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Functional consequences of morphological differentiation between populations of the Cape Dwarf Chameleon (*Bradypodion pumilum*)

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Variation in phenotype between species or populations of the same species living in different habitats is often explained in an adaptive context with local habitat differences driving selection on morphological traits relevant in a given ecological context. Previous studies have demonstrated significant differences in limb and tail morphology between populations of the Cape Dwarf Chameleon (*Bradypodion pumilum*) living in closed vs. open habitats. However, the adaptive nature of the observed differences remains unclear. Here, we quantify the structural habitat use in two different populations, test whether the random habitat differs between the two sites and whether or not chameleons select perches randomly. Next, we test whether morphology is correlated with structural habitat use and test for differences in performance between populations. Our results demonstrate that habitats are structurally different, that chameleons in the two populations use perches of different diameters and that, in one of the populations, chameleons select relatively wider perches than available at random. Performance traits (hand and tail grip performance and sprint speed) are correlated with morphology (hand size, tail length and tibia length) and differ between sexes and populations. Moreover, performance is dependent on dowel size. These results suggest that differences in performance between populations are indeed adaptive and indicate the existence of true ecomorphs in chameleons of the genus *Bradypodion*. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **104**, 692–700.

ADDITIONAL KEYWORDS: habitat – limbs – performance – tail.

INTRODUCTION

Convergence in morphology of distantly related species in similar ecological settings is one of the best examples of evolution by natural selection (Darwin, 1859). However, for convergence to occur, habitats must impose similar selective pressures on traits implicated in functions relevant in that specific ecological setting (Arnold, 1983; Aerts *et al.*, 2002). Caribbean *Anolis* lizards are classic examples of convergence, as animals with similar morphologies have radiated independently in similar ecological conditions on the different islands of the Greater Antilles (Williams, 1972, 1983; Losos, 2010). The term ecomorph was coined to describe the independent evolution of a set of habitat specialists that are similar in ecology, morphology and behaviour (Williams, 1983; Losos, 2009). Previous workers have demonstrated

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*Corresponding author. E-mail: anthony.herrel@mnhn.fr the crucial role of the structural habitat (i.e. perch diameter and height) in this context, as many locomotor performance traits are habitat dependent (e.g. Losos & Sinervo, 1989; Losos & Irschick, 1996; Vanhooydonck *et al.*, 2005). Thus, animals living higher in the canopy have larger toe pads and greater adhesive forces than animals living closer to the ground (Elstrott & Irschick, 2004). Similarly, long-legged species running faster than short-legged species on broad dowels lose their performance advantage on narrow dowels (Losos & Irschick, 1996). Yet, replicated adaptive radiations of organisms with similar morphologies in similar ecological contexts have rarely been demonstrated for other species of lizard (Losos, 2010), and even mainland *Anolis* lizards do not appear to have radiated convergently with Antillean ones in structurally similar habitats (Irschick *et al.*, 1997; Velasco & Herrel, 2007; Pinto *et al.*, 2008).

An interesting candidate for showing similar convergence between habitat use and morphology is the chameleon (Losos, Walton & Bennett, 1993; Bickel & Losos, 2002) and, more specifically, the dwarf chameleon of the genus *Bradypodion*. Indeed, the evolution of open and closed habitat morphs differing in coloration and morphology has been suggested to be a recurrent feature in the genus (Tolley *et al.*, 2006; Tolley & Burger, 2007; Tolley, Chase & Forest, 2008; Measey, Hopkins & Tolley, 2009). Specifically, populations of the Cape Dwarf Chameleon (*Bradypodion pumilum*) inhabiting different habitat types (open fynbos habitat vs. closed canopy habitats) show differences in morphological traits thought to be related to locomotor behaviour (Hopkins & Tolley, 2011). Chameleons from open fynbos habitats are smaller in body size, but also have proportionally smaller feet, a trait which has been suggested to be an adaptation allowing these chameleons to grasp narrower perches typical of the fynbos habitat (e.g. Restionaceae and Ericaceae). Conversely, the larger feet of the closed habitat morph inhabiting forested areas would give it a performance advantage in grasping wider perches (see also Losos *et al.*, 1993). Tail length is also greater for the closed habitat morph and has been suggested to play a role in allowing chameleons to move in complex habitats with canopy cover. Indeed, tail morphology is thought to play an important role in chameleon locomotion by providing stability and balance (Zippel, Glor & Bertram, 1999; Boistel *et al.*, 2010). Finally, chameleons from open habitats have relatively longer limbs, a trait which has been suggested to give them a performance advantage in traversing between bushes, or during gap-bridging in the relatively discontinuous vegetation typical of the fynbos habitat. Limb length is correlated with sprint speed in many lizards, as longer limbs allow an animal to take greater strides without needing to increase stride frequency (Bauwens *et al.*, 1995; Bonine & Garland, 1999; Vanhooydonck, Van Damme & Aerts, 2002). As such, we also predict a correlation between limb dimensions and sprint speed in chameleons.

