

Bolting, bouldering, and burrowing: functional morphology and biomechanics of pedal specialisations in desert-dwelling lizards

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Abstract

Animals often move in a variety of complex habitats and they often exhibit morphological variation that can be explained, at least in part, by the habitat in which they live. The habitats of animals are often generally categorised based on dominant structures. Although this scheme can be fruitful, it ignores the intricacies of the microhabitat and the actual habitat utilisation of an animal. This is especially the case for desert habitats, which are often regarded as uniform and simple. Desert-dwelling lizards, however, occupy a range of structures in a desert including trees, rocks, and sand, and they have been noted as being a dominant form in almost all the warm deserts of the world. Along with this disparity in microhabitat, lizards often exhibit pedal specialisations, or modifications, that enhance a given behaviour (e. g., digging or running). Much work has examined the thermal influences on lizard biology, but pedal specialisations have not been discussed in an integrative and comprehensive way. Here, I review the pedal specialisations in desert-dwelling lizards and discuss their functional ramifications. I will also propose links between these specialisations/modifications and characteristics of habitat structure. Some of the pedal specialisations of desert-dwelling lizards include adhesive toe pads for climbing (geckos), toe fringes and webbed feet for maximising the surface area in contact with the substrate (sand-dwelling lizards), a multifunctional foot (sand-dwelling lizards), zygodactylus feet (chameleons), and claws (rock-dwelling lizards). Finally, I propose a frame-

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work for future studies of biomechanics and functional morphology in desert-dwelling lizards.

Introduction

Differences in locomotor morphology are often related to the habitat in which an animal lives (Losos 1990; Bauer *et al.* 1996; Melville & Swain 2000; Herrel *et al.* 2001; Wainwright *et al.* 2002; Johnson *et al.* 2005; Goodman *et al.* 2008; Higham & Russell 2010). For example, skinks that live in habitats that are rock-dominated exhibit longer limbs than those species occupying forest habitats (Goodman *et al.* 2008). However, there are cases where the relationships between morphology and habitat use/occupation are non-existent, weak, or unpredictable (Vanhooydonck & Van Damme 1999; Schulte *et al.* 2004; Birn-Jeffery *et al.* 2012; Logan *et al.* 2012). One possible confounding factor is that many studies categorise animals based on macro- rather than their microhabitat, which might miss key aspects of habitat utilisation that exert selective pressures on morphology. Desert-dwelling lizards offer a diverse system in which the species occupy a range of habitat types. Moreover, microhabitat utilisation of desert-dwelling lizards can be quantified, making it an ideal system for determining the relationship between morphology and habitat. In addition, lizards are often very abundant and dominant in these habitats.

Desert ecosystems often convey the idea of a paucity of life, continuous heat, lack of moisture, and the presence of endless sand (Jaeger 1955). In fact, deserts can be hot or cold, and are chiefly characterised by a dearth of precipitation relative to water loss by evaporation (Bradshaw 1986). Deserts exist everywhere in the world, including polar and sub-tropical areas. Deserts exist on coastal areas (e. g., Namibia, Peru, or Chile), but also inland (e. g., Mojave, Great Basin, or Central Asian) and are often subjected to persistent wind (Bradshaw 1986). Although the climate is often a key topic of desert research, the habitat structure of deserts is extremely complex, diverse, and, in sandy areas, often in flux. In addition, many animals that live in deserts are not only specialised for dealing with temperature and humidity extremes, but also specialised for locomotion in these extreme habitats (e. g., sand dunes). How these animals move and how their pedal specialisations enhance locomotion in these complex habitats will help us understand the evolution of

morphological disparity. It will also reveal how ecological demand influences the form-function relationship.

