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Branching out: perch diameter and orientation affect pull strength in chameleons (genus: *Bradypodion*)

Anthony Herrel[1,2,3], Jody M. Taft[4,5,*], Devon C. Main[4,6], Jessica M. da Silva,[4,6] Krystal A. Tolley[4,6]

[1]UMR 7179 C.N.R.S/M.N.H.N., Département Adaptations du Vivant, Bâtiment d'Anatomie Comparée, 55 rue Buffon, 75005, Paris, France
[2]Naturhistorisches Museum Bern, Bern, Switzerland
[3]Department of Biology, Evolutionary Morphology of Vertebrates, Ghent University, Ghent, Belgium
[4]South African National Biodiversity Institute, Kirstenbosch Research Centre, Cape Town, South Africa
[5]School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa
[6]Centre for Ecological Genomics and Wildlife Conservation, University of Johannesburg, Johannesburg, South Africa

[*]Corresponding author. South African National Biodiversity Institute, Kirstenbosch Research Centre, Cape Town, South Africa. E-mail: jodymtaft@gmail.com

ABSTRACT

Arboreal species tend to have specific adaptations allowing them to effectively negotiate the complexity of their habitats. For example, chameleons have a prehensile tail and limbs adapted to grasping branches. However, the impact of branch diameter and orientation on their movement has been poorly studied. Using ecological, morphological, and pull force data from two species of *Bradypodion* from different habitats, we examined if chameleons use different substrates and if perch orientation and diameter affect pull strength by quantifying their grip forces on different sized dowels. We found that the habitat of *Bradypodion ventrale* is homogeneous, and dominated by sparse patches of narrow, vertical perches. For this species, perch diameter significantly affected pull strength in both horizontal and vertical pull directions, with chameleons performing best on a vertical 1.5-mm dowel and a horizontal 3-mm dowel. In contrast, *Bradypodion pumilum* typically occurs in more variable vegetation, ranging from low shrubs to wooded habitat with high canopy. Our results show that the habitat has perches that are on average wider than for *B. ventrale* with a greater size range. The performance of *B. pumilum* was less impacted by perch diameter and pull direction suggesting that *B. pumilum* is able to use perches of different diameters in their more heterogeneous habitat.

Keywords: grip; habitat; lizard; locomotion; reptiles; southern Africa

INTRODUCTION

Habitat complexity has been shown to be an important driver of the number of species in a community and their functional traits (August 1983, Nooten *et al.* 2019). For example, the partitioning of complex habitats and specialization for specific locomotor substrates has led to the repeated evolution of complex communities in some lizards (Losos 2009). Arboreal habitats are particularly complex and show enormous variation in perch size, orientation (Higham and Jayne 2004, Jayne and Hermann 2011, Foster and Higham 2012, Herrel *et al.* 2013b, Karantanis *et al.* 2018), and compliance (Thorpe *et al.* 2009, Young *et al.* 2016). Given that locomotion on substrates of different diameters and inclines imposes different physical demands, many arboreal animals have evolved a specialized morphology allowing them to efficiently utilize resources and escape predators in this environment (Losos 1990, Molnar *et al.* 2017, Boettcher *et al.* 2019, 2020). Narrow substrates pose particular constraints and may require unique adaptations, including strong grips between opposable digits or adhesive structures such as claws or toe-pads (Bloch and Boyer 2002, Irschick *et al.* 2006, Crandell *et al.* 2014, Thomas *et al.* 2016, Langowski *et al.* 2018), as the risk of falling may be consequential (Sinervo and Losos 1991).

Grip or pull strength, a performance trait suggested to be relevant to narrow-branch arboreal locomotion, has been measured in several taxa using a variety of methods (Clark *et al.* 2004, Personius *et al.* 2010, Herrel *et al.* 2011, 2013a, Wu *et al.* 2013, Thomas *et al.* 2016, Boulinguez-Ambroise *et al.* 2021, Dickinson *et al.* 2022, Young *et al.* 2022). Gripping more generally is an ecologically relevant performance trait and may be selected for in many contexts (Zablocki-Thomas *et al.* 2021). Indeed, being

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able to hold on tightly to a branch is not only relevant for locomotion on narrow branches, but also is probably crucial in the context of predation and combat amongst conspecifics (e.g. Stuart-Fox and Whiting 2005, Stuart-Fox *et al.* 2006). Moreover, it has been shown that the opportunity for selection for this trait is great (i.e. pull strength is heritable and hence can be selected for) as evidenced in a small arboreal primate, whereby the trait had strong maternal effects (i.e. the phenotype of the mother impacts the phenotype of the offspring; see Zablocki-Thomas *et al.* 2021). Despite the importance of gripping, few studies have explored the impact of perch diameter on pull strength (e.g. da Silva *et al.* 2014, Young *et al.* 2022). Yet, diameter is probably a crucial variable that has previously been shown to have an impact on many locomotor performance traits (e.g. Losos and Irschick 1996, Vanhooydonck *et al.* 2006, Higham *et al.* 2015). Moreover, most studies have measured pull strength by pulling animals horizontally along the branch or a grid (Clark *et al.* 2004, Personius *et al.* 2010, Herrel *et al.* 2011, 2013a, Wu *et al.* 2013, da Silva *et al.* 2014, Thomas *et al.* 2016) or by having animals pull on a chain attached to a platform with a food reward (Boulinguez-Ambroise *et al.* 2021). This implicitly measures not only the grip forces exerted by the hand, but also the force generated by the elbow flexors and shoulder retractors. However, dependent on the type of predator this may not always be ecologically relevant. For example, whereas birds or bats may pull small vertebrates such as lizards or frogs vertically away from the perch (Page *et al.* 2012), other predators such as snakes may effectively pull prey horizontally along the branch (A. Herrel personal observations). Given that different muscle groups may be implicated in the two different types of measures (e.g. shoulder retractors versus forelimb adductors), the effect of perch diameter on gripping performance may be different.

