

RESEARCH ARTICLE

Slow but tenacious: an analysis of running and gripping performance in chameleons

Anthony Herrel^{1,*}, Krystal A. Tolley^{2,3}, G. John Measey⁴, Jessica M. da Silva^{2,5}, Daniel F. Potgieter^{2,3},
 Elodie Boller⁶, Renaud Boistel⁷ and Bieke Vanhooydonck⁸

¹UMR 7179 CNRS/MNHN, Département d'Ecologie et de Gestion de la Biodiversité, 57 rue Cuvier, Case postale 55, 75231, Paris Cedex 5, France, ²Applied Biodiversity Research Division, South African National Biodiversity Institute, Private Bag X7, Claremont, Cape Town, 7735 South Africa, ³Department of Botany and Zoology, University of Stellenbosch, Matieland 7602, South Africa, ⁴Department of Zoology, Nelson Mandela Metropolitan University, PO Box 77000, Port Elizabeth, 6031, South Africa, ⁵Department of Conservation Ecology and Entomology, Stellenbosch University, Private Bag X1, Matieland 7602, Stellenbosch, South Africa, ⁶European Synchrotron Radiation Facility, 6 rue Jules Horowitz, B.P. 220, F-38043 Grenoble, France, ⁷IPHEP-UMR CNRS 6046–UFR SFA Université de Poitiers, 40 avenue du Recteur Pineau, F-86022 Poitiers, France and ⁸Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Antwerp, Belgium

*Author for correspondence (anthony.herrel@mnhn.fr)

SUMMARY

Chameleons are highly specialized and mostly arboreal lizards characterized by a suite of derived characters. The grasping feet and tail are thought to be related to the arboreal lifestyle of chameleons, yet specializations for grasping are thought to exhibit a trade-off with running ability. Indeed, previous studies have demonstrated a trade-off between running and clinging performance, with faster species being poorer clingers. Here we investigate the presence of trade-offs by measuring running and grasping performance in four species of chameleon belonging to two different clades (*Chamaeleo* and *Bradypodion*). Within each clade we selected a largely terrestrial species and a more arboreal species to test whether morphology and performance are related to habitat use. Our results show that habitat drives the evolution of morphology and performance but that some of these effects are specific to each clade. Terrestrial species in both clades show poorer grasping performance than more arboreal species and have smaller hands. Moreover, hand size best predicts gripping performance, suggesting that habitat use drives the evolution of hand morphology through its effects on performance. Arboreal species also had longer tails and better tail gripping performance. No differences in sprint speed were observed between the two *Chamaeleo* species. Within *Bradypodion*, differences in sprint speed were significant after correcting for body size, yet the arboreal species were both better sprinters and had greater clinging strength. These results suggest that previously documented trade-offs may have been caused by differences between clades (i.e. a phylogenetic effect) rather than by design conflicts between running and gripping *per se*.

Key words: ecomorphology, trade-off, locomotion, grip strength, lizard, habitat use.

Received 30 July 2012; Accepted 19 November 2012

INTRODUCTION

Chameleons are highly specialized and mostly arboreal lizards that are characterized by a suite of derived characters including a ballistic tongue, independently moveable eyes, and prehensile feet and tail (Gans, 1967). The specialized grasping feet (Renous-Lécuru, 1973) and tail (Ali, 1948; Zippel et al., 1999; Bergmann et al., 2003; but see Boistel et al., 2010) are thought to be related to the arboreal lifestyle of chameleons. Indeed, the bones in both the hands and feet are rearranged during development (Hurle et al., 1987; Rieppel, 1993) to form a grasping appendage allowing chameleons to hold on to narrow substrates (Peterson, 1984; Higham and Jayne, 2004; Fischer et al., 2010). Similarly, the tail has been modified to enhance ventral flexion and its musculature shows a unique arrangement among lizards (Ali, 1948; Zippel et al., 1999; Bergmann et al., 2003). Moreover, arboreal species have been shown to possess longer tails than terrestrial ones on average (Bickel and Losos, 2002).

The specializations for grasping characteristics for chameleons are, however, thought to exhibit a trade-off with running ability. Performance trade-offs occur when different and conflicting

functional demands are imposed on the same phenotypic trait (Arnold, 1992; Vanhooydonck et al., 2001; Levinton and Allen, 2005; Konuma and Chiba, 2007; Herrel et al., 2009). For example, in lizards, selection on burst locomotion capacity has been shown to occur at the expense of endurance capacity (Vanhooydonck et al., 2001), as the demands on the locomotor muscles are conflicting in the expression of either fast- or slow-muscle fibre types (Bonine et al., 2005). Previous studies on chameleon locomotion have demonstrated a trade-off between running and clinging performance, with faster species being poorer clingers (Losos et al., 1993). This trade-off was suggested to reside in differences in design requirements for sprinting *versus* clinging. Specifically, it was proposed that differences in the insertion of the limb flexors between species may give an advantage in generating torque at the expense of producing more rapid movements in the arboreal species (Losos et al., 1993). Moreover, it was suggested that the arboreal species possessed a greater proportion of slow, yet strong, tonic fibers in its limb muscles (Abu-Ghalyun et al., 1988; Mutungi, 1992). From these data, Losos et al. (Losos et al., 1993) concluded that the trade-offs between sprinting and clinging observed in

chameleons are due to their arboreal specialization and may have constrained the direction of their further diversification.