Lizards are often the dominant vertebrate group in desert habitats. The fact that they are ectotherms likely enables them to cope with the extreme climate (Pianka 1986). Desert habitats are extremely complex and often contain three-dimensional structures such as boulders, bushes, trees, sand dunes, or sheet-rock outcrops (Fig. 1). Despite this complexity, lizards occupying desert habitats are often characterised as either arboreal (trees), saxicolous (rocks), or psammophilous (sand). Unfortunately, this categorisation does little to capture the natural movements of lizards and the biomechanical and morphological underpinnings of locomotion. The microhabitat use of desert-dwelling lizards is something we know little about and will be a vital area of future research when considering the ramifications of pedal specialisations. For example, saxicolous lizards might occupy flat rock sheets, irregularly shaped boulders, or vertical (or inverted) rock faces. In addition to this variation in macro-topography, rocks can vary substantially with respect to their rugosity or roughness at the micro level and this could have a significant impact on the ability of lizards to gain purchase on the substrate (Russell & Johnson 2007).

The goals of this paper are (1) to examine the key features of common pedal specialisations of desert-dwelling lizards, (2) to examine what is known about how desert-dwelling lizards use their natural habitat, and (3) to propose and define a framework for future work that might address the consequences of ecological and morphological diversity among desert-dwelling lizards.

Pedal specialisations for desert locomotion: an overview

Lizards exhibit an array of pedal specialisations/modifications for running, climbing, or digging in desert habitats (Solano 1964; Dixon & Huey 1970; Haacke 1976; Carothers 1986; Luke 1986; Russell & Bauer 1988, 1990; Bauer & Russell 1991; Pianka & Vitt 2003; Lamb & Bauer 2006; Korff & McHenry 2011; Li *et al.* 2012). These include, but are not limited to, toe fringes, interdigital webs, modified claws, elongation of foot tendons or toes, adhesive toe pads, parapathecal elements, and prehensile feet (Fig. 2). The relative importance of these modifications will depend on whether the lizard



Figure 1:

Examples of desert habitats, highlighting structural diversity. A: Granite Mountains, Mojave Desert, California, USA. This habitat is commonly occupied by a variety of lizards such as *Uta stansburiana*, *Colonyx variegatus*, and *Sceloporus magister*. B: rocky area in gravel plains, Gobabeb, Namib Desert, Namibia. This area is commonly occupied by lizards such as *Ptenopus garrulus*, *Pachydactylus rangei*, and *Rhoptropus afer*. C: Kelso Dunes, Mojave Desert, California, USA. A common lizard in this habitat is *Uma scoparia*. D: sand dunes, Gobabeb, Namib Desert, Namibia. A common lizard in this habitat is *Moroles anchietae*. E: Kuiseb River, Gobabeb, Namib Desert, Namibia. Arboreal geckos from the genus *Lygodactylus* can be found here. All photos taken by the author.

is arboreal, saxicolous, or psammophilous, and will depend on how the lizards use these types of habitat (e. g., Collins *et al.* in press). For example, claws and adhesive toe pads will be important for climbing (up and down both rocks and trees), but toe fringes and interdigital webs will be important for moving on soft, sandy surfaces. Whatever the function, these aspects of morphology are key for all forms of locomotor movements involving limbs given that these structures are what contact the substrate and exert forces on the ground (Biewener 2003). Forces are distributed across the pedal surface in contact with the ground and pedal specialisations likely maximise and/or enhance running or clinging performance (Higham & Irschick 2013). The specific pedal specialisations will each be discussed in detail below.

Toe fringes

Toe fringes are laterally projecting, elongated scales that originate from epidermal and dermal tissue (Fig. 2; Luke 1986). In addition to being important for locomotion on moving sand, they can be important for “swimming” through sand, running across water, digging, and potentially gliding (Carothers 1986; Luke 1986; Bauer & Russell 1991; Hsieh 2003). Although toe fringes are well suited for studies of convergence, it is difficult to link toe fringes to a particular habitat. As far as locomotion goes, they likely increase context-dependent performance and they might increase efficiency. It is clear that toe fringes are useful on, or in, substrates that are relatively fluid such as water or dune sand.

