiliones	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00
Orthoptera	8.23	2.54	0.10	1.34	0.09	0.00	0.24	0.17	0.70	0.53
Other										
Vegetation	0.00	0.00	0.07	3.57	5.13	0.07	0.14	0.00	0.00	0.00

The %IRI indicates the proportion of IRI of each prey type in relation to the total IRI value for a phenotypic form. Detailed dietary information on each prey type used to calculate the %IRI, including prey abundance, frequency of occurrence and mass, is provided in the Supporting information (Table S1). Bold values highlight the two predominant prey groups for each sex and form.

Table 4. Diet composition in terms of hardness and evasiveness within each of the five phenotypic forms

				Females				Males		
				Hardness				Hardness		
			N	Soft	Intermediate	Hard	N	Soft	Intermediate	Hard
Open-canopy	*Bradypodion melanocephalum*	26	N_S	19	25	19	38	39	37	25
			N_I	57	132	45		100	241	54
			Mass (mg)	423.60	11806.90	315.80		916.70	938.20	211.30
			%IRI	11.20	**80.01**	8.79		37.47	**54.29**	8.24
	Type A	33	N_S	31	26	18	27	25	23	19
			N_I	118	123	46		68	124	44
			Mass (mg)	667.17	487.10	163.40		450.40	339.90	108.80
			%IRI	**52.37**	38.21	9.42		42.56	**44.83**	12.60
Closed-canopy	*Bradypodion thamnobates*	55	N_S	55	46	41	39	35	28	16
			N_I	257	140	105		128	85	32
			Mass (mg)	5201.90	1363.69	1334.73		1570.01	674.38	471.40
			%IRI	**63.96**	20.64	15.40		**64.14**	27.75	8.10
	Type B	17	N_S	16	12	11	25	24	18	14
			N_I	111	31	28		109	33	32
			Mass (mg)	3205.30	541.50	662.10		6741.00	333.40	635.20
			%IRI	**75.60**	12.53	11.86		**81.97**	9.54	8.48
	Type C	14	N_S	14	12	9	10	10	10	9
			N_I	74	50	20		39	51	24
			Mass (mg)	755.72	453.30	128.40		140.80	3193.10	91.20
			%IRI	**59.35**	32.35	8.31		21.37	**66.75**	11.89

N_S, number of stomachs; N_I, number of items; IRI, relative importance index; %IRI, proportion of IRI of each prey functional group in relation to the total IRI value for a phenotypic form. Detailed dietary information on each prey type used to calculate the %IRI is provided in the Supporting information (Table S1).
Bold values highlight the predominant prey functional group for each sex and form.

Table 5. Schoener's index values of dietary overlap between the five phenotypic forms of the *Bradypodion melanocephalum–Bradypodion thamnobates* radiation, separated by sex.

		Females				
		Bradypodion melanocephalum	Type A	*Bradypodion thamnobates*	Type B	Type C
Males	*Bradypodion melanocephalum*	–	**0.75**	**0.67**	0.47	**0.66**
	Type A	**1.00**	–	**0.74**	0.52	**0.75**
	Bradypodion thamnobates	**0.68**	**0.72**	–	**0.70**	**0.81**
	Type B	0.53	0.58	**0.76**	–	0.60
	Type C	0.54	0.52	0.57	0.57	–

Bold values highlight biologically significant dietary overlap between pairwise comparisons.

result may suggest that closed-canopy females require a greater caloric intake than their male counterparts, which is potentially related to their larger body size and fitness. To confirm this, an assessment of the caloric value of all prey types would need to be undertaken.

The lack of support for dietary differentiation between phenotypic forms was surprising given that such differences may be expected where chameleons inhabit different habitats and/or vary in body size (Akani, Ogbalu & Luiselli, 2001; Measey *et al.*, 2013), both of which are characteristics of this

Table 6. Relationships between snout–vent length and prey dimensions and hardness for the top prey items of chameleons in the *Bradypodion melanocephalum–Bradypodion thamnobates* radiation

	Females					Males				
	r^2	Slope	Intercept	F	P	r^2	Slope	Intercept	F	P
Prey width (mm)	0.153	0.582	−0.539	26.010	< 0.001	0.084	0.446	−0.326	12.547	0.001
Prey mass (g)	0.133	1.829	−1.855	22.003	< 0.001	0.038	1.121	−0.738	5.436	0.021
Prey hardness (N)	0.161	1.002	−2.127	27.600	< 0.001	0.076	0.879	−1.917	11.339	0.001

Table 7. Results of the stepwise multiple regression models used to predict the morphological variables that best explain prey dimensions and hardness