Here, we examine if there is an effect of perch diameter and orientation (pull direction) on pull strength in chameleons. Chameleons are an excellent model in this context as they are highly specialized arboreal lizards with modified hands and feet for gripping (Tolley and Herrel 2013). Moreover, due to their slow locomotion, they are unable to run away from predators and the ability to hold on to the perch may be at a premium. Additionally, during intraspecific encounters, chameleons will try to push one another off the branch before escalating into physical combat involving biting (Stuart-Fox and Whiting 2005), particularly in instances of male–male combat (Stuart-Fox 2006, Karsten *et al.* 2009). We focus on two species of dwarf chameleon, *Bradypodion ventrale* and *B. pumilum*, that broadly differ in habitat use (Fig. 1). Whereas *B. ventrale* is a species inhabiting open-canopy, shrubby vegetation, *B. pumilum* is a forest-dwelling species (Tolley and Burger 2007). Dwarf chameleons of the genus *Bradypodion* make an excellent study system as it has been demonstrated that the morphology of the hands

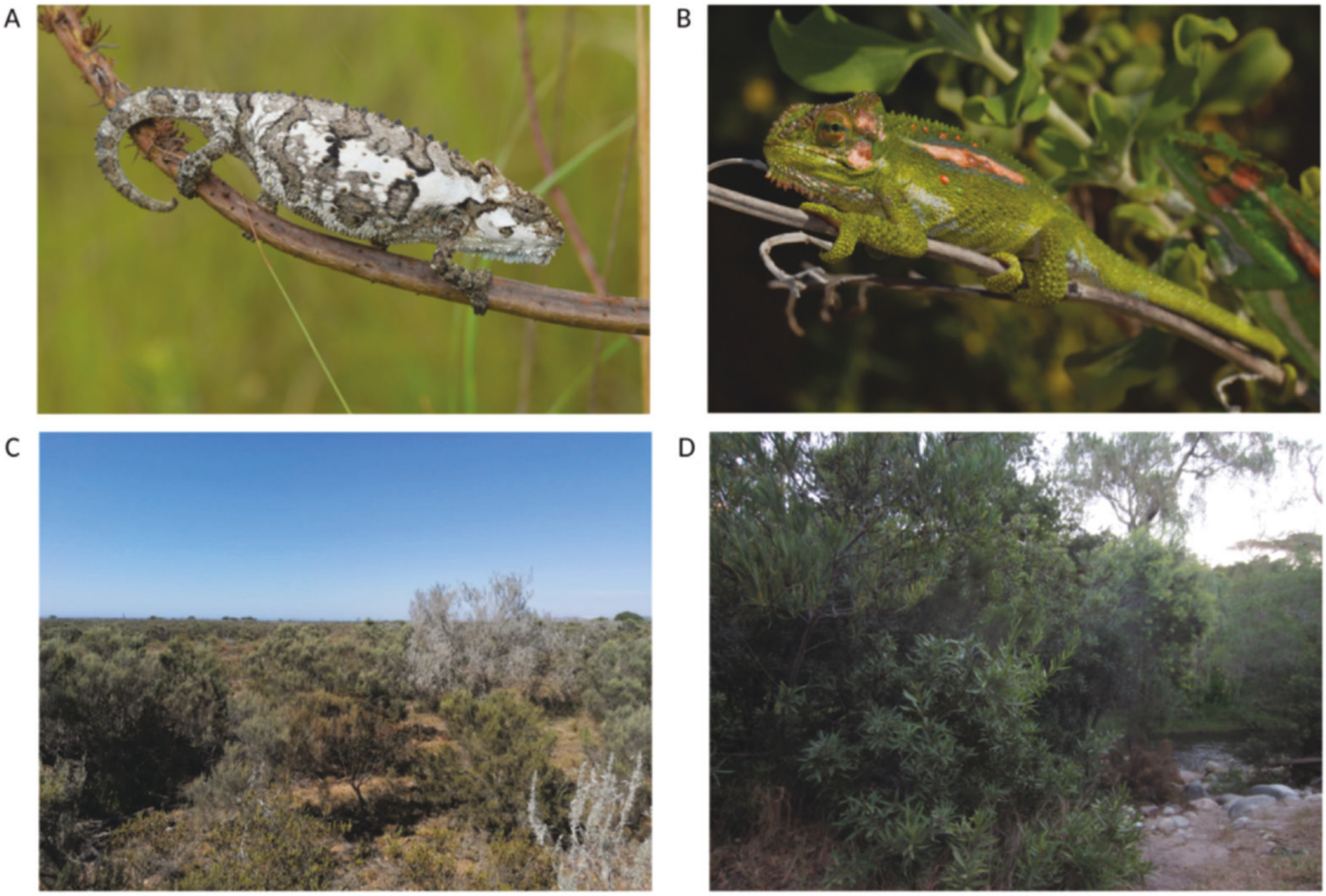

Figure 1. Study species: A, *Bradypodion ventrale* and B, *B. pumilum*; and their respective habitats: C, open bushy habitat and D, dense canopy habitat.

and feet is tightly linked to the substrate used through the impact this has on performance (Herrel *et al.* 2011, 2013a, da Silva *et al.* 2014). By comparing the results for these two species, we test whether the impacts of perch diameter and pull direction can be generalized or are species-specific and therefore depend on the morphology and habitat use of the species.

