



Divergence in locomotor performance, ecology, and morphology between two sympatric sister species of desert-dwelling gecko

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The functional and evolutionary implications of morphological diversification have been addressed for several groups of vertebrates. Although the mechanisms of gecko adhesion have received considerable attention, little is known regarding locomotor performance of geckos in nature, and how this might relate to morphological diversity. In this study we examine locomotor performance of two sympatric sister species of geckos of the genus *Rhoptropus* (*Rhoptropus afer* and *Rhoptropus bradfieldi*) found in the coastal desert regions of Namibia. One species (*R. afer*) commonly runs on sandy substrates and moves between isolated rock sheets, whereas the other species (*R. bradfieldi*) commonly lives and runs on isolated boulders. The morphology of *R. afer* is extremely divergent from its sister species and all other species in the genus. We initially recorded the inclination of the substrate in which the lizards were found in order to characterize the habitat of each species. We then quantified maximum speed and acceleration on a level 1-m trackway, and also during escapes in the field. We found that *R. bradfieldi* occupies steeper surfaces than those occupied by *R. afer*. On the trackway and in nature, *R. afer* runs faster than *R. bradfieldi*, although the differences in locomotor performance between the species are greater for the field measurements. *Rhoptropus afer* commonly runs for more than 2 or 3 m, whereas *R. bradfieldi* commonly runs less than 50 cm during an escape sprint. Our main conclusions are that: (1) *R. afer* attains higher maximum speeds when escaping under controlled and field conditions, although the magnitude differs between conditions; and (2) hindlimb morphology correlates with maximum running speed in *R. afer*, but not in *R. bradfieldi*. Similar to the well-studied *Anolis* lizards, we propose that these two gecko species represent distinct and highly divergent ecomorphs. © 2010 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2010, 101, 860–869.

ADDITIONAL KEYWORDS: acceleration – lizard – locomotion – Namibia – speed – velocity.

INTRODUCTION

Locomotion is a fundamental attribute employed in capturing prey and escaping from predators (Higham, 2007). It therefore significantly impacts an organism's fitness. How an animal moves depends on several factors, including its habitat structure, morphology, physiology, ancestry, and motivation. For example, locomotion during prey capture can differ considerably from locomotion during an escape bout (Irschick

& Losos, 1998; Schriefer & Hale, 2004), highlighting the context-dependent nature of locomotor behaviour. More generally, locomotor performance and/or kinematics can often be linked to the morphology of the locomotor system and/or aspects of the habitat in which an animal lives (Losos, 1990; Garland & Losos, 1994; Miles, Fitzgerald & Snell, 1995; Barbosa & Moreno, 1999; Higham, Davenport & Jayne, 2001; Vanhooydonck & Van Damme, 2001; Bickel & Losos, 2002; Vanhooydonck, Van Damme & Aerts, 2002; Higham & Jayne, 2004). The latter can involve both acute changes in habitat structure (e.g. when an animal encounters an obstacle) or overall characteristics of the locomotor habitat (e.g. arboreal

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versus terrestrial). Understanding what features of an organism enhance locomotion in a given situation is critical to our understanding of the ecological and morphological underpinnings of diversity and adaptation.

The habitat in which an animal lives is likely to dictate the type of performance necessary for survival (Irschick & Losos, 1998). For example, a species that lives in a relatively open area may need to run faster and for longer in order to successfully evade a predator. In contrast, animals living in complexly structured habitats may of necessity employ slower speeds, but exhibit greater manoeuvrability, in order to evade a predator (e.g. Higham *et al.*, 2001). Apart from the level of performance that is necessary to survive, habitat structure itself may limit performance as a result of mechanical constraints. For example, sprinting speed in *Anolis* lizards increases with increasing perch diameter (Irschick & Losos, 1999), and species exhibiting a large decrease in sprint performance with decreasing perch diameter also tend to avoid small-diameter branches in their natural habitat. This again highlights the context-dependent nature of locomotor performance, which is often overlooked in studies of locomotion.