In this article, we test the functional consequences of the observed differences in morphology by measuring performance traits, including sprint speed, hand grip force and tail grip force, probably relevant for these animals in their habitat. Moreover, we test for differences in structural habitat use, and whether or not habitats are used randomly. Finally, we explore correlations between structural habitat (i.e. perch diameter) and morphology. If structural habitat use is indeed related to morphology, and if the morphological traits measured are correlated with ecologically relevant performance traits, such as the ability to hold on to perches of different diameters, the observed interpopulational differences in morphology are probably adaptive.

MATERIAL AND METHODS

ANIMALS

Bradypodion pumilum (Fig. 1; see Table 1 for sample sizes) specimens were caught by hand during night-

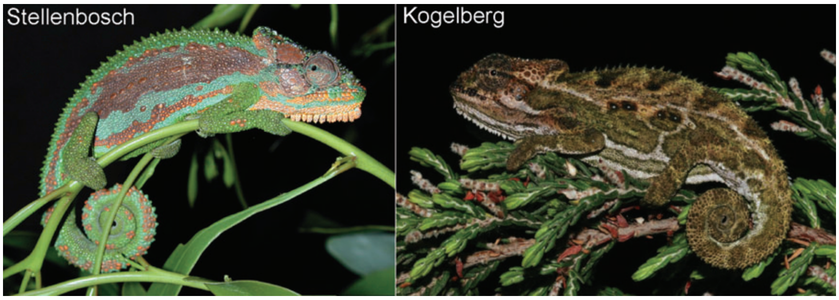

Figure 1. Photographs illustrating animals from the two study populations: left, an individual from the Stellenbosch population; right, an individual from the Kogelberg population. Note that Stellenbosch chameleons typically perch on wider substrates.

Table 1. Summary of ecological, morphometric and performance traits for the two populations investigated in this study

	Kogelberg		Stellenbosch	
	Ecology			
	Male (9)	Female (13)	Male (27)	Female (22)
Perch diameter (mm)	1.93 ± 0.87	2.01 ± 0.71	3.16 ± 1.27	2.40 ± 0.98
	Morphology			
	Male (22)	Female (20)	Male (27)	Female (22)
Mass (g)	2.81 ± 0.69	3.17 ± 1.27	5.45 ± 2.43	5.00 ± 2.69
Snout–vent length (mm)	48.49 ± 5.70	49.25 ± 6.45	63.01 ± 10.49	59.43 ± 10.70
Tail length (mm)	46.84 ± 7.57	41.87 ± 5.23	70.79 ± 14.21	58.66 ± 10.69
Femur length (mm)	9.23 ± 1.25	9.06 ± 1.59	11.67 ± 2.20	10.65 ± 1.94
Tibia length (mm)	7.59 ± 1.06	7.56 ± 1.00	9.47 ± 1.66	8.62 ± 1.81
Medial foot length (mm)	3.65 ± 0.68	3.29 ± 0.87	4.71 ± 1.40	3.96 ± 1.06
Lateral foot length (mm)	4.34 ± 0.90	4.06 ± 0.90	5.87 ± 1.71	4.92 ± 1.19
Humerus length (mm)	10.71 ± 1.74	10.62 ± 1.76	13.51 ± 2.51	12.35 ± 2.14
Radius length (mm)	7.85 ± 1.11	8.17 ± 1.22	10.47 ± 1.75	9.41 ± 1.54
Medial hand length (mm)	3.64 ± 0.81	3.31 ± 0.86	4.95 ± 1.71	4.02 ± 1.13
Lateral hand length (mm)	4.73 ± 0.89	4.19 ± 0.78	6.32 ± 1.74	5.29 ± 1.32
	Performance			
Hand grip force, broad (N)	0.54 ± 0.33	0.33 ± 0.28	0.86 ± 0.65	0.48 ± 0.49
Tail grip force, broad (N)	0.68 ± 0.36	0.75 ± 0.28	1.41 ± 0.55	1.47 ± 0.75
Hand grip force, narrow (N)	0.77 ± 0.37	0.52 ± 0.24	1.62 ± 0.71	1.13 ± 0.55
Tail grip force, narrow (N)	1.22 ± 0.96	0.69 ± 0.49	1.37 ± 0.56	1.29 ± 0.81
Speed hand-timed (cm s^{-1})	3.03 ± 0.76	3.10 ± 0.82	4.88 ± 1.50	3.92 ± 0.81
Speed race track (cm s^{-1})	7.91 ± 2.41	6.94 ± 1.37	14.30 ± 3.68	11.35 ± 3.37