There are four types of fringes in lizards, including triangular fringes (e. g., *Uma* and *Bunopus*), projectional fringes (e. g., *Scincus*), conical fringes (e. g., *Teratoscincus* and *Ptenopus*), and rectangular fringes (e. g., *Basiliscus*). Although it is possible that the different fringe types address different functional challenges, the differences might not be adaptive. Some functional differences have been suggested after preliminary functional studies (Luke 1986). Triangular, projectional, and conical fringes are found on species that occupy sandy habitats and are collectively referred to as denticulate fringes, projecting independently from the toe. The rectangular fringes found on water-running lizards contact one other, preventing water from flowing between adjacent scales. By contrast, the denticulate fringes prevent sand from flowing between adjacent scales. Thus, denticulate fringes provide a greater effective surface area for those lizards that run over sand in desert habitats (Luke 1986). Despite this preliminary functional examination, we still lack a

clear understanding of the biomechanical mechanisms underlying fringe function during locomotion. How does the presence of toe fringes influence the mechanics of locomotion? How do the forces exerted by the feet differ when toe fringes are present?

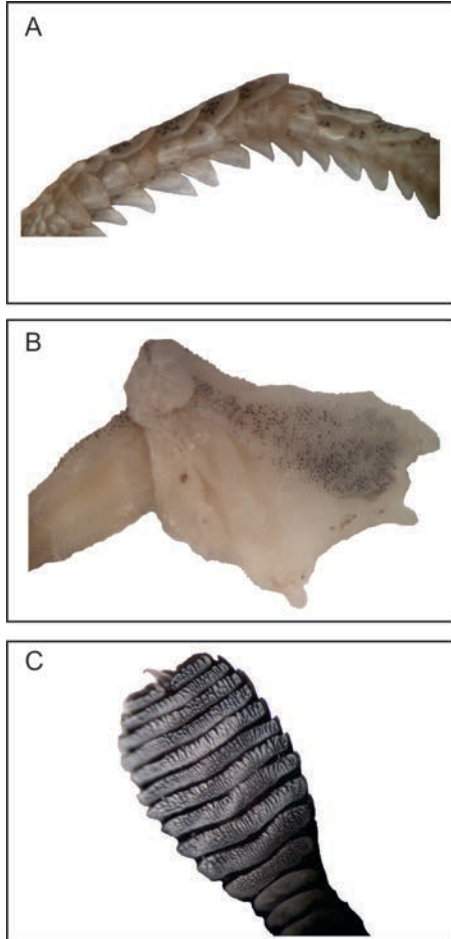


Figure 2:
Examples of pedal specializations, including A: toe fringes (*Meroles anchietae*), B: webbed feet (*Pachydactylus rangeti*), and C: adhesive toe pads (*Rhoptropus bradfieldi*). All photos taken by the author.

Current data regarding the impact of toe fringes on running speed across different species are limited. However, recent work suggests that factors other than toe fringes might predict differences in speed across species. For example, *Callisaurus draconoides* (without fringes) sprints faster than *Uma scoparia* (with fringes) (Irschick & Jayne 1999b). Another recent study examined the sprinting ability of *U. scoparia* and *C. draconoides* on two different substrates (fine dune-sand and coarse wash-sand), and found that *C. draconoides* ran slightly faster on dune sand, but not on the wash sand (Korff & McHenry 2011). The authors concluded that sprinting ability is thus not dominated by environmental differences in the substrate nor the presence of toe fringes. Interestingly, there are populations of *C. draconoides* in Baja California that exhibit toe fringes (Luke 1986; pers. obs.). This variation between populations provides an ideal natural experiment for examining the functional importance of toe fringes.