Laboratory studies of maximum locomotor performance are often extrapolated to movement in a natural habitat (e.g. Brana, 2003). However, this relies on the key assumption that movement is comparable between the two (Hertz, Huey & Garland, 1988; Irschick & Losos, 1998; Irschick & Garland, 2001). If animals exhibit maximum locomotor performance in nature, then selection is likely to act on that attribute. If not, however, quantifying maximum performance in the laboratory may misinterpret or overlook critical aspects of natural behaviour. Additionally, understanding when animals use their maximum level of performance in nature provides insight into the ecological reasons why selection may favour a maximal level of performance (Irschick & Garland, 2001). Many animals exhibit submaximal locomotor performance during undisturbed locomotion in their natural habitat. For example, *Anolis* lizards display very slow locomotor speeds when undisturbed, and habitat structure strongly influences locomotion (Mattingly & Jayne, 2004). It is evident from energy budgeting that animals will utilize submaximal locomotor speeds when maximum performance is not necessary (e.g. foraging versus escape). Thus, it is important to separate undisturbed and provoked locomotion from each other when linking other factors (e.g. morphology and physiology) to behaviour. Although escape locomotion intuitively requires maximal output, it need not be the case if other factors, such as camouflage or a secure hiding place, alleviate the need to escape

at maximal velocity. Although rarely tested, it is also possible that locomotor performance displays greater maxima in nature compared with laboratory studies, probably because of the constraints imposed by laboratory conditions (Irschick *et al.*, 2005).

Given that much of our understanding of the relationship between locomotor performance in the laboratory and in nature has been acquired through the study of *Anolis*, information regarding other groups of lizards is necessary. Several reasons make geckos a pertinent taxon for testing whether comparable patterns of habitat use and performance exist across lizards. First, geckos are extremely diverse, both morphologically and ecologically (Pianka & Huey, 1978; Zaaf *et al.*, 1999; Russell, 2002; Gamble *et al.*, 2008), occurring in deserts, forests, rocky outcrops, and many other habitats. Second, several groups of geckos are secondarily diurnal, making their daytime movements relatively straightforward to observe. Finally, and as is the case for *Anolis* lizards, species within a group of geckos are likely to fall into ecomorphological categories, with some species exhibiting a morphology that is well suited for running fast in open areas, and others exhibiting a morphology well suited for climbing (e.g. Johnson, Russell & Bauer, 2005).

The eight species of geckos of the genus *Rhoptropus* are part of the *Pachydactylus* radiation (Bauer & Good, 1996; Johnson *et al.*, 2005). They occur in Angola and Namibia, are diurnal, and are rupicolous. However, the type of rock that species inhabit ranges in gross aspect from boulders to exposed horizontal sheet rock (Bauer, Russell & Powell, 1996), and also in petrological category (Johnson & Russell, 2009). Different species exhibit considerable variation in locomotor morphology, with *Rhoptropus afer* having longer hindlimb segments, significantly shorter setae, and a smaller subdigital pad area than other species in the genus (Bauer *et al.*, 1996; Johnson *et al.*, 2005; Johnson & Russell, 2009). The morphological traits observed in *R. afer* indicate that it should exhibit higher locomotor speeds than other species, but this remains untested.

Our choice of species to compare was predicated on a combination of phylogenetic relationships, previously documented morphometric data (Bauer *et al.*, 1996), and ecological circumstance (i.e. sympatric). *Rhoptropus afer* is the sister species of *Rhoptropus bradfieldi* and *R. diporus* (Lamb & Bauer, 2001), but *R. afer* is morphologically divergent from all members of its genus (Bauer *et al.*, 1996). Morphometry of body dimensions and limb segments indicates that *R. afer* differs significantly in tibial, metatarsal, and third digit length from its congeners (Bauer *et al.*, 1996), and that all other species show no significant differences in these aspects from each other. *Rhoptropus bradfieldi*, however, exhibits similar



Figure 1. Representative photos of the two species examined in the current study. A, *Rhothropus afer*; B, *Rhothropus bradfieldi*. Both photos were taken by T. Higham.

values for these parameters, relative to body size, to other members of the genus *Rhothropus*. As well as being morphologically distinct sister taxa, *R. afer* and *R. bradfieldi* are also sympatric at the boulder field site employed in this study, allowing us to directly compare segregation of locomotor ecology in the absence of other ecological variables. Both species are active at the same time and experience the same macroclimatic conditions. Both are routinely exposed in the open, and spend long periods in the open. Thus, by comparing *R. afer* and *R. bradfieldi* in a field situation we are comparing morphologically divergent species in terms of features important to the assessment of locomotor performance, but in species that are very closely related.