Table entries are means ± standard deviations. Sample sizes for performance in Kogelberg/Stellenbosch are: 18/22 males and 14/21 females for hand grip on broad dowels; 21/26 males and 18/21 females for tail grip on broad dowels; 20/27 males and 20/22 females for hand grip on narrow dowels; 20/27 males and 17/22 females for tail grip on narrow dowels; 8/12 males and 12/14 females hand-timed; 13/15 males and 7/8 females measured on the race track.

time surveys along a wooded river in Stellenbosch and in a typical fynbos habitat at Kogelberg, South Africa, in November 2008 and February 2010. Animals were brought back to the field station (Kogelberg) or the laboratory at the South African National Biodiversity Institute (SANBI) (Stellenbosch), measured and tested for gripping performance and sprint speed, and released at the exact site of capture. All performance measures were performed at 25 ± 3 °C.

MORPHOMETRICS

For each individual, we measured the following traits using digital calipers (Mitutoyo) as described in Hopkins & Tolley (2011): snout–vent length (SVL), femur, tibia, medial and lateral hindfoot pad length, humerus, radius, medial and lateral forefoot pad length. In addition, we measured the mass of each animal using a digital balance (Ohaus PS121).

HABITAT USE

For each chameleon caught, we took the branch on which it was sleeping and placed it in the bag with the chameleon. On return to the laboratory, the diameter of the perch was measured. No perch diameters were measured for the 2008 Kogelberg sample. Although sleep sites may be different from daytime sites, preliminary data based on radiotracking studies suggest that this is not the case in this species (K. A. Tolley & G. J. Measey, pers. observ.). The random habitat available to the chameleons was assessed by measuring the diameter of all potential perches that crossed a 1-m-long stick held at a height of 1.5 m across the vegetation at 10 random sites at the Stellenbosch site, and at 30 cm off the ground at 20 random sites (across two transects *c.* 300 m apart) at the Kogelberg site (see Irschick *et al.*, 2005a). These heights reflect the perch heights of chameleons observed at both sites, the habitat at the Kogelberg site being homogeneous and characterized by the absence of trees, and an overall vegetation height not greater than 50 cm.

GRIP STRENGTH

One of two dowels (broad, 10 mm; narrow, 5 mm) was mounted on a piezo-electric force platform (Kistler Squirrel force plate, ± 0.1 N; see Herrel *et al.*, in press). The force platform was positioned on a custom-designed metal base and connected to a charge amplifier (Kistler Charge Amplifier type 9865). Forces were recorded during a 60-s recording session at 1000 Hz. During this interval, chameleons were allowed to repeatedly grip a dowel with their tail or hands, and were then pulled away from the dowel. A recording session typically included three to four tail grip trials. To quantify tail strength, animals were pulled from the dowel in the vertical direction, and we extracted peak *Z* forces only using Bioware software (Kistler). It should be noted that animals wrapped their tails around the dowel voluntarily, and thus the number of coils engaged varied across trials and individuals, and was not quantified. Thus, we recorded voluntary maximal tail strength. To quantify hand strength, we let the chameleon hold on to the dowel and pulled it away in the horizontal (*Y*) direction, and extracted peak *Y* forces using Bioware software (Kistler). Each chameleon was tested three times (i.e. three separate recording sessions) on each dowel with at least 30 min of rest between trials and 1 h or more rest between recording sessions with dowels of different sizes. The highest tail and hand grip force for each individual on each dowel was retained for subsequent analysis.

Sprint speed

Animals were tested in one of two ways. Chameleons caught in 2008 were tested on a 2-m-long flat race track equipped with infrared photocells set 25 cm apart. Chameleons were chased down the track and the times were recorded automatically and sent to a laptop computer (Irschick *et al*., 2005b). Chameleons caught in 2010 were tested by chasing them down a 2-m-long track marked at 25-cm intervals. Animals were timed manually using a stopwatch and the times at which animals crossed the 25-cm markers were recorded. The speed in centimetres per second over the fastest interval was calculated and retained for further analysis. Animals were tested on a flat track rather than on perches as selection on sprint speed probably only occurs when animals are crossing the ground between bushes or trees. When in their preferred habitats animals move very slowly and rely on crypsis rather than running to avoid predation (Tolley & Burger, 2007). Moreover, previous studies have shown that sprint speed is highest on a flat substrate (Losos *et al*., 1993).

