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Linking microhabitat structure, morphology and locomotor performance traits in a recent radiation of dwarf chameleons

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Summary

1. Evidence that morphological traits associated with particular environments are functionally adapted to those environments is a key component to determining the adaptive nature of radiations. Adaptation is often measured by testing how organisms perform in diverse habitats, with performance traits associated with locomotion thought to be among the most ecologically relevant.

2. We therefore explored whether there are relationships between morphology, locomotor performance traits (sprint speed, forefoot and tail grip strength on broad and narrow dowels) and microhabitat use in five phenotypic forms of a recent radiation of dwarf chameleon – the *Bradypodion melanocephalum–Bradypodion thamnobates* species complex – to determine whether morphological differences previously identified between the forms are associated with functional adaptations to their respective habitats, which can be broadly categorized as open or closed-canopy vegetation.

3. The results showed significant differences in both absolute and relative performance values between the phenotypic forms. Absolute performance suggests there are two phenotypic groups – strong (*B. thamnobates* and Type B) and weak (*B. melanocephalum* and Types A and C). Relative performance differences highlighted the significance of forefoot grip strength among these chameleons, with the closed-canopy forms (*B. thamnobates*, Types B and C) exceeding their open-canopy counterparts (*B. melanocephalum*, Type A). Little to no differences were detected between forms with respect to sprint speed and tail strength. These results indicate that strong selection is acting upon forefoot grip strength and has resulted in morphological adaptations that enable each phenotypic form to conform with the demands of its habitat.

4. This study provides evidence for the parallel evolution of forefoot grip strength among dwarf chameleons, consistent with the recognition of open and closed-canopy ecomorphs within the genus *Bradypodion*.

Key-words: Chamaeleonidae, lizards, morphometrics, perch diameter, South Africa

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Introduction

Trait utility – evidence that morphological traits associated with particular environments are indeed ecologically pertinent – is a key component for assessing the adaptive nature of radiations, as well as for understanding the underlying mechanisms involved in evolutionary adaptations (Schluter 2000). Trait utility is often measured by testing how organisms perform ecologically relevant functions in diverse habitats. Because locomotion is essential for the survival (e.g. to escape predation, find food) and reproduction (to find mates, defend territories) of many animals, performance traits associated with locomotion are thought to be among the most ecologically relevant (Huey & Stevenson 1979; Arnold 1983; Aerts *et al*. 2000).

Many animals rely on a broad repertoire of locomotor capabilities, such as running/sprinting, jumping, clinging and climbing, to carry out functions relevant to survival; however, optimization of one performance trait often results in a trade-off in another (e.g. Lewontin 1978; Stearns 1992; Irschick & Losos 1999). This is because different performance traits may require very different organismal configurations (e.g. muscle fibre type, skeletal structure), which are beneficial in different environments (e.g. Arnold 1983; Abu-Ghalyun *et al*. 1988; Losos 1990b; Aerts *et al*. 2000). Such trade-offs have been well documented for lizards. For example, a trade-off is commonly observed between speed and stability in cases in which terrestrial and arboreal species are compared. Open-canopy, terrestrial environments, in which organisms tend to be more visible to predators, typically harbour long-legged lizards capable of running rapidly along the ground (i.e. broad substrate) to avoid predation. Conversely, lizards in closed, arboreal habitats tend to have shorter limbs, which often results in them having relatively slower running speeds, but increased stability on the narrow, sometimes vertical, substrates due to the reduced distance between their centre of mass and the surface, which minimizes sideways torque (e.g. Pounds 1988; Losos & Sinervo 1989; Losos 1990a; Sinervo & Losos 1991; Losos, Walton & Bennett 1993; Losos & Irschick 1996; Arnold 1998; Macrini & Irschick 1998; Melville & Swain 2000; Vanhooydonck, Herrel & Irschick 2006).

Chameleons, unlike most lizards, move slowly on all substrates. They are thought to be cruise foragers (Butler 2005) that use their ballistic tongue to capture prey (Zoond 1933; Wainwright, Kraklau & Bennett 1991; Wainwright & Bennett 1992a,b; Herrel *et al*. 2001). To avoid predation, chameleons rely upon crypsis and, in the case of arboreal chameleons, dropping from branches (Brain 1961; Burrage 1973; Tolley & Burger 2007). Although there are a number of primarily terrestrial chameleon clades that utilize low perches at night to decrease predation risk, the majority of Chamaeleonidae radiated during the Eocene into a fully arboreal niche (Tolley, Townsend & Vences 2013). They have specialized adaptations for such habitats, including a prehensile tail and hands/feet, which allow them to grasp perches in a fully arboreal environment (Burrage 1973; Peterson 1984; Tilbury 2010; da Silva & Tolley 2013). These features are particularly useful for clinging and holding onto relatively narrow substrates (Peterson 1984; Higham & Jayne 2004). Because of their vastly different locomotor adaptations and cryptic strategies compared with other lizards (Peterson 1984), the typical performance predictions may not apply to chameleons (i.e. Herrel *et al*. 2011, 2013). Nevertheless, chameleon morphology has been shown to correlate with performance in particular habitats. For example, chameleons in closed-canopy habitats, such as forests and woodlands, tend to possess relatively longer tails and larger feet than do chameleons in open-canopy habitats, such as grasslands and heathlands (Hopkins & Tolley 2011). This may enable them to grip harder on the broader perches found there (Losos, Walton & Bennett 1993; Herrel *et al*. 2011, 2013). The closed-canopy species within the genus *Bradypodion* (dwarf chameleons) also run faster than do their open-canopy counterparts, likely owing to their relatively longer limbs (Herrel *et al*. 2011, 2013). It has been suggested that closed-canopy habitats are less cluttered, and in essence more 'open' at the microhabitat level, with fewer available perches for a chameleon to grasp, compared with open-canopy habitats, which are structurally cluttered at the microhabitat level (Herrel *et al*. 2011; da Silva & Tolley 2013). As such, longer limbs may be essential within closed-canopy habitats to facilitate gap bridging between perches. The associated differences in sprint speed may simply be a by-product of their limb length (e.g. longer limbs allow longer strides to be taken without necessarily increasing stride frequency: Bauwens *et al*. 1995; Bonine & Garland 1999; Vanhooydonck, Damme & Aerts 2002). These correlations demonstrate local adaptations to microhabitat, and thus trait utility. In the case of *Bradypodion pumilum* (the Cape dwarf chameleon), these adaptations led to the suggestion that open and closed-canopy forms should be considered ecomorphs (Measey, Hopkins & Tolley 2009; Herrel *et al*. 2011). However, an essential component of the ecomorph concept is the parallel evolution in multiple lineages of correlations between morphology and ecology (sensu Williams 1972). An assessment of trait utility in another *Bradypodion* clade – the *Bradypodion melanocephalum–Bradypodion thamnobates* species complex – may thus prove beneficial for the classification of dwarf chameleons as ecomorphs.