By quantifying locomotor performance of *R. afer* and *R. bradfieldi* (Fig. 1) in nature and under controlled conditions, we addressed the following three questions. (1) Do the morphological specializations of *R. afer* indicate the attainment of greater maximal speeds than *R. bradfieldi*? (2) Do both of these geckos



Figure 2. Representative photos of the habitat of the two species in the current study. A, isolated sheet-like rock outcrops (arrows) that are common habitat for *Rhothropus afer*. B, boulder field where *Rhothropus bradfieldi* was studied. *Rhothropus afer* occurs in the interstices between the boulders at this site. Both photos were taken near Swakopmund, Namibia, by T. Higham.

commonly employ maximum performance in nature? (3) Do measurements of maximum performance under controlled conditions accurately predict maximum performance in nature?

MATERIAL AND METHODS

FIELD DATA

Field data were collected in habitats near Swakopmund, Namibia, in February of 2010. Two field sites were employed in these experiments, the first being at the base of Rossing Mountain (east of Swakopmund), which is characterized by relatively flat rocky outcrops and hard-packed sand (Fig. 2A), and at which *R. afer* was abundant; the second site was in a boulder field close to the coast and north of Swakopmund (Fig. 2B), at which both *R. afer* and *R. bradfieldi* were common. At the latter site, *R. bradfieldi* only occupied the boulders, employing

their three-dimensional configuration and associated refugia (crevices and low vegetation bordering the boulders) as small islands to which they appear restricted, and never attempting to run between clusters of boulders when chased. Conversely, *R. afer* occupied the ground and flat rocky outcrops surrounding the boulders, never venturing onto the boulder surfaces. Thus, these two species are sympatric, yet occupy structurally distinct substrates.

The first recordings of field escape locomotion involved only *R. afer* at the Rossing Mountain site. When a lizard was first encountered, we measured the inclination of the substrate on which the lizard was found. This was achieved using a PRO 360 digital level (accuracy of $\pm 0.1^\circ$). We used these measurements to characterize the inclination of the habitat in which these species live. All locomotion events were filmed using a Casio Exilim Pro EX-F1 high-speed video camera operating at 300 fps (Casio Computer Co., Ltd., Tokyo, Japan), which was an appropriate frame rate for quantifying velocities and accelerations (Walker, 1998). In order to quantify escape performance in field situations, lizards were startled by quick movements towards them. Because *R. afer* typically runs from a small flat rock to another small flat rock in a continuous locomotor burst, we scaled the video sequences by measuring the distance between two such rocks following the escape. In addition to these in situ quantifications, additional individuals of *R. afer* were collected (by hand) at the Rossing Mountain site and released on a flat rock to film escape speeds on a natural substrate. A grid of 1-m squares was drawn on this rock using chalk in order to measure locomotor performance and to convert distance travelled to metres.

At the second field site (boulder field), *R. afer* was observed as described above. Unlike the Rossing Mountain site, however, the boulder field did not permit extensive field escape observations for this species. For sequences of *R. bradfieldi*, quick movements towards individuals on boulders also elicited escape movements. The field of view was scaled following the escape by marking a distance of 30 or 60 cm on the boulder with chalk while continually filming. This permitted the conversion of escape speeds from pixels s^{-1} to ms^{-1} .

CONTROLLED EXPERIMENTS

A minimum of eight individuals of each species were collected by hand. Whereas individuals of *R. afer* were collected at both field sites, individuals of *R. bradfieldi* were only collected at the boulder field site. Individuals of each species were comparable in size, although *R. bradfieldi* individuals were slightly longer and heavier (Table 1). Each individual was encouraged to run maximally on a custom-built trackway set up in the field location. This trackway was 12-cm wide and approximately 1-m long, with Plexiglas sides and a 600-grit sandpaper horizontal substrate to provide traction. A minimum of four trials was obtained from each individual, and body temperatures were raised to field temperatures (between 30 °C and 35 °C) prior to each trial. Each lizard was given a brief rest between trials. A lateral view of each sequence was recorded at 300 fps using the Casio camera described above. A 10-cm scale on the background was used to convert the sequences to ms^{-1} . In total, seven individuals from each species yielded usable results and were subsequently included in the analyses.