Analyses

All data were $\log_{10}$ transformed before analysis to fulfill assumptions of normality and homoscedascity. Nonparametric statistics were used in cases in which assumptions were not met. We first ran multiple regression models to explore which morphological variables best explained the variation in performance. We ran a multivariate analysis of covariance (MANCOVA) with SVL as covariate to test for differences in limb dimensions between populations and sexes. The results of this analysis confirmed previous analyses (Hopkins & Tolley, 2011), and showed significant differences between populations (Wilks' $\lambda = 0.38$; $F_{13,67} = 8.61$; $P < 0.001$) and sexes (Wilks' $\lambda = 0.48$; $F_{13,67} = 5.51$; $P < 0.001$). The interaction effect was not significant (Wilks' $\lambda = 0.80$; $F_{13,67} = 1.33$; $P = 0.22$). Univariate analyses of covariance (ANCOVAs) confirmed previous results (Hopkins & Tolley, 2011), and showed significant differences between sexes in the size of hands and feet, and between populations in tail length and limb dimensions.

Next, we tested the following: (1) whether random habitats differed between both populations and whether actual habitat use differed from the randomly available habitat for both populations using nonparametric tests of distributions; (2) whether perch diameter was correlated with hand and/or tail dimensions using regression analyses; (3) for differences in performance (grip strength and tail strength on two dowel sizes; sprint speed) between chameleons of both sexes from the two habitats using analyses of variance (ANOVAs); (4) for differences in performance between populations and sexes using ANCOVAs with the morphological trait best correlated with the respective performance trait as a covariate; and (5) whether strength was dependent on dowel size within each habitat using a repeated-measures ANOVA. All analyses were performed using SPSS V. 15.0.

RESULTS

Perch diameters

The distributions of random perch diameters from two transects at the Kogelberg site did not differ from one another ($Z = -1.72$; $P = 0.09$). However, the distributions of random perch diameters differed significantly between the Stellenbosch and Kogelberg sites ($Z = -9.90$; $P < 0.001$), with Kogelberg perches being significantly narrower on average (Kogelberg: 1.35 ± 0.93 mm; Stellenbosch: 3.42 ± 1.71 mm). Animals from the Stellenbosch site used the habitat in random fashion (2.82 ± 1.19 mm; $Z = -1.86$; $P = 0.063$), whereas animals from Kogelberg used perches that were significantly wider on average than the randomly available perches (1.98 ± 0.76 mm; $Z = 4.12$; $P < 0.01$). The diameter of the actual perches used was significantly correlated with the size of the hand ($r = 0.34$; $P = 0.02$) and foot ($r = 0.38$; $P = 0.007$), as well as tail length ($r = 0.45$; $P = 0.001$), for the Stellenbosch population (Fig. 2). However, for the animals from the

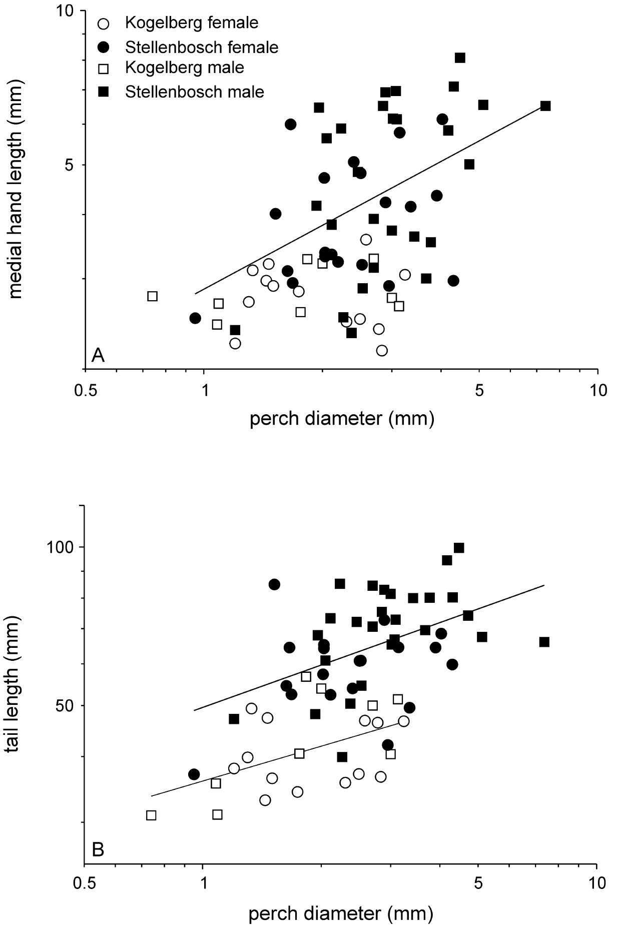

Figure 2. A, Correlation between hand size and perch diameter for animals from two different populations. Although hand diameter is correlated with perch diameter in animals from the forested Stellenbosch site, this is not the case for animals from the Kogelberg fynbos site. B, Correlations between tail length and perch diameter. In both sites, animals with longer tails use wider perches. Open symbols represent animals from the Kogelberg fynbos site; filled symbols represent animals from the forested Stellenbosch site. Squares represent males; circles represent females.