However, the species that were compared in the study by Losos et al. (Losos et al., 1993) belong to two rather divergent clades, *Trioceros* and *Chamaeleo* (Tilbury and Tolley, 2009; Townsend et al., 2011) (Fig. 1). Consequently, the observed trade-off may have been confounded by phylogeny and reflect clade-specific adaptations rather than being a general trade-off typical of chameleons. Here, we explore this question further by measuring running and grasping performance for four species of chameleon belonging to two different clades (*Chamaeleo* and *Bradypodion*). Within each clade we selected a closely related terrestrial [*Chamaeleo namaquensis* Smith 1831 and *Bradypodion occidentale* (Hewitt 1935)] and a more arboreal species (*Chamaeleo dilepis* Leach 1819 and *Bradypodion damaranum* Boulenger 1887) to test (1) whether morphology and performance are related to habitat use and (2) whether the observed trade-off between running and clinging is generally present or is the result of clade-specific adaptations.

MATERIALS AND METHODS

Animals

Bradypodion occidentale specimens ($N=21$) were caught by hand during night-time surveys at the Tygerberg reserve and along the west coast of South Africa during November 2008 and January 2012. *Bradypodion damaranum* ($N=31$) were caught during night-time surveys in Knysna and Outeniqua, South Africa in February 2010. Both species are closely related, yet occur in radically different habitats (Tolley and Burger, 2007; Tolley et al., 2006; Tolley et al., 2008). *Chamaeleo dilepis* ($N=7$) were caught during night-time surveys at various locations throughout South Africa including KwaZulu-Natal and Limpopo Provinces in 2010 and 2011. *Chamaeleo namaquensis* ($N=11$) were caught during daytime surveys in the Swakopmund area, Namibia, in April 2012. These species also occupy radically divergent habitats. The desert habitat of *C. namaquensis* is characterized by the absence of trees (Burrage, 1973). In contrast, although *C. dilepis* has been classified as being 'terrestrial' in some previous studies (Losos et al., 1993; Bickel and Losos, 2002), this species always roosts in trees and only moves over ground to lay eggs or to move between trees in its savannah habitat (A.H. and K.A.T., personal observation), and its primary habitat is arboreal. In contrast, *C. namaquensis* never uses trees and often can be observed to roost on the sand (Burrage, 1973; A.H. and K.A.T., personal observation). In all cases, animals were brought back to the field station, measured and tested for gripping performance and sprint speed, and released at the exact site of capture. All performance measures were performed at $25\pm 3^\circ\text{C}$. As preferred temperatures for chameleons are 25.0°C for *Bradypodion* and 29.3°C for *C. namaquensis* (Andrews, 2008; see Burrage, 1973) these species are performing near to their preferred temperatures.

Morphometrics

For each individual, we measured the following traits using digital calipers (Mitutoyo, Kanagawa, Japan): snout-vent length (SVL); femur, tibia and lateral hindfoot length; and humerus, radius and lateral forefoot length (Hopkins and Tolley, 2011; Herrel et al., 2011). In addition, we measured the mass of each animal using a digital balance (Ohaus PS121, Nanikon, Switzerland).

Morphology

We used a Viscom X8050-16 microtomograph at the Centre of Microtomography of the University of Poitiers (France) to scan a single specimen each of *C. dilepis* (MNHN 2005.3341), a *B.*

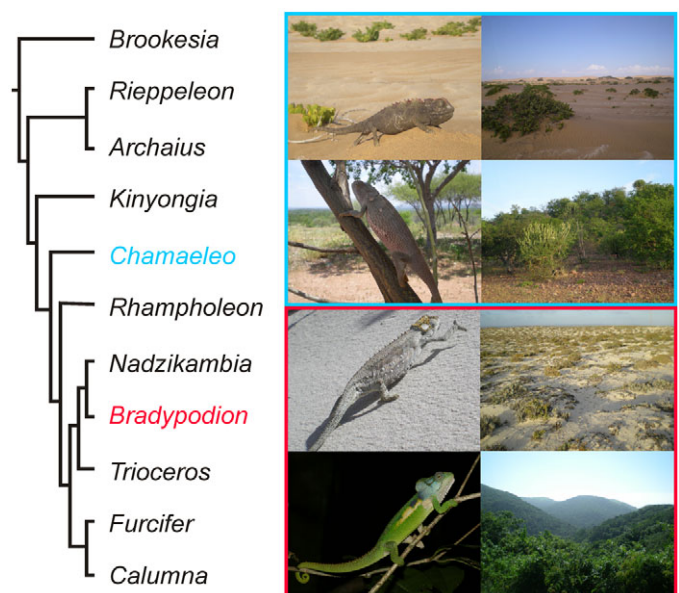


Fig. 1. Cladogram illustrating the relationships between the genera included in the present study (modified from Townsend et al., 2011). Photographs to the right illustrate animals and their habitat. From top to bottom: *Chamaeleo namaquensis*, *Chamaeleo dilepis*, *Bradypodion occidentale* and *Bradypodion damaranum*.