		Females				Males			
Phenotypic form	Prey characteristic	Model	r^2	P	Slope	Model	r^2	P	Slope
Bradypodion melanocephalum	Width (mm)								
	Mass (mg)								
	Hardness (N)					CT	0.131	0.025	3.277
Type A	Width (mm)								
	Mass (mg)					CHL	0.208	0.048	−8.353
						HL			12.259
	Hardness (N)								
Bradypodion thamnobates	Width (mm)	HL	0.170	0.007	1.906				
		LJL			−2.014				
	Mass (mg)								
	Hardness (N)	HL	0.124	0.030	2.125				
		HW			−1.360				
Type B	Width (mm)					HL	0.641	< 0.001	1.583
						CHL			−1.533
	Mass (mg)					InL_Opening	0.322	0.003	1.939
	Hardness (N)	CHH	0.431	0.004	−1.653	HL	0.545	< 0.001	2.318
						CHL			−1.224
Type C	Width (mm)					HL	0.461	0.031	−1.253
	Mass (mg)	HW	0.595	0.007	−5.723	HH	0.706	0.002	−5.532
		CHL			5.987				
	Hardness (N)	InL_Closing	0.360	0.023	−0.654				

LJL, lower jaw length; HL, head length; HH, head height; HW, head width; CT, snout length; InL_Closing, in-lever for jaw closing (LJL-QT); InL_Opening, in-lever for jaw opening (QT-CT); CHL, casque head length; CHH, casque head height.

Table 8. Regression analyses examining the relationship between absolute bite force and prey characteristics

Prey characteristic	Females				Males			
	r^2	Slope	Intercept	P	r^2	Slope	Intercept	P
Width	0.337	0.489	0.494	< 0.001	0.243	0.476	0.467	< 0.001
Mass	0.267	1.718	1.422	< 0.001*	0.183	1.429	1.323	< 0.001*
Hardness	0.219	0.764	-0.375	< 0.001*	0.137	0.832	-0.368	0.001

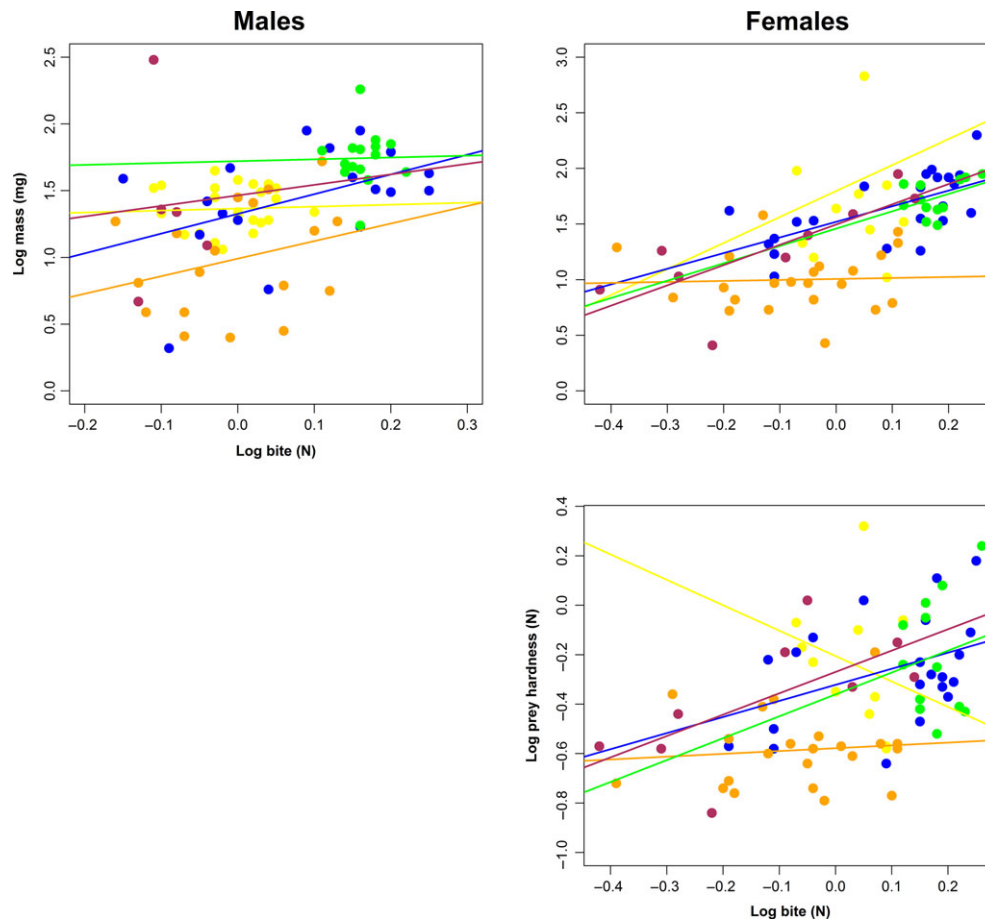*Denotes significant associations after Bonferroni correction.