MATERIALS AND METHODS

We tested the effect of dowel diameter and pull direction (horizontal and vertical) in two species of chameleons, *B. ventrale* ($N = 76$) from Jeffrey's Bay, South Africa, and *B. pumilum* ($N = 20$) from Cape Town, South Africa, in February 2022 (Fig. 2). For each species, all individuals were collected from within a 5-km radius and were from the same overall vegetation, although chameleons occur in, and were collected from, both natural vegetation as well as modified vegetation in peri-urban areas. Chameleons were located at night when they are most visible by torchlight. Pulling data were collected the next day, with chameleons being kept overnight in 5-L plastic boxes with ventilation and vegetation supplied. All animals were released within 24 hr at the exact site of capture, marked by GPS and flagging tape.

All chameleons were measured to the nearest 0.1 mm using digital calipers as in a previous study (da Silva *et al.* 2014). Snout–vent length (SVL), upper arm length, lower arm length, mid-hand width (i.e. the carpal region of the hand), lateral forefoot pad length, and medial forefoot pad length (i.e. the length of the pads composed of the externally fused digits on the lateral and medial side of the hand) were measured on each individual. All analyses were run in IBM-SPSS (v.26).

Pull strength

One of three dowels (narrow: 1.5 mm; intermediate: 3 mm; broad: 8 mm) was mounted on a piezo-electric force platform (Kistler Squirrel force plate, ±0.1 N, Winterthur, Switzerland) (see Herrel *et al.* 2011, 2012, 2013a). The force platform was connected to a charge amplifier (Kistler Charge Amplifier type 9865). Forces were recorded during a 60-s recording session at 500 Hz. During this interval, chameleons were allowed to repeatedly grip a dowel with their hands and were then pulled away from the dowel. A recording session typically included three to four grip trials. To quantify pull strength, we let the chameleon hold on to the dowel and pulled it away in two different ways: (i) in the horizontal (Y) direction, in line with the branch; and (ii) in the vertical (Z) direction perpendicular to the branch (Fig. 3). We extracted peak Y (horizontal) and Z (vertical) forces using the Kistler Bioware software. Each chameleon was tested three to four times on each dowel within a single recording session and was given at least 30 min of rest between trials. The highest grip force for each individual on each dowel was retained for subsequent analysis.

All data were $\log_{10}$-transformed before analyses and all analyses were run separately for the two species. We first ran stepwise multiple regression models to determine which morphological traits best predicted variation in performance on the different dowel diameters and with different pull directions. Next, we ran a repeated-measures analysis of covariance (ANCOVA) followed by *post hoc* tests for horizontal and vertical pull directions to test for an effect of dowel diameter. To ensure the analysis was size-corrected, the traits that best explained performance were included as covariates. Given that the effect of diameter was significant, we ran repeated-measures ANCOVAs with the traits that best explained performance as covariates for each dowel diameter to test whether pull direction impacted pull strength. For each repeated-measures ANCOVA, we tested assumptions for sphericity and when violated we used the Greenhouse–Geisser correction.

Habitat and perch use

We assessed whether perch use differs between the two species and therefore might relate to differences in pulling ability. Therefore, a dataset was collected of perching site diameters and angles used by chameleons encountered during additional surveys at the same field sites (Jeffrey's Bay and Cape Town), during 2022–2023 (*B. ventrale*: $N = 159$, *B. pumilum*: $N = 65$) from natural and peri-urban areas. Each chameleon encountered was also measured for SVL (nearest 0.1 mm). The datasets were highly skewed and did not meet assumptions of normality or homogeneity of variance even after $\log_{10}$-transformation. Thus, nonparametric Mann–Whitney U tests were used for comparisons using the log-transformed data. Perch angles that were recorded as 0° could not be log transformed and were therefore retained as 0°. To first assess whether body size (log SVL) influences perch diameter or angle used by chameleons, log-transformed data were run using general linear regressions separately by species. There was a significant positive relationship between (log) diameters used and (log) body size but not (log) angle (see Results). Therefore, the comparison of perch diameters was made using a nonparametric analysis of covariance (Quade's test) using SVL as a covariate.

The structure of the vegetation in *B. ventrale* and *B. pumilum* habitats were compared by measuring diameter and angle of available perches along randomly placed 100-m-long transects (*B. ventrale*: $N = 7$, *B. pumilum*: $N = 4$). Every 10 m, all perches in a 1-m swathe were measured for diameter (mm) and angle (angles between 0 and 90° relative to the ground). For *B. ventrale*, perches were measured 10 cm below the top of the vegetation given that the bushes normally were 1–1.5 m in height and chameleons are usually found at this height, totalling 875 perches measured. For *B. pumilum*, perches were measured at a height of 1.5 m, totalling 321 perches measured. Although the canopy for *B. pumilum* is often higher (up to several metres), chameleons use the entire range of heights available, and we consider 1.5 m height as representative of the available perches. While this approach provided an overall assessment of structural differences between species habitats, it is possible that individual chameleons select perches preferentially to those available in their respective habitats. Thus, the Mann–Whitney U test was used assess whether the diameters and angles from the random transects were significantly different from the perches used by chameleons for each species, which could indicate whether chameleons specifically chose perching sites.