The *B. melanocephalum–B. thamnobates* species complex is a recent radiation of dwarf chameleons from KwaZulu-Natal (KZN) Province, South Africa (Tolley, Chase & Forest 2008) that is classified as being taxonomically problematic due to discordance between phylogeny and morphology (Tolley *et al*. 2004). The complex is comprised of five recognizable phenotypic forms (Fig. 1), all with distinct differences in ecology and distribution (da Silva & Tolley 2013). Two forms are classified taxonomically – *B. melanocephalum* (Gray 1865) and *B. thamnobates* (Raw 1976) – and the remaining three (regarded as Types A, B

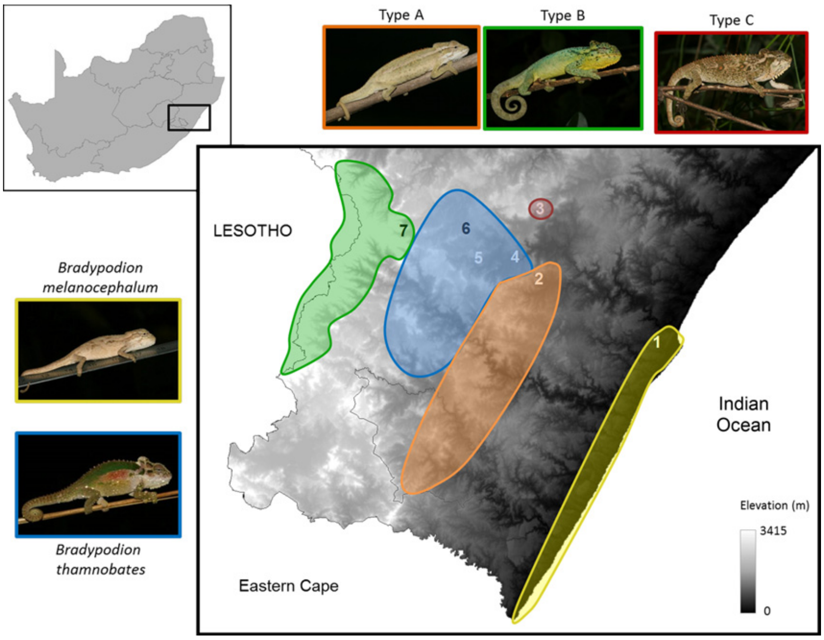

Fig. 1. Photographs and general distributions of the five dwarf chameleon forms within the *Bradypodion melanocephalum–Bradypodion thamnobates* species complex from southern KwaZulu–Natal Province, South Africa. Only male forms are shown, although females resemble males in overall coloration (refer to Fig. 1 in da Silva & Tolley 2013). Numbers indicate field sites sampled in this study: 1, Durban; 2, Hilton; 3, Karkloof; 4, Howick; 5, Dargle; 6, Nottingham Road; 7, Kamberg Nature Reserve.

and C by da Silva & Tolley 2013) designated as morphotypes (Tolley & Burger 2007; Tilbury 2010). Type A appears most similar to *B. melanocephalum* in size and colour, leading many to classify it as another population of the species (Tolley *et al.* 2004; Tilbury 2010); however, it has been found to be most similar to *B. thamnobates* genetically (Tolley *et al.* 2004: Fig. 2, samples CT16 and CT17). Types B and C have morphological features outwardly similar to *B. thamnobates* (e.g. prominent casque and large gular lobes), yet differ in size and coloration. Mitochondrial DNA has grouped Type B with *B. thamnobates* (Tolley *et al.* 2004: Fig. 2, sample CT71), while Type C has been found to group with both *B. melanocephalum* and *B. thamnobates* (Tolley *et al.* 2004: Fig. 2, samples B304 and B305).

Similar to their congener *B. pumilum* (Herrel *et al.* 2011), these forms appear to fall into two broad habitat categories – either open (*B. melanocephalum* and Type A) or closed canopy (*B. thamnobates*, Types B and C) – and have morphological features that appear to reflect adaptations to these habitats (see da Silva & Tolley 2013). However, some morphological features, particularly the limbs and tail, do not always correlate with these broad habitat categories (da Silva & Tolley 2013), potentially reflecting differences at the microhabitat level and/or the recent divergence of this radiation.

To understand whether or not the phenotypic differences in this group of chameleons are adaptive, we examined whether performance could be predicted by morphology and/or microhabitat. We expected similar patterns to be revealed as have been observed with other *Bradypodion* species (Herrel *et al.* 2011, 2013). Therefore, we hypothesized that absolute differences in performance will be correlated with overall body size, but that the phenotypic forms would exhibit functional adaptations (i.e. relative differences in maximal sprint speed, forefoot and tail grip strength) associated with their microhabitats. In particular, we predicted that (i) relative sprint speed would be determined by limb length; (ii) closed habitat chameleons, which possess proportionally larger feet (da Silva & Tolley 2013), would have a relatively stronger grip on both wide and narrow perches than do the shorter-footed open-canopy chameleons; (iii) closed-canopy chameleons would possess a proportionally stronger tail grip on wide perches because their longer tails can wrap more coils around a thick substrate compared with the smaller tails of the open-canopy chameleons, increasing the contact area and creating more friction, thereby allowing for a stronger grip (Herrel *et al.* 2013), while on narrow perches, all forms would be expected to perform comparably; and (iv) morphological traits that correlate well with grip strength, will also show strong correlations to microhabitat (perch diameter). Confirmation of these predictions would corroborate the parallel evolution of open and closed-canopy ecomorphs within the *B. melanocephalum–B. thamnobates* species complex, as well as the genus.

Materials and methods

STUDY SITES AND SAMPLING PROCEDURES

A total of 171 dwarf chameleons (85 females; 86 males) representing the five phenotypic forms (see da Silva & Tolley 2013) within the *B. melanocephalum–B. thamnobates* species complex were sampled from seven sites within southern KZN (Fig. 1) in January and February 2010. To obtain an adequate sample size, *B. thamnobates* was sampled from three sites, whereas the remaining four forms were sampled from a single site each. Animals were collected at night and georeferenced using global positioning system (GPS) coordinates recorded at the location each chameleon was found. Marked flagging tape was placed on the perch of each chameleon to indicate the exact location at which each chameleon was found. Each chameleon, along with a section of their perch, was then placed in a separate cloth bag and brought back to the field base overnight, where they were measured and their performance tested the subsequent day. The diameter of the perch was measured to the nearest 0·01 mm using digital callipers. Once all data were collected, animals were released at their exact point of capture.