Kogelberg population, perch diameter was correlated only with tail length ($r = 0.50$; $P = 0.02$) and not with the size of the hand ($r = 0.05$; $P = 0.83$) or foot ($r = 0.06$; $P = 0.80$). Differences in perch use were significant between populations ($F_{1,66} = 9.04$; $P = 0.004$), but not between sexes ($F_{1,66} = 0.93$; $P = 0.34$); the interaction effect was also nonsignificant ($F_{1,66} = 3.24$; $P = 0.08$). Animals from the Stellenbosch site used wider perches on average.

PERFORMANCE

Hand size was significantly correlated with grip strength on broad (Stellenbosch: $r = 0.90$, $P < 0.001$; Kogelberg: $r = 0.84$, $P < 0.001$) and narrow (Stellenbosch: $r = 0.75$, $P < 0.001$; Kogelberg: $r = 0.84$, $P < 0.001$) dowels in both populations. Tail length was significantly correlated with tail grip strength in both populations and on both substrates (Stellenbosch broad: $r = 0.60$, $P < 0.001$; Stellenbosch narrow: $r = 0.39$, $P < 0.001$; Kogelberg narrow: $r = 0.61$, $P < 0.001$), with the exception of the broad substrate in the Kogelberg population ($r = 0.19$; $P = 0.25$). Tibia length was correlated with sprint speed timed by hand ($r = 0.76$; $P < 0.001$) and as measured on the race track ($r = 0.61$; $P = 0.002$) for the Stellenbosch population. In contrast, for the Kogelberg population, tibia length was correlated with sprint speed measured on the race track ($r = 0.75$; $P < 0.001$), but not with sprint speed when timed by hand ($r = 0.37$; $P = 0.11$).

The effect of dowel size on hand grip strength (repeated measures ANOVA) was significant for animals from both populations (Stellenbosch: $F_{1,43} = 69.99$; $P < 0.001$; Kogelberg: $F_{1,32} = 38.63$; $P < 0.001$), with animals being able to exert higher forces on narrow (Stellenbosch: 1.40 ± 0.67 N; Kogelberg: 0.62 ± 0.34 N) relative to broad (Stellenbosch: 0.68 ± 0.60 N; Kogelberg: 0.43 ± 0.32 N) dowels (Fig. 3). The effect of dowel size on tail performance was, however, not significant (Stellenbosch: $F_{1,45} = 0.85$; $P = 0.36$; Kogelberg: $F_{1,34} = 0.04$; $P = 0.84$; Fig. 4).

ANOVAs indicated significant differences in gripping performance between populations (Wilks' $\lambda = 0.65$, $F_{4,61} = 8.32$, $P < 0.001$) and sexes (Wilks' $\lambda = 0.80$, $F_{4,61} = 3.88$, $P = 0.007$). The interaction effect was, however, not significant (Wilks' $\lambda = 0.97$, $F_{4,61} = 0.51$, $P = 0.73$). Subsequent univariate ANOVAs indicated significant differences between populations in all performance traits (hand narrow: $F_{1.64} = 26.67$; $P < 0.001$; hand broad: $F_{1.64} = 5.73$; $P = 0.02$; tail narrow: $F_{1.64} = 4.71$; $P = 0.03$; tail broad: $F_{1.64} = 20.40$; $P < 0.001$; Figs 3 and 4), with chameleons from the Stellenbosch population being stronger. Differences between sexes independent of population were, however, significant only for hand grip strength (narrow: $F_{1.64} = 10.19$; $P = 0.002$; broad: $F_{1.64} = 10.38$; $P = 0.002$), with males being stronger than females. Differences in sprint speed were significant between populations (race track data: $F_{1,39} = 30.97$; $P < 0.001$; hand-timed data: $F_{1,42} = 17.56$; $P < 0.001$), but not between sexes (race track data: $F_{1,39} = 3.06$; $P < 0.09$; hand-timed data: $F_{1,42} = 1.24$; $P = 0.27$), with Stellenbosch chameleons being faster than Kogelberg ones. Interaction effects were nonsignificant (all $P > 0.05$).