Interdigital webs

A webbed foot can be used either as a “shovel” or a “snowshoe” (Russell & Bauer 1990; Bauer & Russell 1991). In the former case, lizards can dig, typically in sand, with the increased surface area and surface preventing sand particles from passing between the digits. The functional benefit associated with increased surface area can also be implicated in running on top of soft sandy substrates, thus implicating the analogy of snowshoes, which adopt a similar function. One gecko, *Pachydactylus rangei*, utilises webbed feet in the Namib Desert for both excavating a burrow and running over soft sand (see Fig. 2). However, the functional benefits in terms of mechanics or efficiency have yet to be determined. There might also be trade-offs associated with interdigital webbing that have yet to be identified. For example, the range of motion of each digit might be constrained with the existence of webbing. In addition, it is not clear how the mechanics of propulsion during locomotion are influenced by the presence of webbing. Assessing the mechanics of locomotion in *P. rangei* in comparison with closely related taxa lacking interdigital webbing would provide a functional understanding of this interesting and rare pedal specialisation.

Modified claws

Claws are important for clinging to substrata, especially those surfaces that are rough (Fig. 2; Zani 2000). The functional implications are relatively unexplored, but anecdotal information suggests that geckos with their claws removed are no longer able to cling to the underside of horizontal surfaces (Bellairs 1969). Additionally, geckos without claws appear to struggle when climbing up rough vertical surfaces (Mahendra 1941). This struggle, however, does not appear to occur when these same geckos climb smooth surfaces. Thus, the adhesive system appears to be important for smooth surfaces, whereas the claws become important on rough surfaces, such as rocks. Why some geckos lack claws but exhibit extensive adhesive systems is not fully understood.

In an overview of claw morphology (Mahendra 1941), noted the importance of joint structure at the proximal origin of the claw. In Gekkonidae, the articulation of the penultimate phalanx with the last phalanx is substantially dorsal to the insertion of the contractor tendon, which bends the claw in the ventral direction. This distance between the tendon and the joint effectively increases the mechanical advantage and enhances the ability for the claw to be forcefully pushed into the substrate. Although not examined in detail, it might be hypothesised that climbing lizards have an increased ability to contract their claws.

Claw morphology can be related to habitat within certain groups of lizards. A study of neotropical iguanian lizards examined the relationship between habitat use (arenicolous, arboreal, and saxicolous) and claw morphology, and found that those species that often climb (arboreal and saxicolous) exhibit higher and more sharply curved claws (Tulli *et al.* 2009). Non-climbers tended to have longer and less-curved claws. This was also observed in a study that focused on lizards from the genus *Liolaemus* (Etheridge 2000). Coupling these conclusions with a previous study of clinging performance (Zani 2000) suggests that increased claw height and sharp curvature enable lizards to climb by “hooking” into the substrate while still maintaining stability. The longer and flatter claws of terrestrial lizards might increase the effective limb length and increase the surface area of the digit, much like toe fringes. Biomechanical analyses of claw morphology and locomotion on different substrates will help answer some of these questions.

Although claw morphology is an attractive area for connecting behaviour with morphology, a recent study highlights that this relationship can be somewhat complex (Birn-Jeffery *et al.* 2012). One important consideration is what an animal actually does in its natural habitat. Although claw morphology might be expected to differ between arboreal and terrestrial species (Tulli *et al.* 2009), animals often occupy a range of habitats and thus exhibit a generalised morphology. Quantification of claw function, including manipulation of claw morphology, will be beneficial in future research. In addition, phylogenetic constraint might limit the variation in claw function in relation to habitat. Thus, any quantification of claw morphology in relation to habitat should include phylogenetic information.

Elongation of foot tendons and/or toes

A long foot increases the effective limb length of a lizard and enables it to increase locomotor speed by increasing the lever in contact with the substrate (Higham & Russell 2010). In the genus *Rhoptropus*, the elongate metatarsus and phalanx 1 of digit III (Bauer *et al.* 1996) results in a longer digit and thus increased locomotor speeds (Higham & Russell 2010). This is one way of increasing the length of the foot and it is somewhat constrained by the presence of the adhesive system on the distal phalanges. How other desert-dwelling lizards increase the length of their feet and how this impacts locomotor mechanics would be important to consider in the context of pedal specialisations.

