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Subdigital adhesive pad morphology varies in relation to structural habitat use in the Namib Day Gecko

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Summary

1. Morphological features that lead to increased locomotor performance, such as faster sprint speed, are thought to evolve in concert with habitat use. The latter depends on available habitat structure and how the animal moves within that habitat. Thus, this behavioural variation will impact how natural selection acts on locomotion and morphology.

2. Quantifying the interplay between escape behaviour and locomotor morphology across habitats that vary in structural composition could reveal how selection acts on locomotion at local levels. Substrate features, such as incline and topographical variation, are likely key drivers of morphological and functional disparity among terrestrial animals. We investigated the impact of habitat variation and escape behaviour on morphology, including the adhesive system, of *Rhoptropus afer,* a diurnal and cursorial gecko from Namibia. Substrate incline and topographical variation are likely important for this pad-bearing gecko due to the trade-off between adhering and sprinting (i.e. using adhesion results in decreased sprint speed).

3. We corroborate the hypothesis that the adhesive system exhibits the greatest degree of reduction in populations that utilize the flattest terrain during an escape. Our findings suggest that the adhesive apparatus is detrimental to rapid locomotion on relatively horizontal surfaces and may thus be counterproductive to the evasion of predators in such situations. A broad scale analysis of geckos would determine whether diversity of adhesive morphology is driven primarily by habitat use.

4. Phenotypic plasticity of the adhesive system and interspecific competition are plausible candidates for driving our results. However, it is unclear whether the differences we observed have a genetic basis. Future work should focus on how variation of the adhesive system impacts downstream locomotor components such as kinematics and mechanics and how the integration of these traits is related to habitat use.

Key-words: gecko adhesion, habitat, locomotion, performance, phenotypic plasticity, predator evasion

Introduction

Structural habitat complexity may influence the evolution of locomotor traits and performance in several ways. For example, animals must effectively negotiate numerous topographical features (e.g. inclines) that impact such properties as sprint speed. Natural selection should, therefore, act differentially on locomotor performance and result in morphological features that are particularly suited to increase performance relative to the physical challenges that are encountered (Arnold 1983; Schluter & McPhail 1992; Irschick & Losos 1998; Dickinson *et al.* 2000; Donohue *et al.* 2001; Calsbeek 2008). Such morphological changes are sources of functional diversity (e.g. sprinting performance under different physical constraints) and may lead to habitat partitioning and subsequent high rates of diversification (Wainwright 1991, 2007). However, behaviour can modulate what structures are employed during locomotion and how they are used. Thus, the physical constraints imposed by the habitat may be accommodated to some degree through modified behaviour, thereby altering the trajectory and intensity of morphological adaptation (Smith 1974; Moermond 1979; Kotler 1984; Main 1987; Cooper 1997a,b; Cooper & Wilson 2007). Although this may be so, few studies have teased apart the differential impacts of behaviour and morphology in relation to locomotion in terrestrial vertebrates. Quantifying these important, if

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subtle, impacts is likely critical for an enhanced understanding of how animals are adapted to the habitats that they occupy.

The interactions of behavioural modulation, habitat use and locomotor morphology may appropriately be observed through a comparison of terrestrial habitats that differ in the magnitude and frequency of inclined substrata (Irschick 2003). During upslope locomotion, for example, gravity resists forward progression, increasing the work required, for the animal to move away from a predator in the case of a predator-prey interaction (Taylor, Rowntree & Caldwell 1972; Preuschoft 1990; Farley & Emshwiller 1996; Roberts & Belliveau 2005; Biewener & Daley 2007). Running downslope requires energy absorption via eccentric muscular contraction and thus also increases the cost of locomotion relative to level running (Minetti *et al.* 2002). In this case, gravity acts to assist the animal in its forward progress, but may also lead to an increase in instability (Minetti *et al.* 2002; Gabaldón, Nelson & Roberts 2004; Biewener & Daley 2007). Experimental evidence indicates that lizards avoid steep declines during escape manoeuvers (Irschick & Losos 1999). However, small lizards potentially use inclines and declines in their escape from larger predators because the relative magnitude of dimensional changes in terrain, and the effects of upslope and downslope locomotion are size-dependent (Birn-Jeffery & Higham 2014). In other words, the locomotion of smaller animals is affected less than large animals when moving upslope or downslope. For example, Cooper & Wilson (2007) found that the relatively small Striped plateau lizard, *Sceloporus virgatus*, runs upslope for shorter distances than it does horizontally or downslope, suggesting that it uses inclines to its advantage. The manner in which such patterns change across habitats could reveal how selection acts, at a local level, on mechanistic links between escape trajectories and the morphological adaptations to the structural features used during the escape (Irschick 2003).