RESULTS

We provide an overview of the descriptive statistics of morphometric data collected for each species and show that all limb

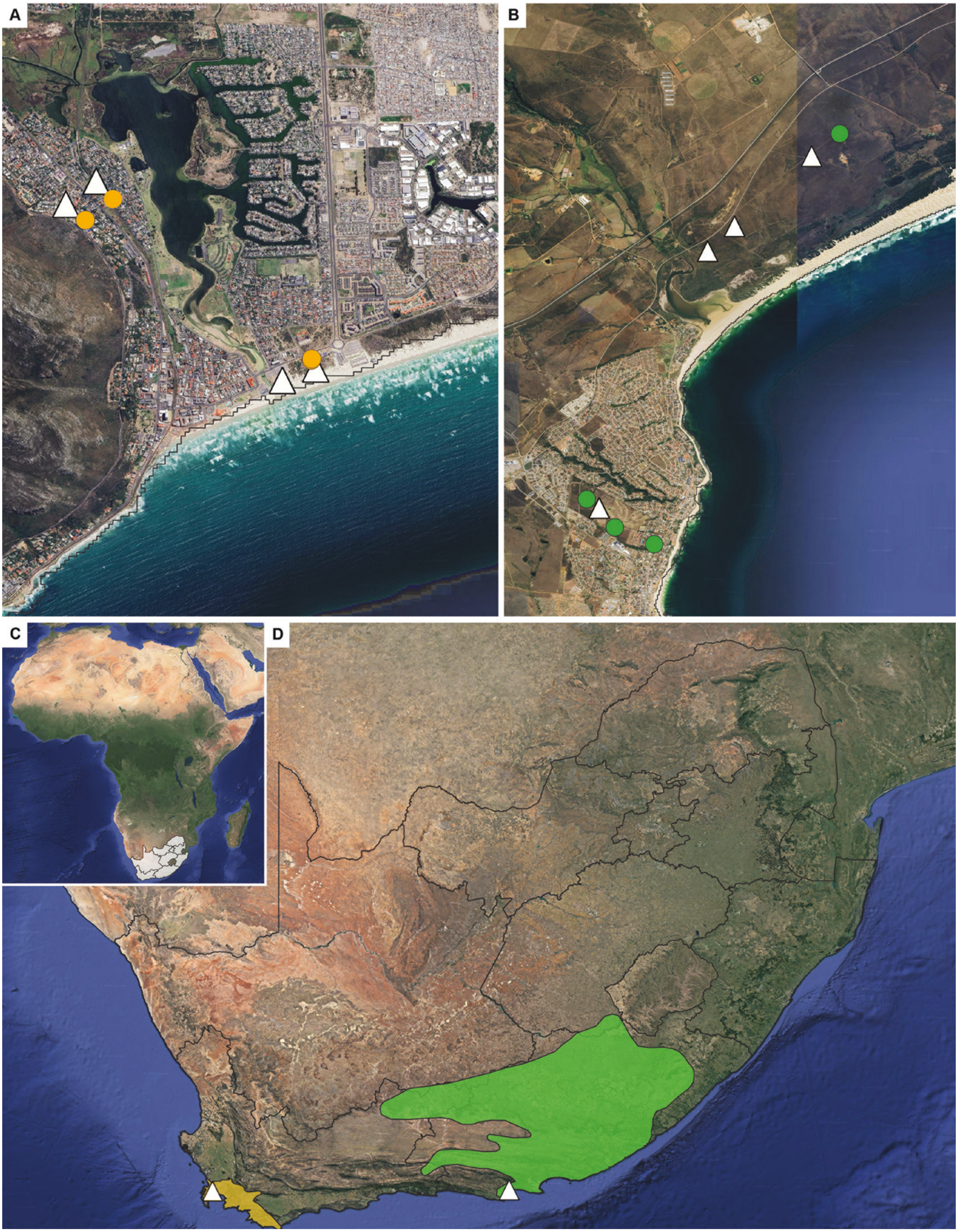

Figure 2. The study area and sample sites for: A, *Bradypodion pumilum* and B, *Bradypodion ventrale*. Habitat transects are indicated by white triangles and sample localities are shown by circles; *B. pumilum* in gold, *B. ventrale* in green. C, South Africa is shown in grey. D, the natural ranges for *B. pumilum* (gold) and *B. ventrale* (green), and study sites shown by white triangles.

traits measured significantly correlated with SVL (Table 1). Additionally, we provide the raw means and standard deviations for both species on the different dowel diameters and with pull directions (Table 2).

Pull strength: *Bradypodion ventrale*

The stepwise multiple regression models identified mid-hand width as the best predictor of pull force on the 1.5-mm dowel for both horizontal ($R^2 = 0.87$) and vertical ($R^2 = 0.22$) pull directions (Table 3). For the pull force on the 3-mm dowel, upper arm length ($R^2 = 0.34$) was retained for the horizontal pull direction whereas lower arm length and mid-hand width ($R^2 = 0.41$) were retained for the vertical pull direction. Finally, whereas for the 8-mm dowel no significant model was retained for the horizontal pull direction, the upper arm was retained as the single best predictor of pull force in the vertical direction ($R^2 = 0.20$). Repeated-measures ANCOVA testing for differences between forces when gripping dowels of different diameters showed significant differences for both the horizontal ($F_2 = 6.11$; $P \le .01$) and vertical ($F_1 = 5.00$; $P \le .05$) pull directions (Table 4). *Post hoc* tests showed that differences were significant between all dowel sizes. For the horizontal pull direction forces were highest on the 3-mm dowel and lowest on the 1.5-mm dowel. For the vertical pull direction forces were highest on the narrowest dowel (1.5 mm) and lowest on the broad 8-mm dowel (Fig. 4). When comparing vertical and horizontal pull directions differences were significant on the 1.5-mm ($F_1 = 6.85$; $P \le .05$) and 8-mm ($F = 10.22$; $P \le .01$) dowels but not on the 3-mm dowel ($F_1 = 0.81$; P = ns). Whereas for the 1.5-mm dowel forces were higher in the vertical pull direction, on the 8-mm dowel forces were higher in the horizontal pull direction (Fig. 4). Forces in the different pull directions were significantly correlated to one another, yet relationships were strongest on the 3-mm dowel (Table 5).