Figure 4. Regression plots showing significant correlations between absolute bite force and prey characteristics for the five phenotypic forms within the *Bradypodion melanocephalum–Bradypodion thamnobates* radiation. Yellow, *B. melanocephalum*; blue, *B. thamnobates*; orange, Type A; green, Type B; maroon, Type C.

radiation. This is because, in novel habitats, lizards may be faced with different dietary resources and, consequently, may need to adapt to their new environments through changes in their external head morphology, as well as their internal digestive systems (Herrel *et al.*, 2008). However, many studies investigating patterns of diet utilization and selection in lizards have reported an overall similarity in the diets of related species (Kaliontzopoulou *et al.*, 2012). Even closely-related sympatric species, which theory suggests are able to coexist by partitioning dietary resources (Hutchinson, 1959; Hardin, 1960; Pianka, 1973; Schoener, 1974), often show largely overlapping diets, indicating little selection for divergence in dietary patterns (Herrel *et al.*, 2001a; Sutherland, 2011). Indeed, most lizards are food generalists and include a large variety of prey in their diets (Greene, 1982). The dwarf chameleons examined in the present study appear to fit this generalization.

Because chameleons are opportunistic cruise foragers, they should encounter similar proportions of soft, intermediate, and hard prey that are available in their habitat (Measey *et al.*, 2011, 2013; Carne & Measey, 2013). If this is the case, the data suggest that there is limited abundance of hard prey types within each habitat. Alternatively, these results could suggest that there is a seasonal effect of certain prey types in particular habitats and/or that chameleons are exhibiting dietary preferences or avoidances (refer to Measey *et al.*, 2011; Carne & Measey, 2013). For example, a recent study examining the foraging behaviour of *Bradypodion ventrale* and *Bradypodion taeniabronchum* found that both chameleons were more likely to take hard prey in winter, when there was a clear reduction in the availability and volume of prey. However, in summer, both species avoided hard prey items. If there is a seasonal effect on prey within the habitats of the *B. melanocephalum*–*B. thamnobates* radiation, then

any constraints in food availability that act on head morphology may not necessarily be seen in summer. A detailed survey of the available invertebrate diversity in each habitat, as well as chameleon diet, during different seasons would need to be undertaken to test these hypotheses.

Despite the general absence of dietary differences between phenotypic forms within this radiation, positive correlations between head morphology, absolute bite force, and prey size (mass and hardness) were detected within all but Type A chameleons, highlghting the functional importance of overall head size in prey acquisition, similar to that found for two ecomorphs of *B. pumilum* (Measey *et al.*, 2011). However, if the associations of bite force and prey size are only by-products of head or body size, then what do the differences in cranial morphology between forms actually indicate and what is driving its evolution? According to current evidence, habitat is likely to be the most significant factor shaping variation within this radiation, along with the associated influences from natural and sexual selection (da Silva & Tolley, 2013).

Currently, the five phenotypic forms are allopatric in distribution and occupy habitats that differ at both macro- and microscales (da Silva & Tolley, 2013). However, according to a biogeographical study investigating the relationship between palaeoclimatic fluctuations and cladogenesis within *Bradypodion*, the ancestral habitat for these chameleons is considered to be forest (Tolley, Chase & Forest, 2008). Subsequent to the Plio-Pleistocene transition approximately 2–3 Mya, these chameleons have become spatially displaced, with some forms retaining the ancestral, forested habitat (*B. thamnobates* and Types B and C) and others progressing into open habitats (*B. melanocephalum* and Type A). This spatial displacement and the associated differences in macro- and microhabitats, which primarily involve differences in their exposure to predators and communication ability, resulted in different selective pressures acting upon these chameleons. Sexual selection appears to be the predominant force within the closed-canopy habitats, driving the development of conspicuous secondary sexual characteristics, such as a proportionally larger head and casque, which results in a greater absolute bite force (da Silva & Tolley, 2013; da Silva *et al.*, 2014b). These features better enable chameleons to communicate to conspecifics from a distance, reducing the need for confrontations, which can be harmful, especially male–male encounters (Stuart-Fox *et al.*, 2006; Tolley & Burger, 2007). Natural selection, on the other hand, appears to be the dominant force driving the appearance of open-canopy chameleons. Open-canopy habitats are more exposed to aerial predators compared

to the closed-canopy forests (Measey *et al.*, 2013). Consequently, the need to communicate to conspecifics is outweighed by the need to avoid predation, thus explaining the diminutive size (in both absolute and relative terms) of *B. melanocephalum* and Type A chameleons and their weaker bite forces (da Silva & Tolley, 2013; da Silva *et al.*, 2014b).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Table S1. Diet composition of dwarf chameleons within the *Bradypodion melanocephalum–Bradypodion thamnobates* species complex.