MORPHOMETRICS

All chameleons were measured to the nearest 0·1 mm using digital callipers (Fig. 2): snout-vent length (SVL), interlimb length (ILL), tail length (TL), thigh length (ThL), crus length (CL), medial hindfoot pad length (MH), lateral hindfoot pad length (LH), proximal hindfoot pad length (PH), brachium length (BL), antebrachium length (AL), medial forefoot pad length (MF), lateral forefoot pad length (LF) and proximal forefoot pad length (PF). Because we worked with live animals, measurements were made externally and are therefore the best approximations for the actual skeletal components listed above. The limits of each component were determined by gently moving the limbs and feet at the joints and positioning each end of the calipers at either end of the bony segment. For consistency, these measurements were taken on the left side of the body. Each measurement was taken once because preliminary precision trials conducted on 10 *B. thamnobates* chameleons and based on three measurements of each variable found little error between the three recordings (±0·77%). The mass of each chameleon was also measured using a Pesola® micro-line spring scale (model 93010: 30 g × 0·25 g ± 0·3%).

PERFORMANCE

Chameleons were first allowed to thermoregulate in a sun/shade setting to attain their preferred body temperature (between 28 and 32 °C; see Segall *et al.* 2013). All performance trials were then performed at ambient temperature. A minimum rest period of 1 h was allowed for each chameleon during the transition between sprinting and gripping tests. Sprint speed was tested by running chameleons along a flat 1-m long track marked at 25-cm intervals. Considering chameleons move very slowly in their regular (perched) habitat and probably do not rely on running to avoid predation in their arboreal habitat (Brain 1961; Burrage 1973; Tolley & Burger 2007), selection related to sprint speed might occur when animals are moving along the ground (Herrel *et al.* 2011). Previous studies of chameleons have also shown that sprint speed is highest on a flat substrate (Abu-Ghalyun *et al.* 1988; Losos, Walton & Bennett 1993); therefore, sprinting performance was tested by chasing chameleons along a flat track. The times at which animals crossed the 25-cm markers were recorded using a stopwatch. For dwarf chameleons, these manual recordings were found to be comparable to readings provided electronically using infrared photocells (Herrel *et al.* 2011). The speed in centimetres per second over the fastest interval was calculated and retained for further analysis.

Grip strength was tested using two different sized horizontal dowels (broad: 9·25 mm; narrow: 4 mm) mounted separately on a piezo-electric force platform (Kistler Squirrel force plate, ±0·1 N: see Herrel *et al.* 2012), which was connected to a Kistler charge amplifier (type 9865). The dowel sizes were chosen as they are representative of branch diameters available to these chameleons (da Silva & Tolley 2013), and hence, might reflect the limit of what they perch on. Moreover, they resemble the dowel sizes used in other dwarf chameleon performance studies (Herrel *et al.* 2011, 2013). Forces were obtained during a 60-s recording session and recorded at 1000 Hz. During the session, chameleons voluntarily gripped the dowel with their tail and forefeet repeatedly (typically, two to four grips each per session) and were then pulled until they released the dowel. Animals were pulled in the vertical direction to measure tail force and in the horizontal direction to measure forefoot grip strength. Even though structural differences exist between chameleon fore- and hindfeet, which might affect their performance, such as the reverse arrangement of fused toes between the medial and lateral segments (Burrage 1973; Peterson 1984), we only investigated forefoot performance because it allowed for comparisons to other species in the genus (*B. pumilum*: Herrel *et al.* 2011; *Bradypodion damaranum*: Herrel *et al.* 2013; Potgieter 2013; *Bradypodion occidentale*: Herrel *et al.* 2013) and, principally, because the forefoot is much easier to measure, resulting in greater precision. Furthermore, the morphometric data show strong correlations between fore- and hind-foot sizes (da Silva & Tolley 2013). Accordingly, the forefoot performance

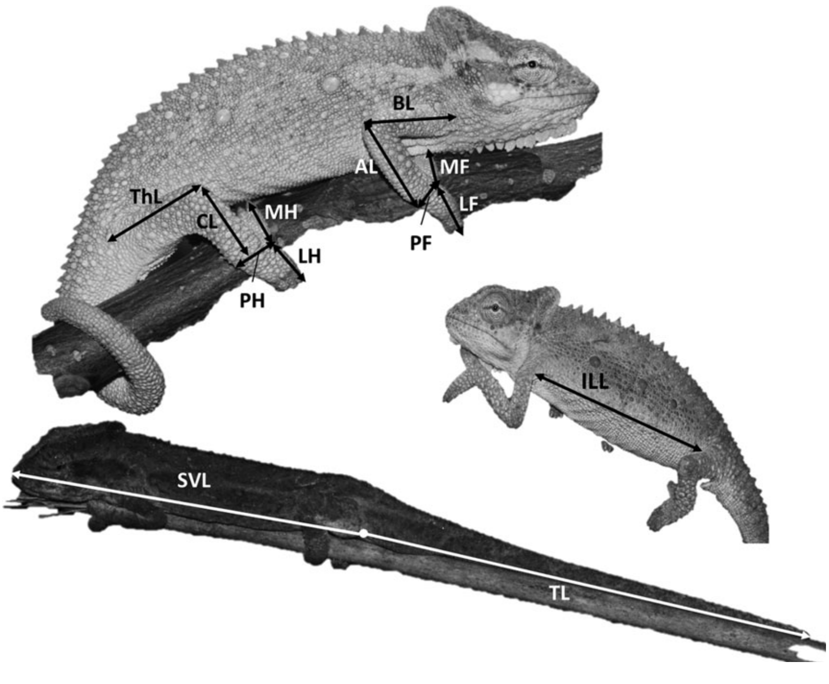

Fig. 2. Thirteen measurements recorded for each chameleon. SVL, snout-vent length; TL, tail length; ILL, interlimb length; ThL, thigh length; CL, crus length; MH, medial hindfoot pad length; LH, lateral hindfoot pad length; PH, proximal hindfoot pad length; BL, brachium length; AL, antebrachium length; MF, medial forefoot pad length; LF, lateral forefoot pad length; and PF, proximal forefoot pad length.

results are expected to hold for the hindfoot as well. Each chameleon was tested in three separate recording sessions for each dowel, with at least 30 min rest between sessions involving the same dowel, and at least 1 h of rest between sessions when changing dowels. The peak forces (*Z*, tail; *Y*, forefeet) were recorded and extracted using Bioware software (Kistler), and the highest tail and forefeet grip values per individual per dowel were retained for subsequent analysis.