occidentale (MNHN 2000.2530) and a *B. damaranum* (Bayworld R8671). The X-ray source used consisted of a microfocus Viscom 150kV open tube, used between 86 and 100kV and 0.270 and 0.760mA. We used a detector composed of an image intensifier with a 1004×1004 pixel camera with a pixel size of 147 μm . The geometry was set to get a 24.5–50 μm voxel size in the reconstructed 3-D images. The reconstruction was performed using the software ImageJ (<http://rsb.info.nih.gov/ij>) and FDK algorithms of DigiCT v.2.4.3 (Digisens, Ferney-Voltaire, France; with plugin: SnapCT, acceleration in GPU). The data sets consist of 1200–3600 projections taken over 360 deg, and 20 integrations by projection. We also used the ID19 long imaging beam line of the European Synchrotron Radiation Facility (Grenoble, France) with large spatial coherence (Boistel et al., 2011). We used a monochromatic beam with an energy bandwidth ($\Delta E/E$) of $10E-4$ obtained with a double Si111 Bragg monochromator. We used a detector composed an optical system coupled to a cooled charge-coupled FReLoN camera (Labiche et al., 2007). We acquired tomographic data from hand of adult *C. namaquensis* (MNHN 282) scanned at 20keV with a propagation distance of 300 mm. The effective pixel size at the converter screen position was 7.45 μm . The data set for a complete sample consists of several scans of 1500 projections taken over 180 deg with vertical displacements between each scan, with a small overlap for scan alignment. The reconstruction was performed using the filtered back-projection algorithm (PyHST software, European Synchrotron Research Facility, Grenoble, France). Three-dimensional images were produced in 16 bits and subsequently converted into 8 bit voxels for visualization. Three-dimensional processing and rendering was obtained after semi-automatic segmentation of the skeleton (Boistel et al., 2011) using 'generate surface' and volume rendering in AVIZO 7.01 (VSG, SAS, Merignac, France).

Grip strength

One of two dowels (broad, 10 mm; narrow, 5 mm) was mounted on a piezo-electric force platform (Kistler Squirrel force plate, $\pm 0.1\text{ N}$,

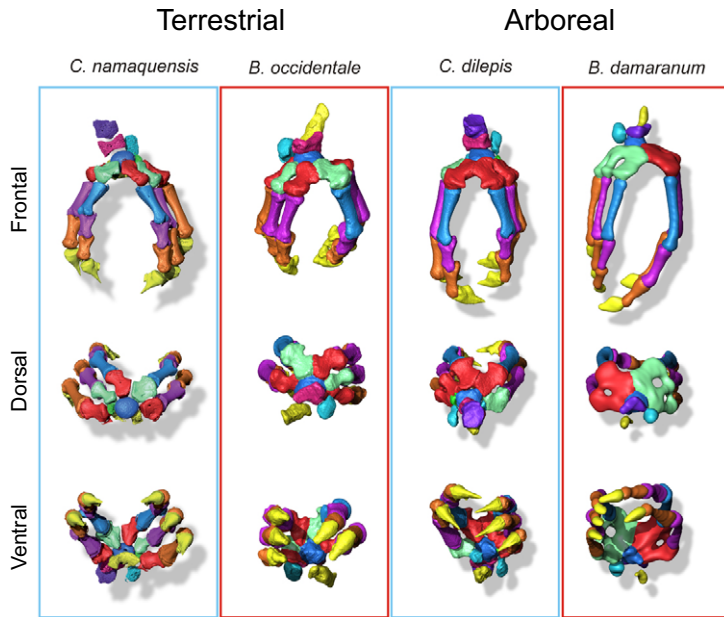


Fig. 2. Three-dimensional reconstructions of the hands of the four species included in this study based on micro-computed tomography (μ CT) data in frontal, dorsal and ventral view. From left to right: *Chamaeleo namaquensis*, *Bradypodion occidentale*, *Chamaeleo dilepis* and *Bradypodion damaranum*. Colors illustrate similar skeletal elements in the different species. Non-fused carpal elements are colored alternately red and green to indicate that elements are not fused. When adjacent elements have the same color this indicates fusion of the carpal elements as suggested by our μ CT data. Note, however, that the resolution of the scan of *B. damaranum* was lower and consequently it is more difficult to detect the independence of different elements.

Winterthur, Switzerland) (see Herrel et al., 2012). 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 grip trials. To quantify tail strength, animals were pulled from the dowel in the vertical direction, and we extracted peak Z forces 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 (i.e. forelimb only), 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. Foot grip strength (hind limb) was not measured as the morphology of the animals does not allow a straightforward measurement without hurting the animals. 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 at least 1 h of 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. Note that not all animals wanted to grip on the broad dowel and consequently sample sizes vary for the different dowel sizes.

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 (Herrel et al., 2011). Chameleons caught between 2010 and 2012 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 substrate consisted of wood covered with cork or hard foam, allowing the animals adequate grip for running. Irrespective of the method used, we calculated the speed over the fastest 50 cm

interval and retained it 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. An analysis of covariance (ANCOVA) testing for differences between the two methods using *B. occidentale* specimens showed no differences between speeds measured on the race track *versus* those timed by hand ($F_{1,18}=0.012$, $P=0.42$).