Following these experiments, several external morphological measurements were taken from both the hindlimb and forelimb using Kobalt digital calipers (accuracy of ± 0.1 mm). The measurements were femur length (upper hindlimb), tibia/fibula length (lower hindlimb), foot (pes) length (to the distal end of digit III), humerus length (upper forelimb), and distal arm length (ulna/radius plus manus, to the distal end of digit III) (lower forelimb). The snout-vent length (SVL) was also measured. Body mass was obtained using a PESOLA scale. Additional animals were included in the morphological analyses despite not participating in the experiments.

DATA ANALYSIS

Video sequences from field and trackway escapes were first converted from MOV to AVI format using MPEG STREAMCLIP for WINDOWS v1.2. The AVI files were then imported into MATLAB R2008a. For field escapes using the metre square grid, the average velocity was obtained by quantifying the distance travelled and dividing this by the elapsed time from

Table 1. Average (\pm SEM) morphological measurements from *Rhoptropus afer* and *Rhoptropus boultoni*

Species	SVL	Mass	HL _{upper}	HL _{lower}	HL _{foot}	F _{upper}	F _{lower}
<i>R. afer</i>	41.8 \pm 1.6	3.2 \pm 0.3	12.3 \pm 0.5	12.7 \pm 0.4	12.4 \pm 0.4	8.5 \pm 0.3	12.6 \pm 0.6
<i>R. boultoni</i>	54.0 \pm 2.3	7.0 \pm 0.8	13.3 \pm 0.5	13.0 \pm 0.5	10.8 \pm 0.6	11.7 \pm 0.3	15.0 \pm 0.5

All measurements are in mm, with the exception of mass, which is in grams. SVL = Snout vent length; HL_{upper} = Upper hindlimb; HL_{lower} = Lower hindlimb; HL_{foot} = Hindfoot; F_{upper} = Upper forelimb; F_{lower} = Lower forelimb.

start to finish. The field of view for these trials was much larger, thus precluding frame-by-frame digitizing. Given these limitations, acceleration data were obtained only from the trackway trials.

For the trackway trials, the tip of the snout was digitized in each frame for each sequence using DLTdv3 (Hedrick, 2008) in MATLAB. Velocity was calculated as the first derivative of the displacement data (from the digitized x coordinate of the snout). The velocity data were then imported into IGOR PRO v5, and smoothing splines were applied, with smoothing factors ranging from 1 to 2. Acceleration was then calculated as the derivative of velocity using the smoothed velocity data. Instantaneous maximum velocity and maximum acceleration were extracted from each sequence. The maximum value from each individual was then retained for further analyses.

STATISTICS

Differences in substrate inclination between the two species were assessed using a two-sample Student's t -test. Because escape speed and acceleration did not exhibit a correlation with body mass or SVL in either of the two species examined, we used the raw speeds rather than the residuals of a regression of performance and body size. We assessed differences in performance variables using two-sample Student's t -tests. Rather than incorporating multiple observations per individual, we extracted and used the single maximum value for each individual. To assess whether speeds were comparable between field and controlled conditions, two-sample Student's t -tests were used.

In order to account for differences in morphology as a result of body size, we first regressed each linear measurement against SVL. We also regressed mass against SVL to assess whether mass differed between the species for a given SVL. We then used two-sample Student's t -tests to analyse differences in morphology by using the residuals of these regressions.

To determine the relationship between morphology and performance on the trackway, we used multivariate regressions that included body mass and each limb segment length as the independent variables. For all statistical analyses, we used a P value of 0.05 as our criterion for statistical significance.

RESULTS

The inclination of the substrate was significantly greater for *R. bradfieldi* compared with *R. afer* (Fig. 3; Student's t -test, $P = 0.002$). As noted above, these values represent the incline of the starting position of each individual, not necessarily the trajectory of the escape.