STATISTICAL ANALYSES

All analyses were carried out using SPSS, version 17.0 (SPSS Inc 2008). All data were $\log_{10}$-transformed prior to analysis to fulfil assumptions of normality and homoscedasticity. Ordinary least squares regressions were then conducted to verify that the assumptions were met. Each $\log_{10}$-transformed variable was entered as the dependent variable, separately, and a plot of the z-predicted (*x*-axis) against z-residual (*y*-axis) values was constructed. All plots showed that the error variance (z-residual) is consistent with the varying values in the predicted variables (z-predicted), confirming homoscedasticity. To remove the effect of body size on performance, all data were size-corrected using a linear regression executed on all individuals, and the unstandardized residuals saved for use in subsequent analyses. The regression and a principal component analysis (PCA) indicated that all body and performance measurements followed similar trajectories and fit within a single principal component, with log SVL possessing the highest component score (Braña 1996; Kratochvíl *et al.* 2003; McCoy *et al.* 2006). Accordingly, all measurements were size-corrected using log SVL.

Although a previous study revealed significant morphometric differences between the five phenotypic forms and sexes examined in this study (da Silva & Tolley 2013), a multivariate analysis of variance (MANOVA) using a general linear model (GLM) was carried out to verify that the subset of data, which included only individuals used in the performance tests used here, would reproduce those results. The full model specified SEX and FORM as fixed factors, SEX × FORM as the interaction, and all size-corrected variables as the dependent variables. All *P*-values were subjected to Holm's sequential Bonferroni (Holm 1979) correction to minimize the possibility of Type I errors (Rice 1989).

Performance

For grip strength tests, repeated-measures ANOVAs were carried out to assess whether performance was dependent on dowel size for each phenotypic form and both sexes. MANOVAS were then conducted on each of the five performance variables using both absolute ($\log_{10}$-transformed) and relative (size-corrected) values to test for differences between forms. As above, all *P*-values were subjected to Holm's sequential Bonferroni correction. To explore which morphological variables best explained the variation in sprint speed and forefoot grip strength on both dowels for each chameleon form, separately, multiple linear regression models were carried out on size-corrected variables. The same models were run for each phenotypic form and sex. Specifically, the three performance variables were entered separately as the dependent variable in a linear regression, with all size-corrected variables used as the independent variables. Akaike Information Criterion (AIC) was calculated using the residual sum of squares from each model, and the difference between the lowest AIC and all others (Δ_i) was determined. Akaike's weights (w_i) were then calculated for each model, with the one exhibiting the highest w_i acknowledged as the best model (Burnham & Anderson 2002). Because TL was the only tail variable measured in this study, a linear regression was conducted simply to assess the degree of correlation between it and tail grip strength on both dowels.

Habitat

To determine whether the perch diameter used by chameleons (i.e. microhabitat) is correlated with their morphology, linear regression analyses were run on $\log_{10}$-transformed data using perch diameter as the independent variable and variables making up the forefoot, hindfoot and tail (MF, LF, PF, MH, LH, PH, TL) as the dependent variables. Only these morphometric variables were included because they are directly involved in gripping perches. As above, AIC and w_i were calculated for each model.

Results

The initial MANOVA revealed morphological differences between the five phenotypic forms (Wilks' $\lambda = 0{\cdot}267$, $F_{4,169} = 4{\cdot}899$, $P < 0{\cdot}001$) and sexes (Wilks' $\lambda = 0{\cdot}539$, $F_{1,169} = 10{\cdot}959$, $P < 0{\cdot}001$), confirming previous results for this species complex (da Silva & Tolley 2013; refer to Table 1 for raw data). Given the significant sex effect, all subsequent analyses were carried out separately by sex.

PERFORMANCE

The effect of dowel size on forefoot grip strength was significant for both sexes in all five phenotypic forms (Table 2), with animals exerting higher forces on the narrow dowel compared with the broad dowel (Table 1). In contrast, only Type A males from the KZN Midlands showed a significant difference in tail performance between the two dowels (Table 2), with these animals also showing a stronger grip on the narrow dowel (Narrow: 0·78 ± 0·36 N; Broad: 0·60 ± 0·36 N). Overall, chameleons exhibited stronger grip forces with their tails than with their forefeet (Table 1).

Absolute and relative performance differences were uncovered between forms for both males and females, albeit to varying degrees (Table 3). Both sexes showed the same pattern in terms of absolute differences, typically with the largest forms being the strongest (i.e. *Bradypodion thamnobates* and Type B). In addition, these two largest forms showed similar performance levels between them, for almost all traits (Table 3). Similarly, the smaller forms (*B. melanocephalum* and Types A and C) were comparable to each other for most performance traits.

Relative performance values showed fewer differences between forms and sexes. After Bonferroni correction, female forms were only found to differ from each other in forefoot grip strength on the broad dowel (Table 3; Fig. 3). This was attributed to *B. thamnobates* having a substantially stronger grip than *B. melanocephalum* and Type A. Male forms differed from each other in forefoot grip strength on both dowels, as well as tail grip strength on the broad dowel (Fig. 3). These differences were also attributed to the stronger gripping ability of *B. thamnobates*, particularly for forefoot strength, and *B. melanocephalum* and Type B for tail grip strength.

Model selection using linear regression to find the morphological variables that best explain performance did not

Table 1. Summary of mean microhabitat, morphological and performance data for male (M) and female (F) dwarf chameleons used in this study, grouped by phenotypic form. Standard deviation shown in brackets