Analyses

All data were \log_{10} transformed before analysis to fulfil assumptions of normality and homoscedasticity. We tested for differences between clades and habitat groups (terrestrial *versus* arboreal) in morphology and performance using multivariate analyses of variance (MANOVA). Next, we ran ANCOVAs to test for differences in morphology and performance with SVL as a covariate. Tests of heterogeneity of slopes were non-significant for all morphological traits in *Bradypodion*. For *Chamaeleo*, heterogeneity of slopes was detected for tail length ($F_{1,13}=4.70$, $P=0.049$), femur length ($F_{1,14}=7.33$, $P=0.017$) and radius length ($F_{1,14}=7.17$, $P=0.018$). In *Bradypodion*, slopes were heterogeneous for sprint speed ($F_{1,48}=4.99$, $P=0.03$) and the grip strength on broad ($F_{1,34}=6.27$, $P=0.017$) and narrow ($F_{1,48}=25.88$, $P<0.01$) dowels. In *Chamaeleo*, slopes were heterogeneous for grip strength on the broad dowel only ($F_{1,14}=4.93$, $P=0.043$). For these traits residuals were calculated and compared using ANOVAs. Thirdly, we ran multiple regression models to explore which morphological variables best explained the variation in performance within each clade. For sprint speed we used all morphological variables as potential predictors. For hand grip strength we used SVL, mass, humerus length, radius length and hand length as potential predictors. Finally, for tail grip strength we used tail length, SVL and body mass as potential predictors. All analyses were performed using SPSS V. 15.0 (IBM, Armonk, NY, USA).

RESULTS

Anatomy

In the species studied here, the proximal hand involves the fusion of the carpal elements of the second row in all species (Fig. 2). As such, these elements form a true ball and socket joint with the carpal elements of the first row (see Renous-Lécure, 1973). Noticeable on

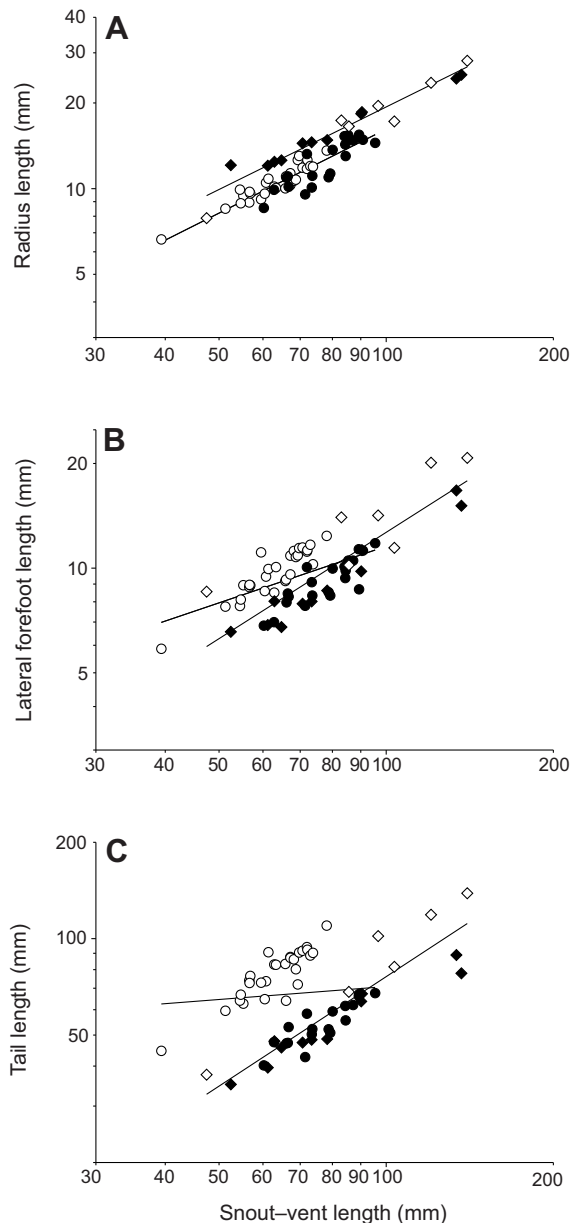


Fig. 3. Differences in (A) radius, (B) lateral forefoot and (C) tail length between species. Open symbols represent arboreal species, closed symbols terrestrial species. Diamonds represent *Chamaeleo* species and circles represent *Bradypodion* species. Note how in contrast to the lateral forefoot and tail, the radius does not differ between habitat groups. Lines represent within-clade regressions.

the micro-computed tomography scans are the longer phalangeal elements present in the two arboreal species independent of their phylogenetic affinity. Moreover, a distinct fusion of the carpals is observed in the two arboreal species (Fig. 2). In the terrestrial species, these elements remain unfused and are clearly individualized on the scans.

Morphometrics and performance

A MANOVA run on the morphological data detected significant clade (Wilks' lambda=0.14, $F_{9,54}=36.72$, $P<0.001$), habitat (Wilks' lambda=0.11, $F_{9,54}=47.79$, $P<0.001$) and interaction (Wilks' lambda=0.52, $F_{9,54}=5.47$, $P<0.001$) effects, indicating that

differences in morphology between animals living in different habitats (terrestrial versus arboreal) are clade dependent (Figs 3, 4). A MANOVA run using the performance data similarly detected significant clade (Wilks' lambda=0.15, $F_{5,46}=53.43$, $P<0.001$), habitat (Wilks' lambda=0.48, $F_{5,46}=10.13$, $P<0.001$) and interaction (Wilks' lambda=0.61, $F_{5,46}=5.78$, $P<0.001$) effects, indicating that differences in performance between terrestrial and arboreal chameleons are clade dependent.