When testing for differences in hand grip strength between populations and sexes, with hand size as a covariate, differences between populations remained significant (Wilks' $\lambda = 0.73$; $F_{2,69} = 12.79$; $P < 0.001$; Fig. 2). Differences between sexes (Wilks' $\lambda = 0.92$;

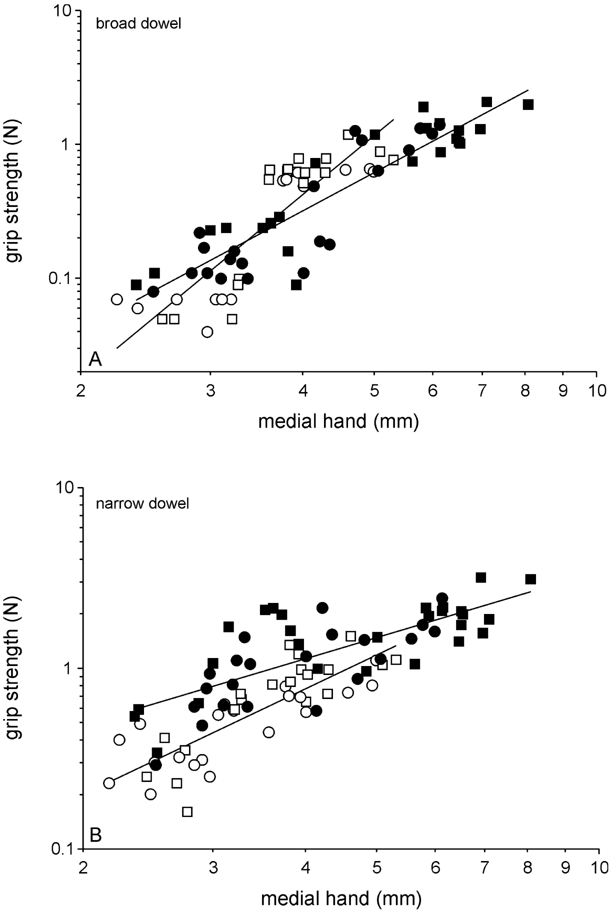

Figure 3. A, Correlations between hand size and grip strength on a broad dowel. For both populations, animals with larger hands have greater grip strength. B, Correlations between hand size and grip strength on a narrow dowel. Again correlations are significant for animals from both sites. It should be noted that smaller animals perform relatively better on narrow relative to broad dowels, again suggesting the relevance of perch diameter in determining grip strength. Open symbols represent animals from the Kogelberg fynbos site; filled symbols represent animals from the forested Stellenbosch site. Squares represent males; circles represent females.

$F_{2,69} = 3.04$; $P = 0.054$) and the interaction between populations and sex (Wilks' $\lambda = 0.99$; $F_{2,69} = 0.48$; $P = 0.62$) were nonsignificant. Subsequent univariate ANCOVAs indicated that only hand grip strength on a narrow dowel was significantly different between populations ($F_{1,70} = 23.78$; $P < 0.01$) and sexes ($F_{1,70} = 5.30$; $P = 0.02$), with animals from Stellenbosch being stronger than animals from Kogelberg, and males stronger than females. Differences in tail grip strength between populations and sexes were rendered nonsignificant when tail length was introduced as a covariate (MANCOVAs, all $P > 0.05$). Only the effect of sex on tail grip strength on a broad dowel remained significant, with females being stronger than males ($F_{1,75} = 5.00$; $P = 0.03$; Fig. 4A). ANCOVA on sprint speed, with tibia length as covariate, indicated significant differences between populations (race track data: $F_{1,38} = 17.33$; $P < 0.001$; hand-timed data: $F_{1,40} = 8.42$; $P = 0.006$), with animals from Stellenbosch running faster (Fig. 5). Sex and interaction effects were nonsignificant (all $P > 0.05$).

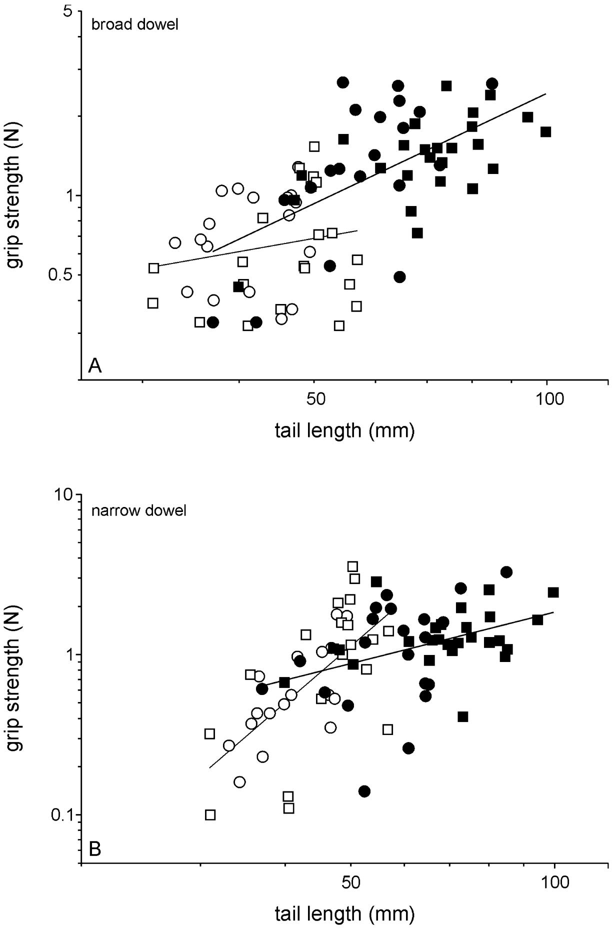

Figure 4. A, Correlations between tail length and tail grip strength on a broad dowel. B, Correlations between tail length and tail grip strength on a narrow dowel. Animals with longer tails can exert higher forces on both substrates in both populations. Open symbols represent animals from the Kogelberg fynbos site; filled symbols represent animals from the forested Stellenbosch site. Squares represent males; circles represent females.