	Bradypodion melanocephalum		*Bradypodion thamnobates*		Type A		Type B		Type C	
	M	F	M	F	M	F	M	F	M	F
Morphology										
n	25	15	20	25	20	25	14	12	6	7
Mass (g)	2·1 (0·5)	4·4 (0·9)	6·2 (3·8)	8·8 (5·9)	2·6 (0·9)	2·2 (0·7)	8·4 (1·9)	13 (4·5)	1·8 (0·3)	1·9 (0·5)
SVL (mm)	49·1 (4·4)	56·8 (2·9)	60·0 (14·6)	66·4 (16·6)	48·2 (7·3)	44·5 (5·4)	69·5 (4·3)	77·5 (6·8)	40·6 (3·2)	41·6 (3·9)
TL (mm)	54·7 (5·4)	51·7 (3·7)	66·7 (17·9)	65·5 (18·1)	52·5 (7·9)	44·8 (4·1)	79·4 (7·9)	85·5 (10·7)	44·8 (3·3)	41·3 (4·1)
ILL (mm)	27·6 (3·2)	33·4 (2·0)	32·9 (8·4)	37·9 (10·6)	25·5 (4·1)	24·2 (3·6)	38·0 (3·8)	44·8 (5·8)	20·9 (2·4)	21·1 (1·4)
BL (mm)	9·4 (1·1)	10·0 (0·7)	11·9 (3·1)	12·7 (3·5)	9·5 (1·6)	8·9 (1·3)	14·7 (1·1)	15·4 (1·5)	7·7 (0·3)	7·9 (0·7)
AL (mm)	7·8 (0·9)	8·4 (0·5)	9·9 (2·8)	10·5 (2·9)	8·1 (1·5)	7·3 (0·9)	11·9 (0·7)	12·9 (1·3)	6·4 (0·5)	6·2 (0·5)
MF (mm)	4·4 (0·6)	4·9 (0·4)	6·1 (1·5)	6·4 (1·6)	4·7 (0·7)	4·3 (0·5)	7·1 (0·4)	7·9 (0·8)	4·2 (0·4)	4·1 (0·3)
LF (mm)	5·3 (0·5)	5·7 (0·5)	7·3 (1·9)	7·8 (1·8)	5·5 (0·7)	5·1 (0·5)	8·9 (0·5)	9·2 (0·8)	4·9 (0·6)	4·7 (0·6)
PF (mm)	1·9 (0·2)	2·0 (0·2)	2·9 (0·8)	3·0 (0·9)	1·9 (0·3)	1·9 (0·3)	3·6 (0·5)	3·6 (0·4)	1·6 (0·1)	1·8 (0·2)
ThL (mm)	9·1 (0·9)	9·6 (0·6)	11·3 (3·4)	11·8 (3·3)	9·4 (1·6)	8·7 (1·1)	13·4 (1·1)	15·1 (1·5)	7·1 (0·6)	7·4 (0·7)
CL (mm)	7·7 (0·6)	8·4 (0·5)	9·5 (2·5)	10·3 (2·8)	7·8 (1·3)	7·3 (0·9)	11·3 (0·6)	12·5 (1·1)	6·3 (0·6)	6·3 (0·4)
MH (mm)	4·2 (0·3)	4·5 (0·4)	6·0 (1·8)	6·4 (1·7)	4·5 (0·8)	3·9 (0·4)	7·0 (0·7)	8·0 (1·0)	3·7 (0·5)	3·4 (0·4)
LH (mm)	5·6 (0·5)	5·8 (0·5)	7·7 (2·0)	8·0 (2·1)	5·7 (0·9)	5·1 (0·8)	9·2 (1·0)	9·8 (1·4)	4·7 (0·4)	4·9 (0·4)
PH (mm)	2·1 (0·3)	2·2 (0·3)	3·3 (1·1)	3·3 (1·2)	2·3 (0·5)	1·9 (0·4)	3·6 (0·6)	4·2 (0·7)	7·7 (0·3)	2·0 (0·3)
Performance										
n	23	15	20	25	20	25	13	12	5	7
Speed (cm s^{-1})	6·30 (1·60)	5·94 (1·31)	7·48 (3·51)	7·79 (1·85)	5·99 (1·92)	5·21 (1·29)	9·96 (2·06)	9·13 (1·84)	4·52 (1·27)	4·04 (0·84)
Max. forefoot grip force (N)										
Broad	0·08 (0·03)	0·07 (0·03)	0·18 (0·14)	0·17 (0·09)	0·05 (0·03)	0·05 (0·02)	0·19 (0·12)	0·21 (0·16)	0·06 (0·02)	0·05 (0·02)
Narrow	0·47 (0·11)	0·55 (0·13)	1·16 (0·90)	1·13 (0·68)	0·39 (0·19)	0·30 (0·12)	1·49 (0·41)	1·70 (0·53)	0·28 (0·09)	0·26 (0·06)
Max. tail grip force (N)										
Broad	0·82 (0·31)	0·68 (0·31)	1·36 (0·87)	1·52 (1·00)	0·60 (0·36)	0·62 (0·25)	2·23 (1·27)	2·17 (1·12)	0·44 (0·10)	0·50 (0·16)
Narrow	0·95 (0·42)	0·62 (0·24)	1·34 (0·99)	1·65 (1·34)	0·78 (0·39)	0·56 (0·27)	2·17 (0·94)	2·19 (1·45)	0·40 (0·11)	0·38 (0·15)
Microhabitat										
n	25	15	17	23	19	23	14	10	6	7
Perch diameter (mm)	1·77 (0·95)	2·06 (0·94)	2·38 (0·87)	2·18 (1·47)	1·55 (0·76)	2·18 (1·00)	2·80 (1·58)	2·24 (1·00)	1·58 (0·58)	1·78 (0·73)

ILL, interlimb length; BL, brachium length; AL, antebrachium length; LF, lateral forefoot pad length; LH, lateral hindfoot pad length; MF, medial forefoot pad length; MH, medial hindfoot pad length; SVL, snout-vent length; TL, tail length; PF, proximal forefoot pad length; ThL, thigh length; CL, crus length; PH, proximal hindfoot pad length.

show a pattern that could be generalized to fit all forms (Table 4). In some cases, several candidate models, often involving multiple morphological variables, exhibited significant correlations with performance (Tables S1–S3, Supporting Information); however, the best fitting models tended to include a single morphological variable (Table 4). Of the three performance variables that underwent model selection (sprint speed and forefoot grip strength on broad and narrow dowels), forefoot grip strength on the narrow dowel showed significant correlations for almost all forms and sexes (Table 4). As forefoot size increased (particularly the medial forefoot and metacarpus), so did the grip strength of both sexes of the open-canopy forms, *B. thamnobates* females and Type B males. In contrast, AL, not forefoot size, was the best predictor of grip strength on the narrow dowel for *B. thamnobates* from the closed-canopy habitat. On the broad dowel, forefoot size and grip strength were not correlated for most forms; and in two cases, correlations were negative, suggesting overall that chameleons do not perform well on the broad surface and, in some cases, performance drops significantly. Sprint speed exhibited the greatest variation among forms and sexes, with the best model generally incorporating a combination of fore- and hind-limbs and feet. Only three groups showed significant correlations between TL and grip strength (Broad dowel: *B. melanocephalum* females; Narrow dowel: Type B females and Type C males). No performance-morphology associations were uncovered for Types B and C females for any of the five performance traits, which could potentially be attributed to their low sample sizes (n = 11 and 8, respectively).