Chameleons of the genus *Bradypodion* living in different habitats differed significantly in morphology (Wilks' lambda=0.06, $F_{9,39}=65.16$, $P<0.001$). Univariate F -tests indicated that differences were significant for all traits except hand and foot length (hand: $F_{1,47}=0.01$, $P=0.93$; foot: $F_{1,47}=0.02$, $P=0.88$). When taking into account differences in SVL (ANCOVA), however, differences in morphology were significant for all traits except femur ($F_{1,46}=0.81$, $P=0.37$), tibia ($F_{1,46}=1.05$, $P=0.31$) and humerus ($F_{1,46}=1.50$, $P=0.23$) length. Overall differences in performance were significant (Wilks' lambda=0.49; $F_{5,31}=6.48$; $P<0.001$). Yet univariate F -tests showed differences in grip strength on the broad dowel only (hand: $F_{1,35}=13.41$, $P=0.001$; tail: $F_{1,35}=5.94$, $P=0.02$). However, when taking into account differences in body size (SVL using ANCOVA or ANOVA on residuals), performance differences were significant for all traits except tail grip strength on the narrow dowel ($F_{1,34}=4.04$, $P=0.052$). However, arboreal species were both faster and stronger than terrestrial ones. Stepwise regressions retained a significant model for sprint speed ($R^2=0.63$, $P<0.001$) with hand length ($\beta=0.57$) and body mass ($\beta=0.28$) as significant variables. Thus, animals with bigger hands and greater body mass run faster. Variation in hand grip strength on a broad dowel was best explained by hand length ($\beta=0.80$) and body mass ($\beta=-0.52$; $R^2=0.36$, $P<0.001$), indicating that animals with larger hands, yet lower body mass, had greater grip strength. In contrast, variation in grip strength on a narrow dowel was best explained by SVL only ($R^2=0.63$, $P<0.001$), with longer animals having greater grip strength. Variation in tail grip strength on a broad dowel was explained by tail length only ($R^2=0.44$, $P<0.001$), with longer tails being correlated with greater tail grip strength. However, on a narrow dowel tail grip strength was best explained by variation in overall body mass ($R^2=0.40$, $P<0.001$), with heavier animals having greater tail grip strength.

Chameleons of the genus *Chamaeleo* living in different habitats were also different in morphology (Wilks' lambda=0.07, $F_{9,7}=9.84$, $P=0.003$). Univariate F -tests indicated that differences in morphology were significant only for tail length ($F_{1,15}=6.23$, $P=0.025$), hand length ($F_{1,15}=5.20$, $P=0.038$) and foot length ($F_{1,15}=5.11$, $P=0.039$). When taking into account differences in SVL, differences in body mass (ANCOVA, $F_{1,14}=22.00$, $P<0.001$), tail length (ANOVA on residuals, $F_{1,15}=23.45$, $P<0.001$), humerus length (ANCOVA $F_{1,14}=5.66$, $P=0.032$), hand length (ANCOVA, $F_{1,14}=12.05$, $P=0.004$) and foot length (ANCOVA, $F_{1,14}=18.74$, $P=0.001$) were significant. Differences in performance were also significantly different between arboreal and terrestrial chameleons (Wilks' lambda=0.36, $F_{5,11}=3.92$, $P=0.028$). Univariate F -tests indicated significant differences in all traits except sprint speed ($F_{1,15}=0.06$, $P=0.81$). When taking into account body size, differences in performance remained, with the exception of sprint speed, which did not differ between species ($F_{1,14}=0.06$, $P=0.81$). Stepwise multiple regressions between sprint speed and morphology retained no significant model, indicating that variation in sprint speed was poorly explained by variation in morphology across these two species. Variation in hand grip strength was explained by hand length only (broad dowel: $R^2=0.81$, $P<0.001$; narrow dowel: $R^2=0.74$,