The zebra-tailed lizard, *C. draconoides*, has one of the longest feet of phrynosomatid lizards and can run incredibly fast, reaching speeds close to 6 m s^{-1} (Irschick & Jayne 1999a, b). This species has a multifunctional foot that exhibits substrate-specific mechanisms for locomotion (Li *et al.* 2012). On a solid substrate, springs (tendons), skeletal elements, and muscles work to enable *C. draconoides* to store and release elastic energy. On a soft, sandy substrate, the foot acts like a force-generating paddle as it penetrates the surface of the sand. It is clear that the importance of this pedal specialisation is related to the openness and hardness of the habitat and the speeds at which the lizard must run.

Adhesive toe pads of geckos

Adhesive toe pads are sub-digital structures that consist of a series of lamellae that are shrouded in arrays of hair-like setae (Fig. 2; Russell 1975, 1979, 1986, 2002; Russell & Bauer 1989; Autumn & Peattie 2002; Johnson *et al.* 2005; Johnson & Russell 2009). They are formed from β -keratin and, in geckos, they often branch at the tips into spatulae. Gecko adhesion has been the subject of many studies and the disparity in morphology between genera is striking (Loveridge 1947; Russell 1976; Gamble *et al.* 2012). In addition to the diversity of sub-digital pad structure, there appears to be a number of “solutions” with respect to other aspects of the manus and pes when it comes to obtaining an adhesive system (Russell 1976). One aspect of the adhesive system that appears to have many solutions relates to digit I (Russell 1976) because it typically has only two phalanges, thereby limiting the ability to hyperextend the digit. In fact, the hyperextension in digit I typically occurs between the first phalanx and the first metacarpal/metatarsal (Russell 1976). This constraint has, in some cases, resulted in the reduction and disuse of digit I altogether. One important exception is within the *Pachydactylus* radiation, in which hyperphalangy of digit I (resulting in three phalanges instead of two) has permitted the expansion of the sub-digital adhesive toepad. In addition, hyperextension in this radiation can include the distal two phalanges. This radiation is commonly found in African deserts and the ability to utilise digit I during locomotion might have contributed to their success.

Although typically thought of as an adaptation for climbing in arboreal habitats, perhaps driven by the focus on the arboreal tokay gecko (*Gekko gekko*), adhesion is also important for any climbing gecko (e. g., saxicolous) because it provides a “stickiness” via van-der-Waals interactions, which are weak intermolecular forces (Autumn *et al.* 2000). Vertical orientations seem to be common in rocky outcrops that are typically found in deserts; thus, the adhesive system of geckos might play a role in the ability to move up, down, and around rocks. This is supported by the fact that secondarily padless species (or those with reduced toe pads) in these same general habitats are terrestrial, have longer toes, and are faster (Johnson *et al.* 2005; Johnson & Russell 2009; Higham & Russell 2010; Collins *et al.* in press). Many of the species from the *Pachydactylus* radiation in Southern Africa often climb on rocks and those that do have well-developed adhesive systems.

In addition to adhesion, what selective advantage might exist for having a sub-digital adhesive system arranged how it is? As highlighted almost 40 years

ago, little attention has been paid to the spreading of the digits over 180° or more, which is often associated with well-developed toe pads (Russell 1976). It has been proposed that this arrangement of the toes facilitates moving in lateral as well as upward and downward directions on vertical surfaces (Russell 1975). This type of habitat is typified by vertical rock faces, which are often found in desert habitats. Future work should test this hypothesised advantage of the spreading of the digits in conjunction with adhesion, and the *Pachydactylus* radiation could be an ideal group in this context.