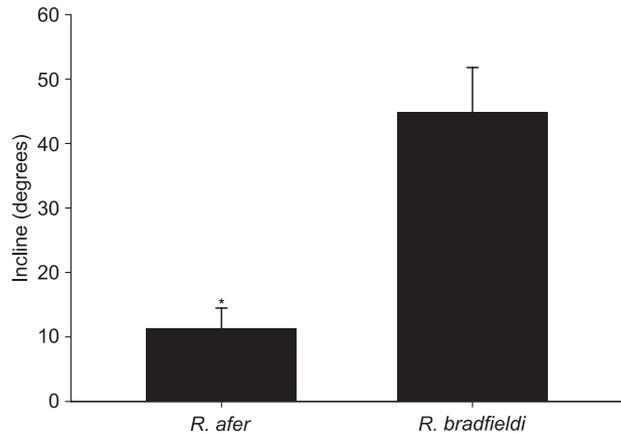


Figure 3. The average incline at which *Rhoptropus afer* (left) and *Rhoptropus bradfieldi* (right) were first encountered in their natural habitat. *Significant difference ($P < 0.05$), using a two-sampled Student's t -test.

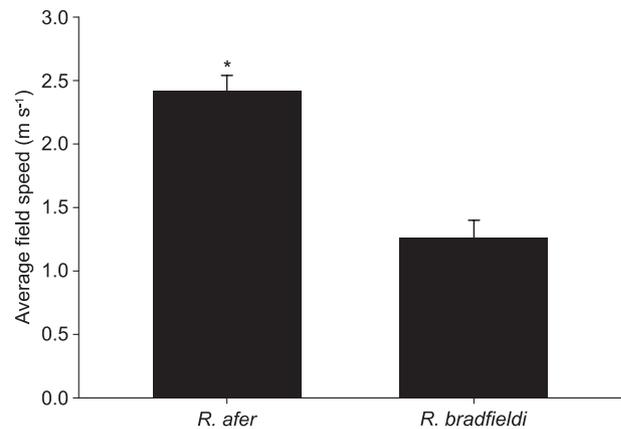


Figure 4. The average field speed for *Rhoptropus afer* (left) and *Rhoptropus bradfieldi* (right). Note that *R. afer* ran approximately twice as fast as *R. bradfieldi* in the field. *Significant difference ($P < 0.05$), using a two-sampled Student's t -test.

Average field speeds were significantly faster for *R. afer* compared with *R. bradfieldi* (Fig. 4; Student's t -test; $P < 0.0001$), with the average difference between the species being 1.22 m s^{-1} . Although maximum escape speed on the artificial trackway was greater for *R. afer* (average maximum = 2.1 m s^{-1}) compared with *R. bradfieldi* (average maximum = 1.6 m s^{-1}) (Fig. 5A; Student's t -test, $P = 0.04$), the difference between the species was not as great as that for comparative field data. *Rhoptropus afer* accelerated at an average maximum of 92 m s^{-2} , compared with 64 m s^{-2} for *R. bradfieldi*, although this was not a significantly greater acceleration (Fig. 5B; Student's t -test, $P = 0.15$). Interestingly, the average escape speeds in the field for *R. afer*, but not *R. bradfieldi*,