Table 2. Repeated measures ANOVA assessing the dependence of grip strength on dowel size within both sexes of each phenotypic form

			Max. Forefoot grip strength		Max. Tail grip strength	
Morph	Sex	*n*	*F*	*P*	*F*	*P*
Bradypodion melanocephalum	M	23	271·81	<0·001	0·24	0·631
	F	15	257·37	<0·001	0·64	0·435
Bradypodion thamnobates	M	20	550·56	<0·001	0·22	0·647
	F	25	521·00	<0·001	0·01	0·910
Type A	M	20	396·04	<0·001	12·15	0·003
	F	25	259·66	<0·001	1·04	0·320
Type B	M	13	449·59	<0·001	1·09	0·315
	F	12	230·94	<0·001	0·18	0·682
Type C	M	5	159·31	0·001	1·918	0·225
	F	7	212·71	<0·001	0·44	0·531

M, male; F, female; *n*, sample size; *F*, test value; *P*, significance value.

HABITAT

Model selection examining the best morphological correlates of perch diameter found significant correlations for all but Type C chameleons (Table S4) and was particularly strong for females of the closed habitat form, *B. thamnobates*. Of the best fitting models, PH was correlated with perch diameter in females; although in males, no consistent pattern was observed (Table 5). Overall, different morphological variables were found to associate with perch diameter (Table 5) compared with those that associated with grip strength (Table 4).

Discussion

Chameleons within the *B. melanocephalum*–*B. thamnobates* species complex possess functional adaptations in forefoot size and performance that correspond to their use of either open or closed habitats. These results reflect those observed for other *Bradypodion* species (Herrel *et al.* 2011, 2013; Potgieter 2013), providing additional support for the existence of open and closed-canopy ecomorphs within the genus. No habitat-specific correlations were uncovered between limb length and sprint speed, or between TL and tail strength, indicating that selection is not acting upon these traits in terms of the habitat associations and measurements made.

As expected, the absolute differences detected between the five chameleon forms followed the same pattern for

Table 3. MANOVA results investigating absolute and relative performance differences between phenotypic forms

	Males (n = 86)				Females (n = 85)			
	Absolute		Relative		Absolute		Relative	
Performance	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Sprint speed (cm s^{-1})	10·406	<0·001*	1·331	0·266	8·069	<0·001*	1·139	0·344
Max. forefoot grip force (N)								
Broad	18·509	<0·001*	4·669	0·002*	22·585	<0·001*	3·961	0·006*
Narrow	26·643	<0·001*	5·187	0·001*	27·066	<0·001*	2·227	0·073
Max. tail grip force (N)								
Broad	14·910	<0·001*	3·636	0·009*	14·207	<0·001*	2·510	0·048
Narrow	14·932	<0·001*	1·972	0·107	14·410	<0·001*	1·874	0·123

F, test value; *P*, significance value.
*Significant after Bonferroni correction.

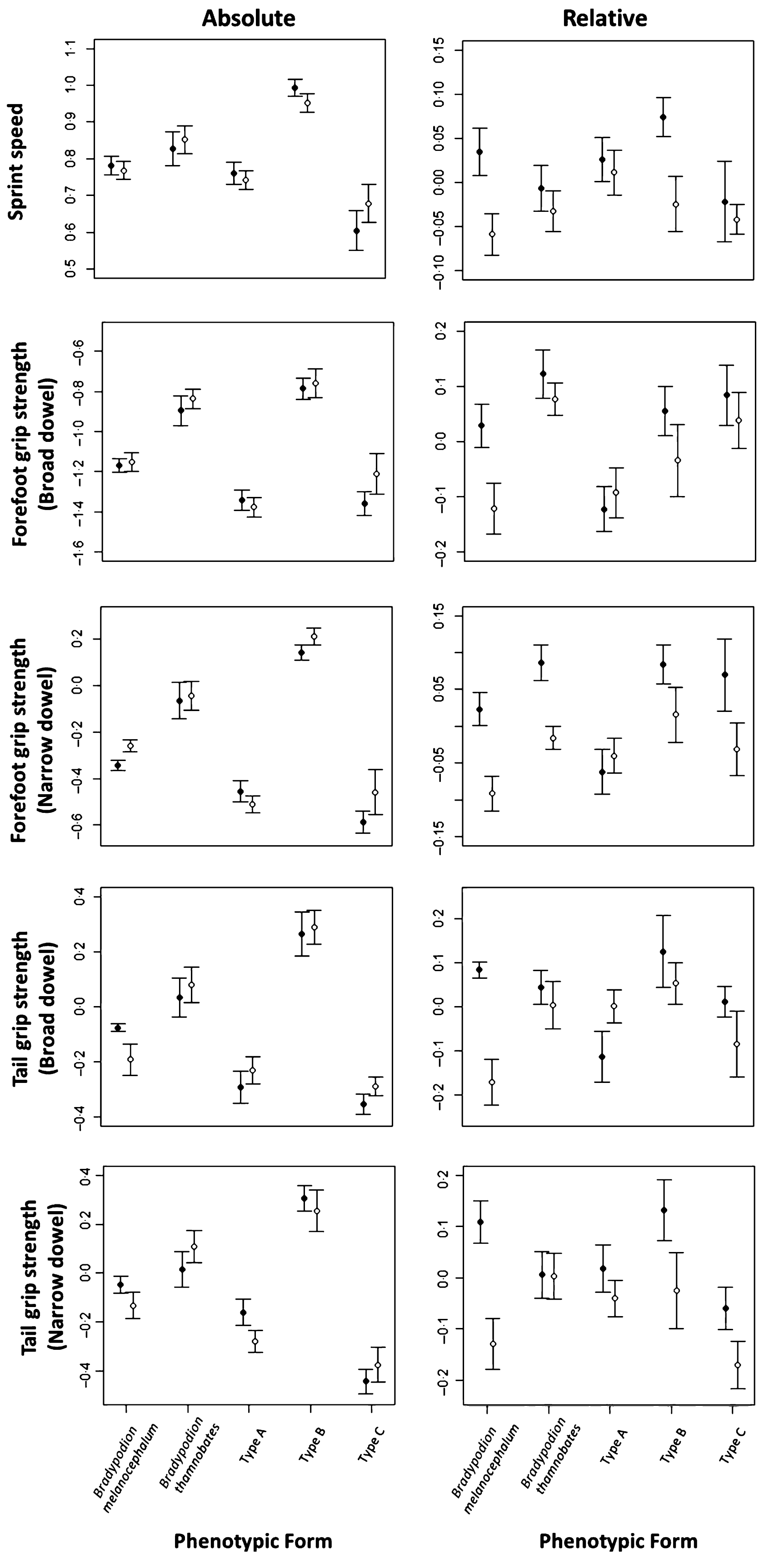

Fig. 3. Error plots of mean absolute values (left) and mean relative values (right) for the five performance variables tested for the *Bradypodion melanocephalum–Bradypodion thamnobates* species complex. Error bars represent standard error. Absolute force equates to $\log_{10}$-transformed values, whereas relative force depicts size-corrected values. Solid circles represent males; empty circles, females.