DISCUSSION

Our data suggest that the Kogelberg fynbos habitat and the wooded Stellenbosch habitat are indeed different with respect to the availability of structurally different perches, with the fynbos habitat being

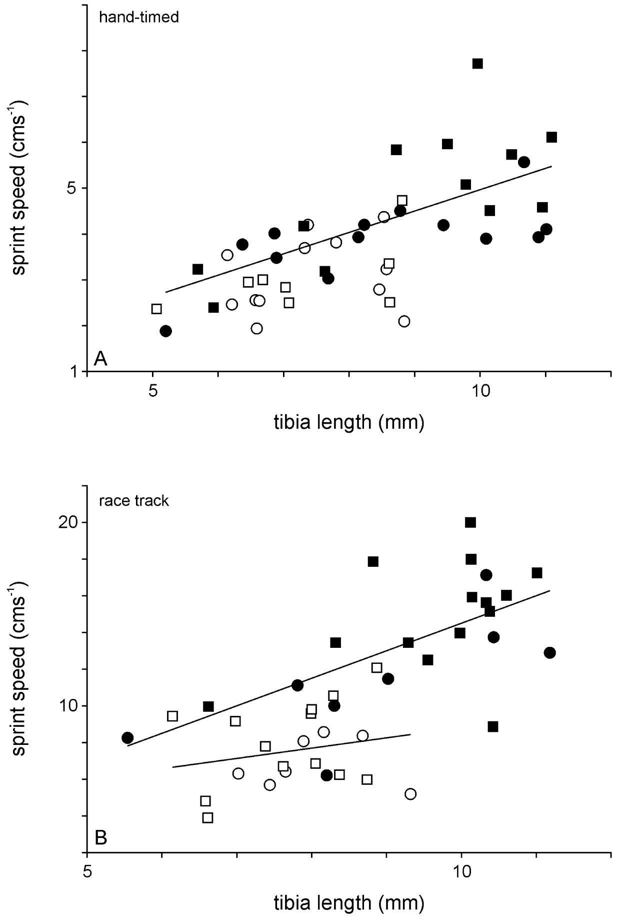

Figure 5. A, Correlations between tibia length and sprint speed for animals captured in 2010 that were timed manually. B, Correlations between tibia length and sprint speed for animals captured in 2008 and measured on a race track equipped with photocells. Independent of the type of method used, animals with longer tibia run faster and animals from the forested Stellenbosch population run faster for a given tibia length than animals from the Kogelberg fynbos population. Open symbols represent animals from the Kogelberg fynbos site; filled symbols represent animals from the forested Stellenbosch site. Squares represent males; circles represent females.

characterized by narrower perches. Unexpectedly, although Stellenbosch chameleons used the available habitat randomly, Kogelberg chameleons avoided the use of the narrowest perches available in the habitat (majority of available perches ranged from 0.7 to 1.0 mm in diameter). Despite the fact that the Kogelberg individuals avoided the narrowest perches, the actual perch diameters used still differed between the two populations, with Stellenbosch chameleons using wider perches on average. Moreover, within each population, individuals used the habitat nonrandomly, as perch diameter was correlated with aspects of morphology, such as hand size (Stellenbosch only) and tail length (both populations). Thus animals prefer to sleep on perches of specific diameters that match their morphology. Indeed, although sleeping individuals grasp the perch with their feet, they are also known to wrap their tails around branches, especially when sleeping on isolated twigs (K. A. Tolley & G. J. Measey, pers. observ.). One important caveat of our data that remains to be tested is whether night-time perch diameters, as measured here, also reflect daytime habitat use. Preliminary data based on radiotracking of this species suggest similarity in the use of the habitat, with animals using perches of similar diameters both day and night (K. A. Tolley, pers. observ.).