Pull strength: *Bradypodion pumilum*

The stepwise multiple regression model for *B. pumilum* showed different results. For the horizontal pull direction, the only variable that explained force was upper arm length (Table 3). For the vertical pull direction, however, the upper and forearm length were the best predictors of variation in pull force (Table 3). Unlike *B. ventrale,* repeated-measures ANCOVA

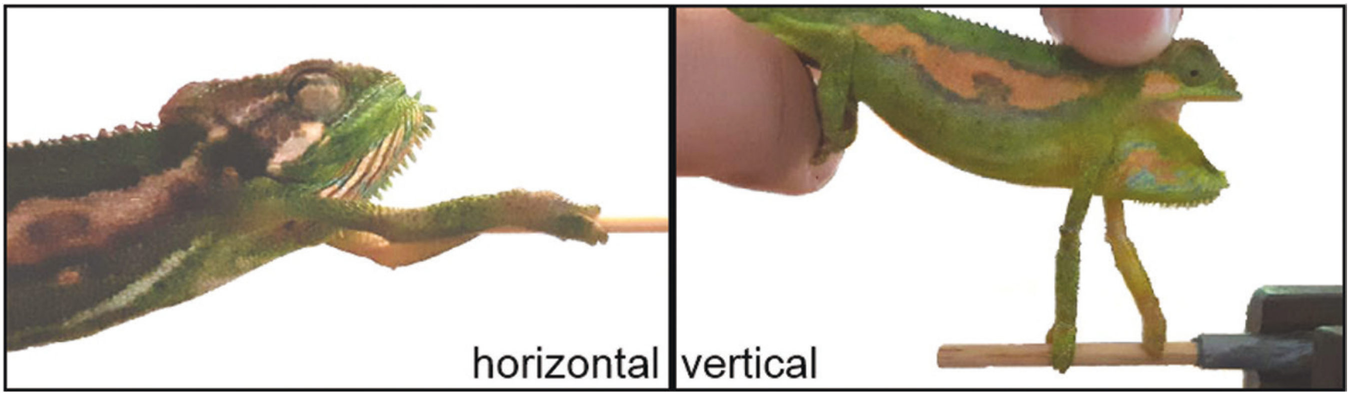

Figure 3. Images illustrating the different pull directions (horizontal and vertical) on dowels of different diameters used to measure pull strength in chameleons. Illustrated are trials with *Bradypodion pumilum*.

Table 1. Descriptive statistics for morphological traits (mm) measured for two species of dwarf chameleon, as well as results of the Pearson correlation tests between snout–vent length and all other morphometric measurements.

	***Bradypodion ventrale* (*N* = 76)**					***Bradypodion pumilum* (*N* = 20)**				
	Minimum	**Maximum**	**Mean ± SD**	**Pearson correlation**	***P***	**Minimum**	**Maximum**	**Mean ± SD**	**Pearson correlation**	***P***
Snout–vent length	67.02	91.24	81.72 ± 5.66			49.36	78.10	66.48 ± 8.25		
Upper arm length	14.05	19.18	16.66 ± 1.19	0.79	≤ .01	10.66	16.73	14.27 ± 1.64	0.88	≤ .01
Lower arm length	10.97	15.40	12.73 ± 0.91	0.72	≤ .01	7.37	12.46	10.56 ± 1.51	0.91	≤ .01
Mid-hand length	2.31	3.90	2.98 ± 0.33	0.55	≤ .01	1.62	3.27	2.52 ± 0.31	0.82	≤ .01
Lateral fore-foot pad length	4.24	7.32	5.74 ± 0.58	0.58	≤ .01	3.88	6.93	5.68 ± 0.88	0.73	≤ .01
Medial fore-foot pad length	3.11	5.81	4.67 ± 0.53	0.41	≤ .01	3.07	5.24	4.33 ± 0.52	0.75	≤ .01

N, sample size; SD, standard deviation.

Table 2. Raw mean values with standard deviations (SD) and variances for pull forces on different sized dowels, in two different pull directions for two species of dwarf chameleon.

Dowel diameter	Pull direction	Minimum	Maximum	Mean ± SD	Variance
Bradypodion ventrale ($N = 76$)					
1.5 mm	Horizontal	0.51	1.82	0.98 ± 0.27	0.07
	Vertical	1.54	3.17	2.38 ± 0.41	0.17
3 mm	Horizontal	0.86	2.31	1.67 ± 0.37	0.13
	Vertical	1.19	2.99	2.07 ± 0.44	0.19
8 mm	Horizontal	0.64	1.89	1.20 ± 0.26	0.06
	Vertical	0.61	2.84	1.45 ± 0.46	0.21
Bradypodion pumilum ($N = 20$)					
1.5 mm	Horizontal	0.49	1.06	0.74 ± 0.18	0.03
	Vertical	0.97	2.29	1.58 ± 0.35	0.12
3 mm	Horizontal	0.74	1.96	1.32 ± 0.34	0.12
	Vertical	1.22	2.93	1.92 ± 0.44	0.19
8 mm	Horizontal	0.35	1.11	0.77 ± 0.23	0.05
	Vertical	0.67	1.66	1.25 ± 0.22	0.05

N, sample size.