Table 4. Results of regression analyses on the morphological variables found to best reflect the five performance variables under investigation

		Males				Females			
Performance variable	Phenotypic form	Model	β	R^2	P	Model	β	R^2	P
Sprint speed	*Bradypodion melanocephalum*	**Antebrachium**	**0·412**	**0·169**	**0·041**	**Crus** **Medial forefoot**	**−0·683** **0·657**	**0·612**	**0·002**
	Bradypodion thamnobates	**Thigh**	**0·652**	**0·425**	**0·002**	Proximal hindfoot Antebrachium	−0·314 0·394	0·197	0·089
	Type A	Medial forefoot	0·377	0·142	0·112	**Lateral hindfoot** **Antebrachium**	**0·375** **0·357**	**0·309**	**0·030**
	Type B	**Medial hindfoot** **Brachium**	**0·627** **0·378**	**0·505**	**0·015**	Lateral forefoot	0·570	0·325	0·053
	Type C	**Medial hindfoot** **Proximal hindfoot** **Antebrachium**	**0·244** **0·732** **0·436**	**0·001**	**0·001**	Thigh	−0·371	0·138	0·326
Maximum forefoot grip strength (broad dowel)	*B. melanocephalum*	Antebrachium	0·378	0·143	0·135	**Medial forefoot**	**−0·317**	**0·100**	**0·025**
	B. thamnobates	Brachium	0·395	0·156	0·084	Lateral forefoot	0·295	0·087	0·153
	Type A	Medial forefoot	0·363	0·131	0·127	Medial forefoot	0·341	0·116	0·111
	Type B	**Proximal forefoot**	**0·524**	**0·275**	**0·045**	Antebrachium	−0·500	0·25	0·098
	Type C	**Medial forefoot**	**−0·780**	**0·608**	**0·038**	Medial forefoot	0·636	0·404	0·066
Maximum forefoot grip strength (narrow dowel)	*B. melanocephalum*	**Medial forefoot**	**0·411**	**0·168**	**0·042**	**Proximal forefoot**	**0·561**	**0·315**	**0·024**
	B. thamnobates	**Antebrachium**	**0·486**	**0·219**	**0·038**	**Antebrachium** **Medial forefoot**	**0·383** **0·307**	**0·304**	**0·018**
	Type A	**Antebrachium** **Proximal forefoot**	**−0·493** **0·489**	**0·351**	**0·031**	**Medial forefoot**	**0·716**	**0·513**	**< 0·001**
	Type B	**Proximal forefoot**	**0·612**	**0·374**	**0·015**	**Proximal forefoot**	0·402	0·161	0·196
	Type C	Medial forefoot	−0·509	0·259	0·244	Medial forefoot	0·077	0·154	0·296
Maximum tail grip strength (broad dowel)	*B. melanocephalum*	Tail	0·248	0·061	0·233	Tail	**0·539**	**0·291**	**0·031**
	B. thamnobates		0·342	0·117	0·140		−0·177	0·031	0·397
	Type A		0·058	0·003	0·814		0·228	0·052	0·296
	Type B		−0·069	0·005	0·807		0·233	0·050	0·486
	Type C		0·260	0·067	0·574		0·252	0·064	0·513
Maximum Tail Grip Strength (Narrow dowel)	*B. melanocephalum*	Tail	−0·035	0·001	0·867	Tail	0·107	0·011	0·694
	B. thamnobates		−0·018	0·000	0·939		**0·432**	**0·187**	**0·031**
	Type A		0·105	0·011	0·669		0·071	0·005	0·748
	Type B		−0·040	0·002	0·888		0·608	0·370	0·036
	Type C		**0·822**	**0·675**	**0·023**		0·254	0·065	0·509

R^2, coefficient of determination; β, beta coefficient depicting direction of correlation; P, significance value.
Text in bold highlights significant morphology-performance correlations. Refer to Table 1 for sample sizes.

Table 5. Morphological variables found to best reflect perch diameter across all phenotypic forms and sexes

	Males					Females				
Phenotypic form	n	Model	β	R^2	P	n	Model	β	R^2	P
Bradypodion melanocephalum	25	**PF**	**0·429**	**0·184**	**0·032**	15	**PH** **TL**	**0·537** **0·478**	**0·653**	**0·001**
Bradypodion thamnobates	17	**PF**	**0·513**	**0·263**	**0·035**	23	**MF** **PH**	**−1·195** **1·177**	**0·712**	**0·000**
Type A	19	LH	−0·274	0·075	0·256	23	**PH**	**−0·417**	**0·174**	**0·049**
Type B	14	**MH** **PH** **TL**	**1·022** **−0·441** **−0·511**	**0·659**	**0·011**	10	PF MF	−1·285 1·353	0·421	0·195
Type C	6	LF	0·471	0·221	0·287	7	LH	0·308	0·095	0·371

n, sample size; β, beta coefficient depicting direction of correlation; R^2, coefficient of determination; P, significance value; TL, tail length; MF, medial forefoot pad length; LF, lateral forefoot pad length; PF, proximal forefoot length; MH, medial hindfoot pad length; LH, lateral hindfoot pad length; PH, proximal hindfoot pad length.
Text in bold highlights significant correlations between morphology and perch diameter.

each performance trait investigated, demonstrating the effect of overall body size on performance. Forms that utilize closed-canopy habitats are stronger and faster than those that use open-canopy habitats. Indeed, the forms generally fit into one of the two absolute performance categories – strong (Type B and *B. thamnobates*) and weak

(*B. melanocephalum*, Types A and C). For many animals, body size is highly heritable (Peters 1983) and has been shown to be influenced by habitat use (e.g. Asplund 1974; Fleming 1991), which might also be the case here. Moreover, each form reaches different absolute body sizes (da Silva & Tolley 2013), which is not a consequence of phenotypic plasticity, as demonstrated by a common garden experiment on *B. thamnobates* and *B. melanocephalum* (Miller & Alexander 2009). Accordingly, the differences in absolute performance are likely indicative of ecological differences between them. The one exception might be with the Type C chameleons. These chameleons are the smallest (in absolute terms) of all the forms in this study, yet their primary habitat is forest. If they were to follow the other forest forms, they should be among the larger chameleons. Considering that the individuals sampled in this study were collected in secondary vegetation along the forest edge and not in the forest itself due to accessibility problems (da Silva & Tolley 2013), they may not be representative of mature adults, but rather subadults, thus biasing the data.