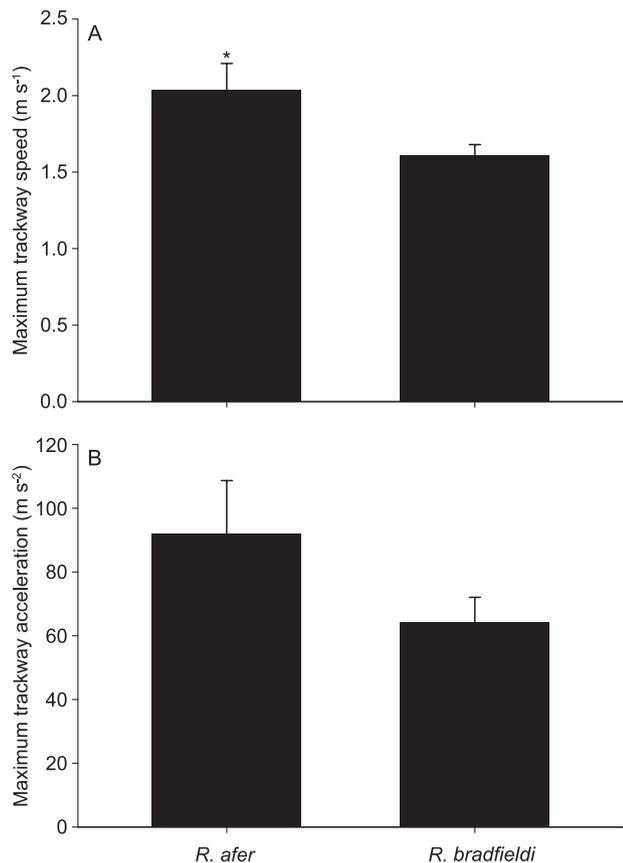


Figure 5. The maximum trackway speed (A) and acceleration (B) for *Rhoptropus afer* (left bars) and *Rhoptropus bradfieldi* (right bars). Note that *R. afer* ran significantly faster ($P < 0.05$) than *R. bradfieldi*, but that the maximum accelerations were not significantly different. *Significant difference ($P < 0.05$), using a two-sampled Student's *t*-test.

were faster compared with the maximum escape speeds recorded in the trackway trials.

We found that *R. afer* exhibited longer total hindlimb length compared with *R. bradfieldi* (Student's *t*-test, $P = 0.002$), which was most evident in the distal elements [pes (foot) length, Student's *t*-test, $P = 0.003$; Fig. 1]. The average mass of *R. afer* for a given SVL was considerably less than that for *R. bradfieldi* (Student's *t*-test, $P = 0.02$). Using multiple regressions, the hindfoot (pes) length of *R. afer*, but not any other element, was significantly and positively correlated with maximum trackway escape speed (Fig. 6A; $r^2 = 0.97$; $P < 0.0001$). In contrast, none of the lengths of the hindlimb segments of *R. bradfieldi* were correlated with trackway performance (Fig. 6B).

DISCUSSION

Our study highlights the differences in performance between closely related, but morphologically dis-

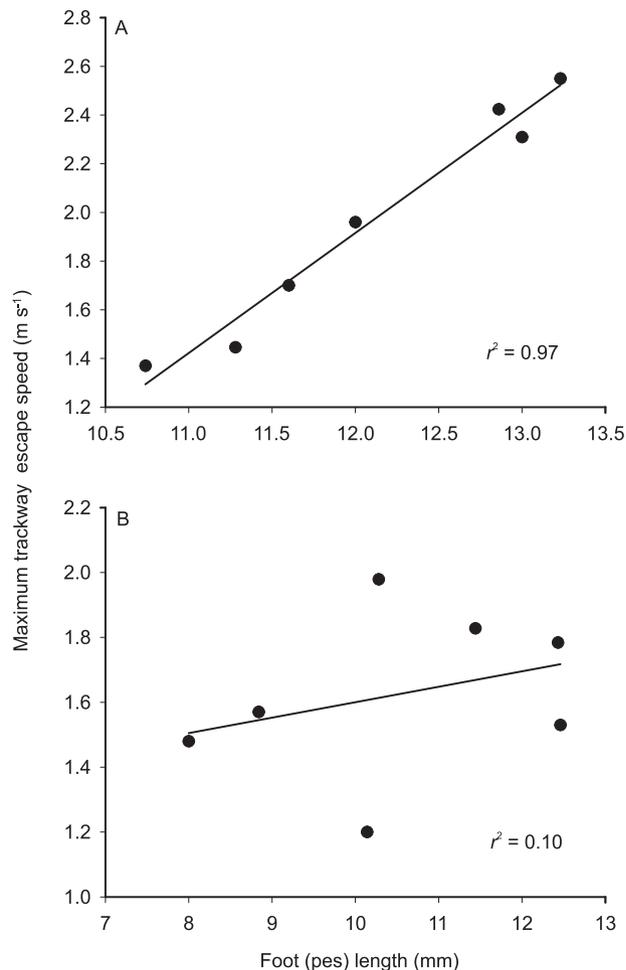


Figure 6. The foot (pes) length of *Rhoptropus afer* (A) and *Rhoptropus bradfieldi* (B) plotted against maximum trackway speed. Note that there is a significant, and positive, correlation for *R. afer* ($r^2 = 0.97$), but not for *R. bradfieldi* ($r^2 = 0.10$).