Table 3. Results from the stepwise multiple regression model assessing the morphological traits that best explain pull strength for two species of dwarf chameleon.

	Variable	R^2
Bradypodion ventrale		
Horizontal		
1.5 mm	Mid-hand length	0.87
3 mm	Upper arm length	0.34
8 mm	—	—
Vertical		
1.5 mm	Mid-hand length	0.22
3 mm	Mid-hand length + forearm length	0.41
8 mm	Upper arm length	0.20
Bradypodion pumilum		
Horizontal		
1.5 mm	Upper arm length	0.55
3 mm	Upper arm length	0.69
8 mm	Upper arm length	0.58
Vertical		
1.5 mm	Upper arm + forearm length	0.79
3 mm	Upper arm length	0.81
8 mm	Forearm length	0.74

showed no differences between dowel sizes for either the horizontal or the vertical pull direction (Table 4). When comparing forces between the different pull directions, differences were significant only for the largest 8-mm dowel (Table 4). Forces measured in different pull directions were significantly and strongly correlated to one another (all $R > 0.74$; see Table 5).

Habitat and perch use

Assessment of perch use by linear regressions with (log) body size (SVL) and (log) perch diameter showed a significant positive relationship for both species (*B. ventrale*: $R^2_{1,159} = 0.14$, $P \leq .01$; *B. pumilum*: $R^2_{1,63} = 0.09$, $P \leq .05$), but not for (log) angle (*B. ventrale*: $R^2_{1,159} \leq 0.01$, $P =$ ns; *B. pumilum*: $R^2_{1,64} = 0.04$, $P =$ ns). Comparison of the diameters of perches used showed no significant difference between species ($F_{1,222} = 0.83$, $P =$ ns). Furthermore, the angles used did not differ significantly between species (Table 6) and both species used the entire range of perch angles (from 0 to 90°).

Comparison of perches used by chameleons to those randomly available showed that *B. ventrale* uses significantly wider diameter perches (median = 2.56 mm) than those available (median = 2.32 mm) in the habitat ($U = 1.99$, $P \leq .05$). Although the median angle used was more vertical (median = 65°) than those available (median = 60°), the difference was not significant ($U = -0.04$, $P =$ ns). In contrast, *B. pumilum* uses significantly narrower perches ($U = -3.42$, $P \leq .01$; median used = 1.91 mm, median available = 2.73 mm) and more angled perches ($U = 2.67$, $P \leq .01$; median used = 70°, median available = 45°) than those available in the habitat.

For the comparison of habitat structure between species, the nonparametric Mann–Whitney *U* test showed that the distribution of perches available for *B. ventrale* and *B. pumilum* differed significantly in both diameter and angle (Table 7). The *B. ventrale* habitat consists of narrower but more vertically oriented perches than those available in the *B. pumilum* habitat.

DISCUSSION

Our results show some interesting differences in the pulling forces exerted on dowels of different diameters exerted by the two species. For *Bradypodion ventrale*, distal limb segment sizes explained force on narrow dowels, irrespective of pull direction. This is probably because hand size is a good proxy for the size and strength of the intrinsic hand flexors (flexores brevi superficialis and profundus; see Molnar *et al.* 2017). Interestingly, on the intermediate sized dowel, the best predictors were more proximal elements such as the forearm, possibly reflecting the size of the flexor digitorum longus and the proximal biceps brachii

Table 4. Results of repeated-measures analysis of variance for two species of dwarf chameleon.

Source		Type III sum of squares	d.f.	Mean square	*F*	*P*	Mauchly's *W*	*P*
Bradypodion ventrale								
Horizontal dowels	Sphericity assumed	0.10	2	0.05	6.11	≤ .01	0.93	.07 (ns)
Vertical dowels	Greenhouse–Geisser	0.07	1	0.05	4.99	≤ .01	0.65	≤ .01
1.5-mm dowel[a]	Greenhouse–Geisser	0.05	1	0.06	6.85	≤ .05	1.00	≤ .01
3 mm dowel[a]	Greenhouse–Geisser	0.01	1	0.01	0.81	.37 (ns)	1.00	≤ .01
8 mm dowel[a]	Greenhouse–Geisser	0.06	1	0.07	10.22	≤ .01	1.00	≤ .01
Bradypodion pumilum								
Horizontal dowels	Sphericity assumed	0.01	2	0.01	0.69	.51 (ns)	0.76	.10
Vertical dowels	Sphericity assumed	0.01	2	0.01	0.54	.58 (ns)	0.68	.07
1.5-mm dowel[a]	Greenhouse–Geisser	0.01	1	0.01	1.33	.26 (ns)	1.00	≤ .01
3-mm dowel[a]	Greenhouse–Geisser	0.02	1	0.01	1.36	.26 (ns)	1.00	≤ .01
8-mm dowel[a]	Greenhouse–Geisser	0.02	1	0.02	5.91	.03 (ns)	1.00	≤ .01

d.f., degrees of freedom; ns, not significant.

[a] Comparisons between horizontal and vertical pull directions on a given dowel diameter.