In addition to absolute differences, relative performance differences were detected in forefoot grip strength on both sized dowels and tail grip strength on the broad dowel, indicating that selection may be acting upon these performance traits, and their associated morphological traits, in response to habitat. As expected, forefoot grip strength produced the same pattern on either dowel, with the closed-canopy forms (including Type C) exerting greater forces for their size than the open-canopy forms. The widest perches in the open habitats do not exceed 6 mm, and average around 2 mm, whereas the widest perches in the closed habitats can reach close to 20 mm, and average between 2·50–4·50 mm (da Silva & Tolley 2013). Both dowels appear to be too large for the smaller-footed open habitat chameleons to adequately grasp. Conducting similar tests using dowels that better represent perch diameters more commonly available in open-canopy habitats, and thus that are more representative of the actual perches used by those chameleons (e.g. 1·5–2 mm or narrower), may prove useful for testing the effectiveness of foot size on narrow perches.

The greater forefoot grip strength of the closed habitat chameleons likely emphasizes the importance of stability and balance within this habitat. It could be especially important during intraspecific encounters, which often result in intense fighting. These fights generally involve intense swaying, open-mouthed threat displays, chasing and biting (Burrage 1973; Stuart-Fox *et al.* 2006; Tolley & Burger 2007), with both combatants grasping the branch to maintain balance and support. In open-canopy habitats, where the average plant and perch height is between 0·75 and 1·75 m and the perches are densely clustered in a vertical orientation (da Silva & Tolley 2013), the risk of displacement is far less compared with closed habitats where perches are less densely arranged and perch heights average 1·6–4·5 m (da Silva & Tolley 2013). This may explain why grip strength showed correlations with both limb and foot variables (Tables 4, S2, S3). Grip strength is created by the flexor muscles, which extend from the limbs into the feet, and the extensor muscles in the limbs stabilize the wrist and provide leverage. As such, they cannot function in isolation.

As expected, the tails of each form were found to perform similarly on the narrow dowel, suggesting they are equally suited for grasping narrow perches. On the broad dowel, unexpected differences in tail performance were identified for males. Instead of the closed-canopy chameleons having a proportionally stronger grip owing to their relatively longer tails (see Herrel *et al.* 2013), the tail grip of the open-canopy *B. melanocephalum* was among the strongest for males. This result is especially surprising considering that the other open-canopy form, Type A, which possesses a comparable TL to *B. melanocephalum* (da Silva & Tolley 2013), was the weakest. The much weaker tail grip of Type A males is unlikely to be a consequence of microhabitat, because females from this habitat did not show the same outcome, yet they utilized the same size perches. Moreover, males have longer tails than females, so it would be expected that they would be better able to wrap their tails around the broad dowel, and hence be able to exert a proportionally stronger force; yet, this was not observed. Given that TL alone could not adequately explain tail performance for most forms, other morphological features or adaptations that were not measured here may be involved, such as the length of the distal end of the tail, which is used in prehensile activities and the length of the hypaxial muscles (M. ischiocaudalis and M. inferocaudalis), which work to curl the tail (Zippel, Glor & Bertram 1999; Bergmann, Lessard & Russell 2003). As such, identification of the morphological components involved in tail performance, and whether these differ between forms, may further our understanding. However, if this result is a sampling artefact, then the overall generalization is that all these forms are well suited for grasping onto both broad and narrow dowels with their tails. This would then mirror results found for open and closed-canopy forms of the congeners *B. pumilum* and *B. damaranum* (Herrel *et al.* 2011, 2013). Considering all forms were able to exert greater forces with their tails compared with their forefeet, the importance of the tail for stability and support in each habitat is likely to be high. Indeed, chameleons are known to pull themselves onto branches solely using their tails (Tolley & Burger 2007). This ability allows them to move effectively both horizontally and vertically throughout their habitats (Higham & Jayne 2004; Tolley & Burger 2007; Tilbury 2010; Herrel *et al.* 2011), allowing them to reach or extend further to traverse large gaps. These abilities may be particularly important when added stability or an escape route is required, such as during aggressive confrontations with conspecifics (Herrel *et al.* 2011) and, possibly, predators.

Sprint speed also showed no relative differences between forms, indicating that the direction and strength of selection on this performance trait may be the same within each habitat. This finding is not altogether surprising considering chameleons move extremely slowly and tend to use crypsis instead of running to avoid predation (Brain 1961; Burrage 1973; Tolley & Burger 2007). These results also indicate that sprint speed is not just a by-product of limb length, as suggested as a possible explanation for performance differences between open and closed-canopy *B. pumilum* forms (Herrel *et al.* 2011). Indeed, the combination of limbs and feet correlated best with sprint speed for each form, but this appears to be simply a function of body size. Types A and B – the forms with, proportionally, the longest limbs – did not run faster than the other forms, again supporting the hypothesis that limb length may be more important for bridging gaps rather than increasing speed.

Hindfoot size (especially PH) was found to correlate best with perch diameter in almost all forms and sexes; however, this feature was not tested for performance in this study. Consequently, it is not possible to infer whether grip performance is driven by perch size for the hindfoot. However, considering the associations between the fore- and hindfoot mentioned in the Materials and Methods and the fact that forefoot size did show strong correlations to perch diameter in two forms, the forefoot performance results are expected to hold for the hindfoot as well. As such, these results indicate that microhabitat structure (i.e. the size of perches along which chameleons move) has an effect on dwarf chameleon morphology and has likely contributed to the observed differences in trait utility between forms within this species complex. Although future studies of other species and forms that have radiated into different habitats are needed to test the generality of these observations, these data provide the first evidence of the potential existence of ecomorphs in chameleons.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Table S1. Regression models exploring the best morphological correlate of sprint speed for each of the five phenotypic forms of the *B. melanocephalum*–*B. thamnobates* species complex.

Table S2. Regression models exploring the best morphological correlate of forefoot grip strength on the broad dowel for each of the five phenotypic forms of the *B. melanocephalum*–*B. thamnobates* species complex.

Table S3. Regression models exploring the best morphological correlate with maximum forefoot grip strength (narrow dowel) for each of the five phenotypic forms of the *B. melanocephalum*–*B. thamnobates* species complex.

Table S4. Regression models exploring the best morphological correlate of perch diameter for each of the five phenotypic forms.