parate, species of geckos of the genus *Rhoptropus*. The faster species, *R. afer*, has relatively long limbs (Bauer *et al.*, 1996) compared with all other species in the genus and other pad-bearing geckos. In addition, *R. afer* occupies primarily open areas with substrates of low inclination. In contrast, the slower species, *R. bradfieldi*, has relatively short hindlimbs and occupies boulders that have relatively steep inclines that provide shorter distances for travel. The divergence in performance and morphology of *R. afer* from other species in the genus probably reflects the release of constraints imposed by climbing. Performance differences in the field, however, are greater than those observed under controlled conditions.

Several studies have examined the locomotion of geckos, although all of these have been conducted under laboratory conditions (Farley & Ko, 1997; Zaa-

et al., 2001; Irschick *et al.*, 2003; Vanhooydonck *et al.*, 2005; Autumn *et al.*, 2006; Bergmann & Irschick, 2006; Chen *et al.*, 2006; Russell & Higham, 2009). Based on this body of work, running speeds approaching 2 m s^{-1} appear to be extremely fast for geckos. Thus, *R. afer*, with speeds exceeding 3 m s^{-1} , is the fastest gecko for which speeds have been recorded. It is diurnal and lives in relatively open habitat on the ground, both of which have probably favoured increased locomotor speeds. One constraint that many geckos face that influences running speed is the presence and use of the adhesive system. Engaging the adhesive system and then hyperextending the digits to release the system imposes a lower limit on the duration of the stance phase of the stride. This in turn is likely to limit the ability to run fast in species that rely on the adhesive system. A way of circumventing this constraint is to hold the digits in a hyperextended position during running on a level surface, when adhesion is not necessary. This occurs in the Moorish gecko, *Tarentola mauritanica* (Russell & Higham, 2009) and in *Pachydactylus* clade geckos, including *Rhoptropus* (Russell, 1975). Compared with other species of *Rhoptropus*, *R. afer* exhibits significantly shorter setae and a small subdigital pad area (Johnson & Russell, 2009), further highlighting the departure from adhesion and subsequent attainment of a non-gecko type running style. The observed changes in *R. afer* have yielded an ecomorph that is convergent with that of fast desert-dwelling lizards, such as *Callisaurus draconoides* (Irschick & Jayne, 1999a). This is especially interesting given that this ecomorph is secondarily derived from a typical pad-bearing gecko-like body form, and appears to be unique among geckos.

Several studies have examined lizard locomotion in the field and in the laboratory in attempts to determine how often and when maximum speeds are utilized in nature. For example, Irschick & Losos (1998) examined locomotor performance in eight species of *Anolis* lizards in the laboratory and in the field. They found that sprinting during escape in the field closely approximated maximum sprinting performance (90% of maximum), as measured in the laboratory. However, sprinting during feeding decreased to about 71% of maximum. In our study, we examined how escape sprinting performance compared between field and controlled conditions. We found that, for *R. afer*, velocity in the field was greater than that measured under controlled conditions (about 118% of controlled trackway speeds). In contrast, the field speeds of *R. bradfieldi* were approximately 78% of those measured on the trackway. We would conclude that maximum performance was accurately measured under controlled conditions for *R. bradfieldi*, but not for *R. afer*, given that field speeds exceeded the speed under controlled conditions. One explanation is that

R. afer requires a relatively long distance (several meters) to achieve its maximum sprinting speed, whereas *R. bradfieldi* rarely runs for more than 50 cm at a given time. Added to this, it is evident that *R. bradfieldi* employs its adhesive system on the steep inclines of the boulder surfaces it typically negotiates, imposing a limitation on velocity in such circumstances (Russell & Higham, 2009). On the horizontal trackway such constraints are released, permitting faster speeds to be attained, as was the case for *Tarentola* (Russell & Higham, 2009). Conversely, *R. afer* habitually runs on horizontal, or near-horizontal, surfaces, and probably employs the same locomotor kinematics in the field and on the trackway, albeit in circumstances that inhibit the attainment of maximal sprinting performance. Without knowing what these animals actually do in their natural habitat, one would assume that the controlled trackway conditions revealed maximum sprinting performance in both species, which is incorrect. Thus, future work that incorporates field observations is critical for understanding the environmentally important performance capabilities of animals.