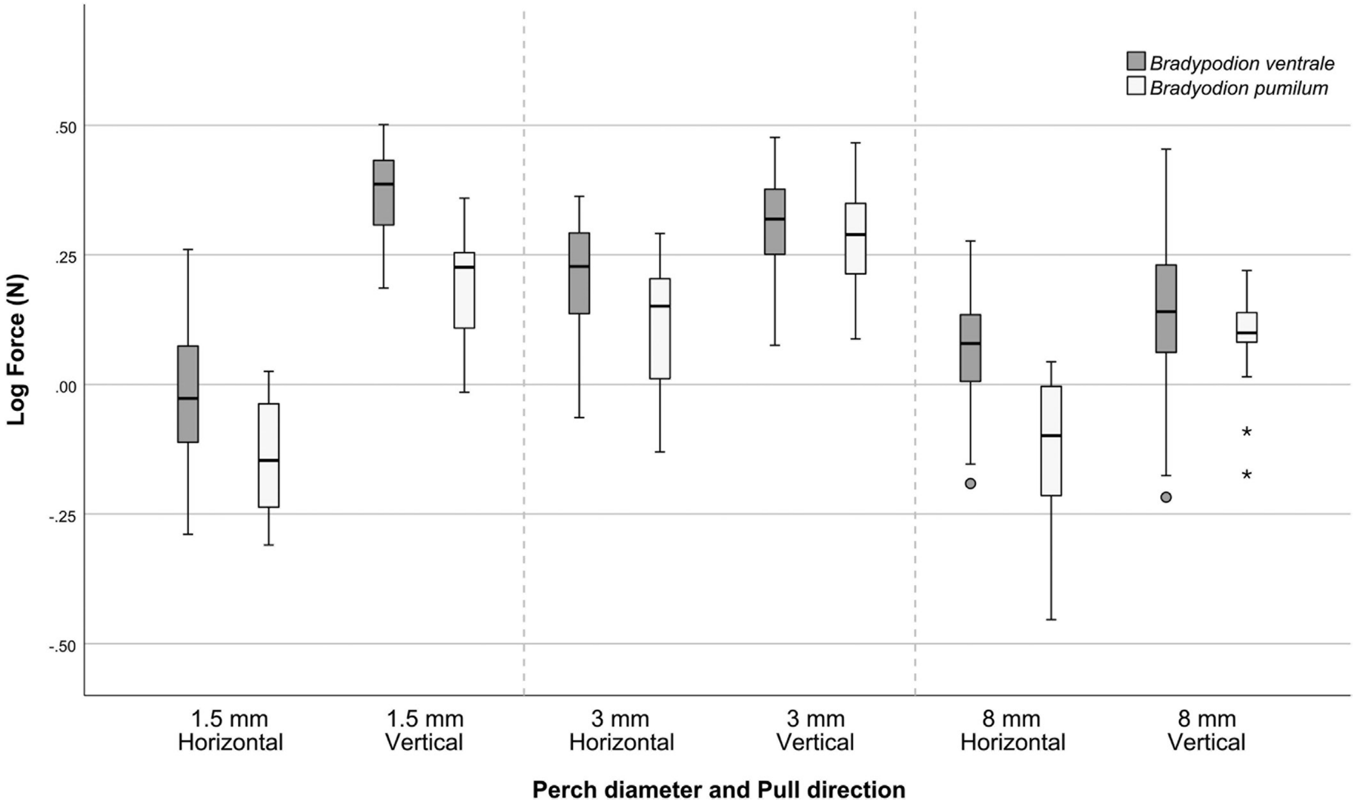

Figure 4. Box plots illustrating the differences between substrate diameters and pull directions for *Bradypodion ventrale* (grey) and *B. pumilum* (white). Illustrated are marginal means ± SEM.

and brachialis muscles (Molnar *et al.* 2017). For vertical pulling, hand flexion is clearly important as indicated by the importance of the mid-hand and forearm. In contrast, during horizontal pulling the elbow flexors were clearly more important as suggested by the importance of upper arm length in explaining variation in pull force. Finally, on the broadest dowel, the most proximal elements were retained in the model also suggesting an important role for elbow flexion when pulled vertically. None of the traits used explained variation in horizontal pull force on the 8-mm dowel, however, suggesting that this may be determined by other structures, such as claws or possibly the humerus retractors, for which no proxy was measured.

In contrast, for *B. pumilum*, proximal limb segments were overall better predictors of variation in force on different dowels and in different pull directions. The forearm and upper arm were consistently retained as best predictors, suggesting that in this species elbow flexion by means of the biceps and brachialis is important when gripping. As we only measured pull forces we cannot discuss whether both species used different strategies to deal with different substrates and pull directions. Future studies using 3D kinematic analyses with X-ray video would be ideal to examine this in greater detail. Overall, these results highlight the different ways in which these two species interact with substrates of different diameters. The habitat of *B. pumilum* is diverse with a combination of large and small trees, bushes, and groundcover and has a large diversity of perch sizes (Table 7; see also Higham *et al.* 2015) with diverse orientations (angles). The branches tend to have large gaps between, and as such *B. pumilum* may rely more on the proximal muscles to maintain its grip and for reaching perches. In contrast, given the hand size of *B. ventrale*, performance on the narrow horizontal dowel appears to be limited. The clumpy, shrubby natural habitat of this species does not have a continuous canopy, although each bush has a dense array of perches. Thus, the structure of this habitat may constitute a trade-off, where moving from bush to bush requires crossing open ground, whereas movement in a bush is accomplished easily with many perches within reach, potentially placing additional pressures on their locomotor system. Overall, these results are similar to those of a previous study comparing the relationships between morphology and pull strength in other species of chameleons. Whereas in the open-habitat morphs, distal segments were better predictors of performance, for the forest morphs more proximal elements better explained performance (da Silva *et al.* 2014). Future studies exploring differences in the muscle anatomy between these two species could be especially insightful in better understanding the observed differences.