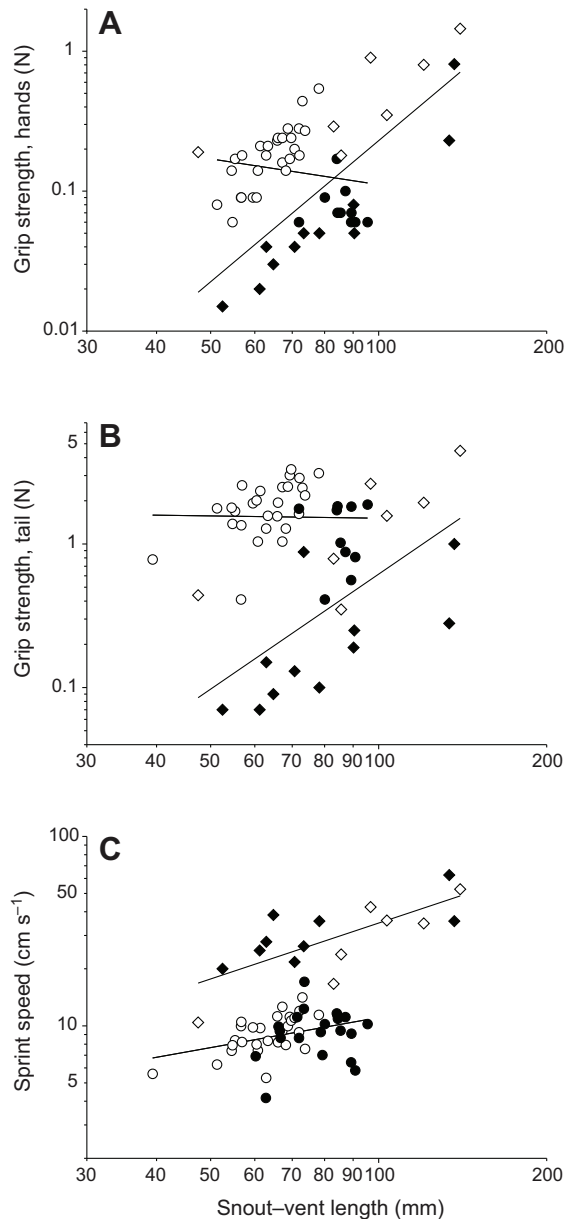


Fig. 4. Differences in performance between species in terms of (A) hand grip strength, (B) tail grip strength and (C) sprint speed. Open symbols represent arboreal species, closed symbols terrestrial species. Diamonds represent *Chamaeleo* species and circles represent *Bradypodion* species. Note how habitat groups differ in hand and tail strength but not in sprint speed. Lines represent within-clade regressions.

$P < 0.001$), with animals with larger hands having greater grip strength. Similarly, tail grip strength was explained by tail length only (broad dowel $R^2 = 0.66$, $P < 0.001$; narrow dowel: $R^2 = 0.80$, $P < 0.001$), with longer tails being associated with greater tail grip strength.

DISCUSSION

Our results show that habitat structure drives the evolution of morphology and performance in chameleons. Terrestrial species in both clades show poorer grasping performance compared with more arboreal species, and have smaller hands and feet (Figs 3, 4). Moreover, hand size best predicts gripping performance. Given that

selection acts at the level of the performance of the whole organism (Arnold, 1983), this suggests that the structural habitat drives the evolution of hand morphology through its effects on grasping performance. These results mimic results obtained for different morphs of the Cape dwarf chameleon (*Bradypodion pumilum*), where individuals inhabiting forest characterized by wider perches have bigger hands and better grasping performance (Hopkins and Tolley, 2011; Herrel et al., 2011). The reasons why larger hands and feet are beneficial to arboreal chameleons have not been explored explicitly, but it seems intuitively obvious that having larger hands and feet would allow chameleons to close their hands or feet around wider perches, thus allowing them to generate a torque preventing them from toppling sideways (Losos et al., 1993; Herrel et al., 2012). All chameleons, even the most terrestrial species, have prehensile hands and feet, the structure of which is highly derived compared with other lizards. The proximal hand, for example, involves the fusion of the carpal elements of the second row to form a true ball and socket joint with the carpal elements of the first row (Renou-Lécure, 1973). Whereas the fusion of the carpals observed in the arboreal species included in our study (Fig. 2) may provide greater structural integrity of the base of the hand associated with the relatively larger grasp forces, the independence of the carpals in the terrestrial species may, in contrast, allow the hand to flatten more, and consequently provide a better grip on a flat substrate. Why terrestrial species generally have shorter phalanges and hands (Fig. 2), or why having longer hands and feet does not provide a benefit to the more terrestrial species, remains unclear. It is possible that the larger hands of the arboreal species prevent the closure around the very fine and narrow substrates occasionally used by the more terrestrial species for roosting (see Herrel et al., 2011). Alternatively, the longer phalanges may prevent effective locomotion on a flat substrate. Yet the functional advantages or handicaps associated with these divergent morphologies remain to be tested experimentally. Moreover, a larger number of species needs to be examined before these observations can be generalized.

Our data also show that arboreal species also have longer tails and better tail gripping performance (Figs 3, 4). Again this is in accordance to what was observed for different populations of the Cape dwarf chameleon (Herrel et al., 2011). The reasons why longer tails appear to provide chameleons with a performance benefit again remains uncertain, but minimally longer tails allow animals to coil their tails around wider perches. Moreover, this may allow chameleons to have more coils around a substrate of a given diameter, allowing for an increased contact area, which positively affects frictional and adhesive forces. In addition, the longer tails of arboreal chameleons are characterized by smaller distal vertebrae in the prehensile part that grow with negative allometry (Bergmann et al., 2003). As vertebrae are smaller, this may permit the generation of tighter coils around the substrate and thus better gripping. Finally, at least some terrestrial chameleons use their short tails as a walking stick to improve balance while walking on wide substrates (Boistel et al., 2010).