A recent study by Irschick *et al.* (2005) outlined criteria for studies hoping to relate laboratory performance to fitness. Equivalent values of maximum performance in the field and in the laboratory not surprisingly resulted in the ideal situation for estimating fitness ('best fitness line'). Most of the species of *Anolis* and lacertid lizards in the study fell within the 'slacker space', meaning that their laboratory performance exceeded their performance in nature. In contrast, desert-dwelling species, such as *C. draconoides* and *Uma scoparia*, which will run for distances of up to 30 m to find shelter (Jayne & Ellis, 1998; Irschick & Jayne, 1999b), and attain maximum running speeds beyond a distance typical of a race-track (between 1 and 2 m), were categorized as 'over-achievers'. Interestingly, in our study *R. afer* would be considered an 'overachiever', whereas *R. bradfieldi* would be a 'slacker'. This probably relates to the results of Irschick *et al.* (2005) in that *R. afer* will run for long distances and thus attain higher maximum sprinting speeds. For *R. bradfieldi*, however, the slower speeds in the field might relate to: (1) the deployment of the adhesive system on inclines and the constraints that that places upon the attainment of maximal velocity; or (2) the fact that they do not normally run under conditions imposed upon them in the controlled trials. Thus, depending upon the taxa being examined, there may be additional confounding factors that need to be understood. One way to avoid the performance-to-fitness study in the laboratory would be to measure performance in the field and relate that to a variable of interest (e.g. limb length), and avoid laboratory measurements altogether.

The relationship between morphology and performance is vital for understanding fitness and natural selection (Arnold, 1983; Wainwright, 1994). In addition, understanding what drives emergent behaviours (i.e. locomotion) will shed light on the mechanisms underlying functional diversification (Wainwright, 2007). We found that hindlimb length and maximum sprinting speed on an artificial trackway were positively correlated for *R. afer*, but not for *R. bradfieldi*. Again, the ecology of the species, and the particular mode of deployment of its locomotor apparatus, probably provides the answer to this observation. When morphology and performance are strongly correlated, one would expect selection on those morphological traits to be strong (Irschick *et al.*, 2007). When maximum performance is a key element for survival in a species, one would also expect morphological features that maximize performance to be prevalent. This appears to be the case for *R. afer*, which can run at high speeds and will often run many metres without pausing. Associated with this is an elongate metatarsus and phalanx 1 of digit 3 (Bauer *et al.*, 1996). The distal phalanges are, however, still associated with the adhesive system, and are thus comparable in size with those of other species. However, the elongated phalanx 1, combined with an elongate third metatarsal, probably provides an increased lever used in propelling the animal faster. Unlike *R. afer*, *R. bradfieldi* typically remains on a single boulder, often escaping short distances (< 50 cm) to cover, or to the other side of the boulder. It moves in a variety of body orientations, and deploys its subdigital adhesive system while doing so. Thus, maximum sprinting performance as recorded on a horizontal surface is not likely to be attainable under field circumstances, and is therefore not likely to be a key attribute for survival. Other factors, such as climbing ability, are likely to be important for the survival of this species. Not surprisingly, the link between morphology and level running performance is weak for *R. bradfieldi*, suggesting that morphological factors related to climbing are probably more important. Such an inference, however, can only be made if an incomplete understanding of locomotor capabilities, circumstances, and mechanics is accounted for. Ultimately, selection on morphology is integrated with the behaviour of the animal in its natural habitat, as highlighted in this study. Future selection studies of whole-animal performance and morphology (Irschick *et al.*, 2008) using these two species will reveal which factors actually enhance fitness.

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