The adhesive system does a very effective job when it comes to clinging to smooth surfaces, but the ability to cling to rough surfaces depends on the microtopography of the habitat (Russell & Johnson 2007). As the habitat gets increasingly rugose, the importance of claws might also increase. Actively modulating both the adhesive system and the claws is one way to ensure full contact with a given surface. It is important to note that the adhesive system is only useful when an animal is on an inclined surface given that geckos do not deploy the adhesive system on a level surface (Russell & Higham 2009). Future work should examine the functional interactions between claws and the adhesive system in habitats that vary in rugosity.

Many species of gecko that occupy sandy desert habitats have secondarily lost the adhesive system or did not have it in the first place (Johnson *et al.* 2005). The *Pachydactylus* radiation found in Southern Africa offers an ideal group for studying the impacts of habitat structure on the morphology and function of the adhesive system (Russell 1976). In several of the genera, including *Chondrodactylus*, *Pachydactylus*, and *Rhoptropus*, there are examples of species that are terrestrial and exhibit reduced or lost adhesive systems (Johnson *et al.* 2005). The loss or reduction of adhesion in these cases might be due, in part, to the functional constraints that are imparted by the adhesive system. For example, the deployment and hyperextension of the system with each stride cycle slows locomotion (Russell & Higham 2009). Therefore, it is likely that selection favours a reduction in the system in species that no longer need to climb extensively (Collins *et al.* in press). Little is known regarding the adhesive system of other groups of desert-dwelling geckos in relation to locomotion and/or habitat despite the fact that they are very common in these habitats, including Peru (Dixon & Huey 1970; Huey 1979; Espinoza *et al.* 1990), Mexico (Grismer 2002), Egypt (El Din 2006), Israel (Espinoza *et al.* 1990), Namibia (Werner 1977), Australia (Kluge 1967; King & Rofe 1976; Pianka 1986; Bauer 1990), and the United States (Jones &

Lovich 2009), among others. A comprehensive analysis of the function of adhesive toe pads during locomotion in multiple desert lineages is needed to fully understand the importance in this type of habitat.

Interestingly, recent work suggests that adhesive toe pads have evolved independently 11 times and have been lost nine times (Gamble *et al.* 2012). Although the loss of adhesive toe pads is commonly associated with increased aridity, this is not necessarily the case for desert-dwelling geckos that occupy rocky habitats. Regardless, the impressive number of gains and reversions provides a rich framework for future investigations into the morphology and function of the adhesive system.

Paraphalangeal elements of geckos

Paraphalangeal elements are cartilaginous structures that are associated with interphalangeal joints. They appear to be quite diverse among geckos, occurring in a variety of locations along the phalanges. A main function of the paraphalangeal elements is likely to help control the adhesive toe pads when the penultimate phalanx cannot impart appropriate pressure on the scansors. In sand-dwelling species such as *P. rangei*, the distal phalanges are reduced and the paraphalanges occur only in the proximal areas of the foot (Russell & Bauer 1988). The paraphalangeal elements, in this case, appear to be associated with digging. The elements project laterally and are associated with the interparaphalangeal muscles. These muscles are also associated with the short flexor muscles of the digit, which might enable the webbing to be controlled during digging (Russell and Bauer 1988). This unique function of paraphalangeal elements in desert-dwelling geckos needs to be experimentally tested.

Zygodactyly

Chameleons are unique among lizards in that they exhibit the ability to grasp small branches with their feet (Peterson 1973, 1984; Higham & Jayne 2004; Higham & Anderson 2013). Effective and stable progression in arboreal habitats, where small branches can be far from the ground, is critical for maintaining stability (Peterson 1973; Cartmill 1985; Foster & Higham 2012). Chameleons accomplish this by having hands and feet in which the metacarpals and metatarsals are grouped into opposing bundles (Gasc 1963; Gans 1967; Peterson 1984; Losos *et al.* 1993; Russell & Bauer 2008). Although