Our data also show that some of effects observed are specific to each clade (*Chamaeleo* versus *Bradypodion*). For example, no differences in sprint speed were observed between the two *Chamaeleo* species, suggesting that at least in the *Chamaeleo* clade no trade-off exists between running and gripping. However, it must be noted that *C. dilepis* is by some considered to be among the more terrestrial species within the clade, as it is often seen crossing roads. As such, this may bias our analyses and other species need to be tested. One other caveat that needs to be mentioned is that all species were tested for sprint speed at similar temperatures. If optimal

performance temperatures are different for different species, then this could introduce a bias in the results. Although preferred temperatures for chameleons are generally low (Andrews, 2008) and optimal performance temperatures are thus likely not too different from the temperature at which animals were run, no data yet exist on the thermal dependence of performance of sprinting in chameleons. Within *Bradypodion*, however, differences in sprint speed were significant after correcting for body size. Yet, arboreal species were faster than terrestrial ones, consistent with what was observed for *B. pumilum* (Herrel et al., 2012). This can be explained by the fact that hand length positively affected both sprint speed and gripping strength in *Bradypodion* species. In the *Chamaeleo* species, however, sprint speed was not dependent on specific morphological traits and did not differ between species. Moreover, limb long-bones, which typically determine sprint speed in lizards (Vanhooydonck and Van Damme, 2001), were not different between terrestrial and arboreal *Chamaeleo* species. These results demonstrate that trade-offs between sprinting and clinging do not exist in *Chamaeleo* (no relationship) or in *Bradypodion* (positive relationship). Consequently, previously demonstrated trade-offs between running and clinging (Losos et al., 1993) likely reflect differences in performance in different functional tasks between clades of chameleons rather than being the result of an intrinsic design conflict between gripping and running. Future analyses examining these relationships across a much broader range of chameleons are needed to fully understand the evolution of running and gripping performance and the associated morphology in chameleons.

ACKNOWLEDGEMENTS

We particularly thank Paul Tafforeau and José Baruchel at the European Synchrotron Radiation Facility for their help. We would like to thank Werner Conradie and Bill Branch from the Port Elizabeth Museum, South Africa, and Ivan Ineich from the Muséum National d'Histoire Naturelle, France, for loaning specimens for scanning. We are grateful to Tommy Collard, Penny Glanville, Stuart Nielsen and Duncan MacFayden for their help in the field. We also thank the Centre de Microscopie de fluorescence et d'Imagerie numérique team at the Muséum National d'Histoire Naturelle in Paris for allowing us access to computers and reconstruction software. This study was carried out under permits from the Namibian Ministry of Environment and Tourism (1616/2011), Northern Cape Province (ODB 2679/2008), Western Cape Province (AAA007-00002-0056 and AAA007-00875), Limpopo Province (O18-CPM403-00001 and CPM333-0002) and KwaZulu-Natal Province (OP4596-2010, OP1647-2009 and OP3794-2011), and under South African National Biodiversity Institute (SANBI) ethics clearance (0010-08 and 002/10).

FUNDING

We would like to thank the South African National Research Foundation (Key International Science Capacity Fund Program), the Partenariat Hubert Curien-National Research Foundation Protea, the South African National Biodiversity Institute, the City of Cape Town, and Oppenheimer and Sons for financial and logistical support. This study was also partially supported by a European Synchrotron Radiation Facility Project through allocation of beam time.