The correlation between morphology and perch diameter suggests that perch diameter may have an important effect on the ability of an animal to grasp the substrate, as has been documented previously (Losos *et al.*, 1993). This is confirmed by our analyses of grip strength on dowels of different diameter. Indeed, these analyses show that the ability of animals to exert force with their hands on a dowel is dependent on dowel diameter, with animals being able to exert greater forces on narrower dowels. Moreover, the correlations between morphology (hand size and tail length) and performance (hand and tail grip strength) suggest that animals in habitats that differ structurally (i.e. differing in perch diameter) may experience different selective regimes, resulting in morphological divergence between populations. Although untested, the ability to hold on to a branch using the feet and the tail is probably relevant to chameleons (see Tolley & Measey, 2007). For example, when males encounter each other on the same branch, this often results in vigorous fighting (Stuart-Fox *et al.*, 2006; Tolley & Burger, 2007; Measey *et al.*, 2009), with males holding on to the substrate with their tails and hindfeet. In addition, in many arboreal species of chameleons, tails are used to hold on to branches when moving vertically through the canopy or when bridging gaps.

If the ability to hold on to a substrate is indeed ecologically relevant, this leads to the prediction that animals living in habitats characterized by wider perches should evolve larger hands and feet, and longer tails. Not only is this observed in the two populations examined here (Hopkins & Tolley, 2011), but animals from habitats characterized by wider perches are also stronger than animals from habitats with narrow perches, suggesting that the selection on morphology is associated with differences in performance. Size-corrected variation in hand strength (i.e. independent of the size of the hands) is, however, only different between populations when measured on narrow dowels, with Stellenbosch animals being stronger than animals from Kogelberg. Although the reason for this observation remains unclear at this point, it suggests the existence of an optimal perch size that is matched to an individual's hand size, as observed previously for other chameleons (Losos *et al*., 1993). Indeed, the diameter of the narrow test dowel closely approximates the selected perch diameter in the wild for the Stellenbosch animals. As such, it would be interesting to measure performance on even narrower dowels, matching the observed perch diameters for the Kogelberg animals, to test for the presence of an optimal dowel size. The fact that strength was different between animals from the two populations when correcting for hand size suggests additional underlying differences in the musculoskeletal system that would be worth investigating.

Sprint speed was also different between populations, with animals from the wooded site at Stellenbosch being faster, even when correcting for differences in limb length. Although it has been suggested that longer limbs might be advantageous for animals from the open fynbos habitat, which is characterized by the absence of forest or trees (Hopkins & Tolley, 2011), our measurements show that animals from wooded sites actually sprint faster. This suggests that, despite the fact that the fynbos habitat is often considered to be spatially heterogeneous (Rebelo *et al*., 2006), for a chameleon, the wooded habitat may actually be more 'open', at least at ground level. Indeed, despite a nearly continuous canopy cover, the forested habitat shows relatively little understorey vegetation, whereas, in the fynbos, the ground is not bare, but is covered in low grasses, sedges, sticks and leaf litter, which can be several centimetres thick. Thus, there are at least two potential explanations that are not mutually exclusive. In the wooded habitat, if chameleons were to fall from the tree during combat or when escaping from predators, they would have to cross relatively open areas where they would remain exposed to ground-dwelling predators, making speed an advantageous trait. Alternatively, in the fynbos habitat, chameleons must routinely cross the ground between the sparsely placed bushes, and, here, longer limbs (but not faster speed *per se*) may provide an advantage when negotiating the ground-covering vegetation.

Differences between sexes in performance were also significant and match previously documented differences in morphology (Hopkins & Tolley, 2011). As interaction effects were nonsignificant, this suggests homogeneous differences independent of habitat type. Males typically have larger hands than females (Hopkins & Tolley, 2011), and our data demonstrate that males also have greater hand grip strength than females. Moreover, on narrow dowels, males show higher levels of gripping performance than females, even when correcting for hand size, thus suggesting selection on performance and the underlying morphological traits associated with the musculoskeletal system. The fact that these intersexual differences are consistent across populations and independent of habitat type suggests that they are related to sex-specific behaviours present in both populations. Unfortunately, the lack of ecological and behavioural data on these animals does not allow us to speculate on the nature of these behaviours.

In conclusion, the habitats at both sites differ significantly in structure, as measured by the available perch diameters, and the use thereof is nonrandom in at least one of the populations. Moreover, perch diameter is correlated with morphology in both populations, indicating that individuals prefer substrates that match their morphology. Morphology is also related to performance within populations and differences between populations in morphology are also reflected in performance. Finally, intersexual differences in morphology also lead to differences in performance, which may also be relevant in a sexual selection context. The logical next step is to test for fitness advantages of variation in performance to determine the relevance of the functional traits identified here in the context of sexual and natural selection. This could be performed by following individuals of known morphology and performance at the population level whilst quantifying reproductive success and survival. Finally, it would be interesting to test the covariation between habitat use, morphology and performance for previously documented morphs in other species (Tolley & Burger, 2007) to test for the generality of the observed differences, and the presence of true ecomorphs in chameleons of the genus *Bradypodion*.

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