When comparing the effect of perch diameter on force, no statistical differences between the two species were noticeable. Dowel size also had no effect on peak force in *B. pumilum*, yet for *B. ventrale* dowel size had a strong effect on force with forces being highest on the 3-mm dowel in the horizontal pull direction and on the 1.5-mm dowel in the vertical pull direction. We expected that such an outcome could be strongly correlated to habitat, and we did find the habitats of the two dwarf chameleon species used in our analyses to differ, with *B. ventrale* habitat consisting of narrower and more vertical perches that of *B. pumilum*. The two species overall, however, used similar diameter and angled perches across their natural and peri-urban habitats. It would be essential in the future to test whether habitat transformation in the peri-urban areas influences perch choice, perhaps resulting in different pulling performance among populations within species that occur in natural and peri-urban areas.

Similarly, whereas for *B. pumilum* differences between the horizontal and vertical pull directions were significant only on the 8-mm dowel, for *B. ventrale* pull direction significantly impacted force on the extreme diameter dowels (1.5 and 8 mm). Overall, these results suggest that *B. ventrale* performs better on the 3-mm dowel (high forces and no differences between vertical and horizontal pull directions), while the closed-canopy species, *B. pumilum*, appears to be more of a generalist capable of performing well on most dowel diameters and for both pull directions. Alternatively, the fact that no statistical differences in performance between diameters were observed in *B. pumilum*

Table 5. Results of Pearson correlation tests between grip forces in different pull directions for two species of dwarf chameleon.

Species	Dowel diameter	Pearson correlation	*P*
Bradypodion ventrale	1.5 mm	0.24	≤ .05
	3 mm	0.58	≤ .01
	8 mm	0.52	≤ .01
Bradypodion pumilum	1.5 mm	0.74	≤ .01
	3 mm	0.91	≤ .01
	8 mm	0.85	≤ .01

Table 6. Summary of perch diameters (mm) and angles (°) available in the habitat of two species of dwarf chameleons.

Species	Diameter			Angle		
	N	Mean (SD)	Range	*N*	Mean (SD)	Range
B. ventrale	1336	1.79 (1.54)	0.02–9.94	1336	68.5 (25.20)	0–90
B. pumilum	200	3.45 (1.48)	1.10–11.30	276	37.1 (26.89)	0–90
F (*P*)	203.3 (≤ .01)			348.2 (≤ .01)		
Levene's test (*P*)	0.01 (ns)			10.2 (≤ .01)		

Sample sizes (*N*), mean and standard deviation (SD) are given. Comparisons are between species for diameter and angle using analysis of variance, *F* (*P*) and for homogeneity of variance, Levene's test (*P*); ns, not significant.

Table 7. Summary of perch diameters (mm) and angles (°) used by two species of dwarf chameleon.

Species	Diameter				Angle		
	N	Mean (SD)	Range	EMM[a]	*N*	Mean (SD)	Range
B. ventrale	109	2.57 (1.29)	0.09–8.64	2.39	94	63 (25.5)	0–90
B. pumilum	126	2.73 (1.57)	0.32–10.0	2.85	32	46 (30.9)	0–90
F (*P*)		4.37 (≤ .05)				10.37 (≤ .01)	
Levene's test (*P*)		1.48 (ns)				2.17 (ns)	

Sample sizes (*N*), uncorrected mean and standard deviation (SD), along with the range of sizes of the perches used are given, and the estimated marginal means (EMM). Comparison of habitat transects by analysis of covariance (ANCOVA) or analysis of variance (ANOVA) are given (*F* and *P* values); ns, not significant.
[a] Covariate value for calculation of the EMM = 68.8.

could be due to the lower sample size for this species. Yet, previous studies have demonstrated that *B. pumilum* adapts its kinematics of locomotion when walking on narrow versus broad perches (Higham *et al.* 2015) confirming the idea that this species is more of a generalist in its locomotion compared to other more habitat-specific species of *Bradypodion*. Moreover, the strong correlations between forces on vertical and horizontal dowels in *B. pumilum* suggest that this may not be a statistical artefact, but rather the result of different strategies in which these species hold on to branches of different diameters.

In conclusion, whereas perch diameter and pull direction have a strong and significant impact on performance in *B. ventrale*, *B. pumilum* was less sensitive to variation in perch diameter. If these assumptions can be generalized across chameleons, then we would expect other forest-dwelling species to show relative independence of performance on perch diameter, similar to *B. pumilum*. Conversely, more open habitat species that presumably must cross the ground between bushes can be expected to show optimal perch diameters for performance that match the perches selected. If so, then anthropogenic habitat modifications impacting the natural habitat might have a greater impact on open habitat specialists whereas forest species may show an ability to adapt to novel but transformed habitats.

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AUTHOR CONTRIBUTIONS

A.H., J.M.T. and K.A.T. designed the research. A.H., J.M.T., D.C.M., J.M.dS and K.A.T. collected and interpreted the data. J.M.T. and K.A.T. conducted the formal analyses for the manuscript. A.H. drafted the manuscript with support from K.A.T. All authors reviewed and edited the manuscript as well as provided approval for publication.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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DATA AVAILABILITY STATEMENT

The data underlying this study are available upon request to the authors.

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