Figure 3:
Images of lizards in their natural habitat to highlight the pedal specializations. A: *Chamaeleo namaquensis* perching on a rocky outcrop near Gobabeb, Namibia. Note the prehensile feet grasping to the rocky projections. B: *Sceloporus orcutti* on a rocky surface in California, USA. Note the claws gripping the surface of the rock. All photos taken by the author.

this pedal specialisation has been implicated in arboreal locomotion in non-desert habitats, desert-dwelling chameleons (*Chamaeleo namaquensis*) also exhibit prehensile feet. This might simply be a consequence of evolutionary history and might not enhance the ability to move in a sandy, desert habitat. In this case, one might expect other aspects of locomotor morphology (or function) to compensate for the prehensile limbs that have been retained. Interestingly, *C. namaquensis* can be found in the middle of a rocky outcrop where they might benefit from having prehensile feet and hands (Fig. 3; Herrel *et al.* 2013). Although not examined in this context, *C. namaquensis* likely exerts adduction forces on the rock projections, generating friction. Future work detailing how these prehensile appendages apply forces to rock surfaces (as compared to arboreal branches) is needed to determine if this species of chameleon utilises its locomotor system in a comparable way as other species of chameleon. In addition, determining whether other features of the locomotor system have been modified in desert-dwelling chameleons is also important.

How desert-dwelling lizards use their habitat

Although detailing the morphological specialisations among lizards is incredibly important, determining how these pedal specialisations are actually used in natural habitats is critical for understanding the functional ramifications of this phenotypic variation. Few studies have examined how desert-dwelling lizards use their habitat, although this type of habitat is ideal for such studies for three reasons. First, desert-dwelling lizards often use sand and desert habitats are often windy. Thus, tracks left from running lizards can be examined over a relatively short time period. The wind will then erase the footprints and another trackway can be analysed. Second, desert habitats are arid and often sunny, providing ideal conditions for viewing lizards as they move throughout their habitat. Third, few obstructions (other than rocks and small bushes) preclude the observations of moving lizards. This is unlike the cluttered habitat of a forest, which can make this process quite challenging.

A key question that has not been addressed in detail is whether species that occupy a general category of habitat (e. g., saxicolous) use their habitats in a similar way, even if the available habitat structure is disparate. For example, one saxicolous species might seek out vertical surfaces, whereas other species might prefer relatively horizontal surfaces. Alternatively, two species

that live in disparate rocky habitats might converge on their microhabitat use by seeking out comparable inclines and/or curvatures. Another source of variation is the type of rock that a saxicolous species prefers. Rocks vary considerably in their composition and topography depending on their source and the climate (Dolgoff 1996). This could have significant implications for the relationships between morphology, ecology, and function.

A recent study examined the microtopography of rock surfaces used by *Rhoptropus* cf. *biporosus*, a species of gecko found on sandstone outcrops in the Gai-As region of Namibia, and compared this to the form, configuration, compliance, and functional morphology of the setal fields (Russell & Johnson 2007). The rock samples analysed in this study were taken directly from the field and were those that were actually traversed during a run. Thus, the actual use of the habitat could be linked to habitat structure and morphology of the pes. The sandstone surfaces examined in this study exhibit comparable degrees of unpredictability with respect to the peaks and valleys (Russell & Johnson 2007). The main conclusion is that the actual surfaces available to the lizard result in only a small fraction of setae actually being able to adhere to the surface. This realistic assessment of locomotion and morphology diverges drastically from the smooth surfaces used in studies that typically examine adhesion in geckos (Irschick *et al.* 1996; Autumn *et al.* 2000). Although this study by Russell & Johnson (2007) examined ecologically relevant morphology, more information is needed regarding how lizards run in their habitat and what they might prefer/avoid.