REFERENCES

- Abu-Ghalyun, Y., Greenwald, L., Hetherington, T. E. and Gaunt, A. S. (1988). The physiological basis of slow locomotion in chameleons. *J. Exp. Zool.* **245**, 225-231.
- Ali, S. M. (1948). Studies on the anatomy of the tail in Sauria and Rhynchocephalia. II. *Chamaeleon zeylanicus* Laurenti. *Proc. Indiana Acad. Sci.* **28**, 151-165.
- Andrews, R. M. (2008). Lizards in the slow lane: thermal biology of chameleons. *J. Therm. Biol.* **33**, 57-61.
- Arnold, S. J. (1983). Morphology, performance and fitness. *Am. Zool.* **23**, 347-361.
- Arnold, S. J. (1992). Constraints on phenotypic evolution. *Am. Nat.* **140** Suppl., 85-107.
- Bergmann, P. J., Lessard, S. and Russell, A. P. (2003). Tail growth in *Chamaeleo dilepis* (Sauria: Chamaeleonidae): functional implications of segmental patterns. *J. Zool.* **261**, 417-425.
- Bickel, R. and Losos, J. B. (2002). Patterns of morphological variation and correlates of habitat use in chameleons. *Biol. J. Linn. Soc. Lond.* **76**, 91-103.
- Boistel, R., Herrel, A., Daghfous, G., Libourel, P.-A., Boller, E., Tafforeau, P. and Bels, V. L. (2010). Assisted walking in Malagasy dwarf chameleons. *Biol. Lett.* **6**, 740-743.
- Boistel, R., Swoger, J., Kržič, U., Fernandez, V., Gillet, B. and Reynaud, E. G. (2011). The future of three-dimensional microscopic imaging in marine biology. *Mar. Ecol. Prog. Ser.* **32**, 438-452.
- Bonine, K. E., Gleeson, T. T. and Garland, T., Jr (2005). Muscle fiber-type variation in lizards (Squamata) and phylogenetic reconstruction of hypothesized ancestral states. *J. Exp. Biol.* **208**, 4529-4547.
- Burrage, B. R. (1973). Comparative ecology and behavior of *Chamaeleo pumilum* (Gmelin) and *C. namaquensis* Smith (Sauria: Chamaeleonidae). *Ann. S. Afr. Museum* **61**, 1-158.
- Fischer, M. S., Krause, C. and Lilje, K. E. (2010). Evolution of chameleon locomotion, or how to become arboreal as a reptile. *Zoology* **113**, 67-74.
- Gans, C. (1967). The chameleon. *Nat. Hist.* **76**, 52-59.
- Herrel, A., Podos, J., Vanhooydonck, B. and Hendry, A. P. (2009). Force-velocity trade-off in Darwin's finch jaw function: a biomechanical basis for ecological speciation? *Funct. Ecol.* **23**, 119-125.
- Herrel, A., Measey, G. J., Vanhooydonck, B. and Tolley, K. A. (2011). Functional consequences of morphological differentiation between populations of the Cape dwarf chameleon (*Bradypodion pumilum*). *Biol. J. Linn. Soc. Lond.* **104**, 692-700.
- Herrel, A., Measey, G. J., Vanhooydonck, B. and Tolley, K. A. (2012). Got it clipped? The effect of tail clipping on tail gripping performance in chameleons. *J. Herpetol.* **46**, 91-93.
- Higham, T. E. and Jayne, B. C. (2004). Locomotion of lizards on inclines and perches: hindlimb kinematics of an arboreal specialist and a terrestrial generalist. *J. Exp. Biol.* **207**, 233-248.
- Hopkins, K. P. and Tolley, K. A. (2011). Ecomorphological variation in dwarf chameleons and the dynamics between natural and sexual selection. *Biol. J. Linn. Soc. Lond.* **102**, 878-888.
- Hurle, J. M., Garcia-Martinez, V., Gañan, Y., Climent, V. and Blasco, M. (1987). Morphogenesis of the prehensile autopodium in the Common Chameleon (*Chamaeleo chamaeleo*). *J. Morphol.* **194**, 187-194.
- Konuma, J. and Chiba, S. (2007). Trade-offs between force and fit: extreme morphologies associated with feeding behavior in carabid beetles. *Am. Nat.* **170**, 90-100.
- Labiche, J.-C., Mathon, O., Pascarelli, S., Newton, M. A., Ferre, G. G., Curfs, C., Vaughan, G., Homs, A. and Carreiras, D. F. (2007). Invited article: the fast readout low noise camera as a versatile x-ray detector for time resolved dispersive extended X-ray absorption fine structure and diffraction studies of dynamic problems in materials science, chemistry, and catalysis. *Rev. Sci. Instrum.* **78**, 091301.
- Levinton, J. S. and Allen, B. J. (2005). The paradox of the weakening combatant: trade-off between closing force and gripping speed in a sexually selected combat structure. *Funct. Ecol.* **19**, 159-165.
- Losos, J. B., Walton, B. M. and Bennett, A. F. (1993). Trade-offs between sprinting and clinging ability in Kenyan chameleons. *Funct. Ecol.* **7**, 281-286.
- Mutungi, G. (1992). Slow locomotion in chameleons: histochemical and ultrastructural characteristics of muscle fibers isolated from iliofibularis muscle of Jackson's chameleon (*Chamaeleo jacksonii*). *J. Exp. Zool.* **263**, 1-7.
- Peterson, J. A. (1984). The locomotion of *Chamaeleo* (Reptilia: Sauria) with particular reference to the forelimb. *J. Zool.* **202**, 1-42.
- Renou-Lécuro, S. (1973). Morphologie comparée du carpe chez les Lepidosauriens actuels (Rhynchocephales, Lacertiliens, Amphisbèniens). *Gegenbaurs Morphol. Jahrb.* **119**, 727-766.
- Rieppel, O. (1993). Studies on skeleton formation in reptiles II. *Chamaeleo hoehnelii* (Squamata: Chamaeleonidae), with comments on the homology of carpal and tarsal bones. *Herpetologica* **49**, 66-78.
- Tilbury, C. R. and Tolley, K. A. (2009). A re-appraisal of the systematics of the African genus *Chamaeleo* (Reptilia: Chamaeleonidae). *Zootaxa* **2079**, 57-68.
- Tolley, K. A. and Burger, M. (2007). *Chameleons of Southern Africa*. Cape Town: Struik Publishers.
- Tolley, K. A., Burger, M., Turner, A. A. and Matthee, C. A. (2006). Biogeographic patterns and phylogeography of dwarf chameleons (*Bradypodion*) in an African biodiversity hotspot. *Mol. Ecol.* **15**, 781-793.
- Tolley, K. A., Chase, B. M. and Forest, F. (2008). Speciation and radiations track climate transitions since the Miocene Climatic Optimum: a case study of southern African chameleons. *J. Biogeogr.* **35**, 1402-1414.
- Townsend, T. M., Tolley, K. A., Glaw, F., Böhme, W. and Vences, M. (2011). Eastward from Africa: palaeocurrent-mediated chameleon dispersal to the Seychelles islands. *Biol. Lett.* **7**, 225-228.
- Vanhooydonck, B. and Van Damme, R. (2001). Evolutionary trade-offs in locomotor capacities in lacertid lizards: are splendid sprinters clumsy climbers? *J. Evol. Biol.* **14**, 46-54.
- Vanhooydonck, B., Van Damme, R. and Aerts, P. (2001). Speed and stamina trade-off in lacertid lizards. *Evolution* **55**, 1040-1048.
- Zippel, K. C., Glor, R. E. and Bertram, J. E. A. (1999). On caudal prehensility and phylogenetic constraint in lizards: the influence of ancestral anatomy on function in *Corucia* and *Furcifer*. *J. Morphol.* **239**, 143-155.