Another recent study examined how a Namibian cursorial gecko, *Rhoptropus afer*, uses its habitat and how habitat availability and use differ between populations (Collins *et al.* in press). When escaping, *R. afer* generally avoided steep inclines and declines as well as heterogeneous substrates, thereby selecting escape routes that were not direct. Variation in the use of available habitat also varied among populations. For example, a population close to the coast in Namibia used substrates that were less inclined than what was generally available (Collins *et al.* in press). Whether this variation at the population level is replicated at an interspecific level is not understood at this point.

Two studies have quantified the locomotor activity of a dune-dwelling lizard (*Uma scoparia*) in its natural habitat (Jayne & Ellis 1998; Jayne & Irschick 2000). A goal of the study by Jayne & Irschick (2000) was to determine how frequently lizards run near their maximal speed. Surprisingly, the lizards often moved very fast during undisturbed locomotion. In addition, bipedal

locomotion was extremely rare ($< 0.5\%$ of all strides). The study by Jayne & Ellis (1998) examined the impacts and use of inclines on the escape behaviour of *U. scoparia*. Surprisingly, *U. scoparia* rarely used level surfaces, despite being considered a terrestrial lizard. In fact, normal escape behaviour included substantial movements up and down inclines (Jayne & Ellis 1998). Additionally, escaping lizards turned minimally, thus commonly moving in relatively straight paths. These types of studies are extremely rare, but yield incredibly important information. Desert-dwelling lizards are ideal for this type of research given that footprints are visible (and speed can often be determined from these footprints) and lizards can be viewed with relative ease. This is in contrast to forest-dwelling lizards, in which the habitat might obstruct the view of the lizard.

Future directions

The biomechanics of desert-dwelling lizards in the field need to be determined. This could include high-speed video of natural movements, but also comparisons of field movements and lab movements. Although locomotor speeds can be obtained under certain conditions without cameras (e. g., footprints left in the sand), the development of field-portable high-speed cameras can enable researchers to examine how natural habitat structure impacts three-dimensional limb movements. Indeed, several studies have utilised field-portable cameras to examine lizard locomotion (Bergmann & Irschick 2010; Higham & Russell 2010). However, we are lacking information about high-speed movements of lizards in their natural habitat.

In addition to high-speed video cameras, wireless accelerometers and gyros are permitting a high-resolution examination of natural animal movements (Hedrick *et al.* 2004). One issue is that desert-dwelling lizards are often small (a few grams), making these measurements difficult. However, technological advancements are likely to reach a stage where very small wireless chips (< 1 g) will be suitable for these small lizards. If these can record three-dimensional accelerations as a desert-dwelling lizard runs through its natural habitat, we can assess whether general habitat categories are linked to actual movements.

Although the variation within a pedal specialisation might not be telling in terms of predicting habitat structure or use, the broad-scale differences in pedal specialisations might predict a general habitat type. For example, toe

fringes are likely suitable for moving under, through, or on soft surfaces such as water or soft sand. By contrast, highly curved claws might be important for moving up rough surfaces such as rocks. Finally, a combination of adhesive toe pads and claws are likely important for desert-dwelling lizards that occupy a range of habitats, including both smooth and rough surfaces. Future work examining the evolution of pedal specialisations across all lizards will permit the identification of convergence in relation to ecology (Losos 2011). Evidence of the operation of natural selection is likely if certain specialisations are arising independently in comparable ecological conditions. At the same time, one must be cautious given that convergence in morphology does not always convey adaptation (for discussion, see Losos 2011).

Finally, a biomechanical understanding of pedal specialisations is lacking. What does it mean to have long claws and toe pads? What are the consequences of having paraphalangeal elements? How do neuromuscular control, neuromuscular anatomy, and muscle mechanics (force, strain, and velocity) change with respect to different pedal specialisations? How do propulsive mechanics and overall patterns of ground reaction forces change with respect to pedal specialisations? This is an exciting time in which we can build upon the excellent morphological work that has been done over the last 50 years and determine the mechanical and ecological ramifications of these pedal specialisations.

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