Anti-predator behaviour, escape behaviour and escape performance are dependent on substrate preference in multiple taxa (Jones, Mandelik & Dayan 2001; Collins *et al.* 2013; Des Roches *et al.* 2014). Although substrate–movement interactions are well known for many lizard taxa, little is known about such interactions in geckos, despite their affinity for specialized substrata (Carillo de Espinoza, Daniel Salas & Yehuda Werner 1990; Bauer & Russell 1991; Autumn & Peattie 2002; Autumn *et al.* 2006; Lamb & Bauer 2006; Russell & Johnson 2007; Johnson & Russell 2009), and the use of their highly specialized adhesive system on these. Interestingly, a study by Cooper & Whiting (2007) found that escape behaviour depends on habitat structure in *Rhoptropus boultoni,* a boulder-dwelling gecko equipped with an adhesive system. However, other studies of ancestrally padless geckos are inconclusive (Persaud, Werner & Werner 2003; Werner *et al.* 2004). Hence, characterizing the interplay between the evolution of the adhesive system and habitat use may reveal consequences of selection on escape behaviour, performance and morphology.

The gekkotan adhesive system, although having originated independently on multiple occasions within this cluster (Gamble *et al.* 2012), is considered to be an evolutionary innovation, permitting the exploitation of inclined and inverted surfaces (Russell 1975, 1979; Irschick *et al.* 1996; Johnson & Russell 2009). Adhesion occurs through a finely tuned, hierarchically arranged locomotor system culminating in adhesive toe pads (Russell 1975; Autumn & Peattie 2002). Toe pads are characterized by subdigital scansors that carry highly organized (Johnson & Russell 2009) fields of microfibrillar setae (10–100+ μm in length) that bear branched tips terminating in spatulae (0·2–0·4 μm wide) that create reversible bonds with the substratum. Adhesion is achieved by a combination of van der Waals forces and frictional loading associated with minute asperities of the locomotor surface (Autumn & Peattie 2002; Autumn *et al.* 2002; Tian *et al.* 2006; Johnson & Russell 2009). During locomotion, the setae are deployed through the unfurling of hyperextended digits subsequent to heel strike. To disengage adhesion, the digits are hyperextended. Engaging and disengaging setae is rapid (~ 20 ms), but this process occupies *c.* 12·7% of stance time (Russell & Higham 2009). Given that the deployment of the adhesive system takes time, there is a trade-off between adhering (used during climbing) and locomotor speed. In locomotion on horizontal surfaces, pad-bearing geckos routinely hold their digit tips (and thus their adhesive apparatus) in a permanently hyperextended configuration and thus employ only the bases of the digits for purchase and thrust application (Bauer, Russell & Powell 1996; Russell & Higham 2009). In cases where geckos have become increasingly terrestrial, selection has favoured the reduction or abandonment of the adhesive system (Bauer, Russell & Powell 1996; Gamble *et al.* 2012). Thus, to more fully understand the physical parameters of locomotion of pad-bearing geckos in relation to potential predator avoidance, it is important to understand the trade-offs that are evident between adhering to a surface and the employment of the fastest possible escape speed when running from a predator.

Despite the now well-understood phenomenon of adhesion in geckos, it is not currently known how the adhesive system differs between species and/or populations in response to habitat structure. Russell & Johnson (2013) found that the theoretical maximum adhesive capacity of all *Rhoptropus* geckos was tempered by the microtopographical roughness of the rock surfaces that they inhabited, with safety factors falling to within normally recognized biological ranges. Thus, all species of *Rhoptropus* are able to effectively exploit these habitat structures and no clear relationship was found between adhesive morphology and microtopography at the interspecific level, although it was recognized that *R. afer* exhibited reduced adhesive capacity relative to its body size.

Utilizing an intraspecific framework to understand how morphology and patterns of habitat use are related to the manner in which the adhesive system is adapted to habitat structure would be beneficial, due to the lack of phylogenetic history that must be accounted for in multiple species comparisons (Losos & Miles 1994), and would reduce the confounding effects of within-species variation that may obscure comparisons at the interspecific level. Additionally, any differences found among populations of a single species would likely be related to recent changes associated with habitat differences at the local level (Losos & Miles 1994; Herrel, Meyers & Vanhooydonck 2001; Kaliontzopoulou, Carretero & Llorente 2010). To approach the problem in this way, we chose *R. afer* (Fig. 1b,c) as our study species.

Rhoptropus afer (Peters 1869) is a member of the well-studied *Pachydactylus* radiation (FitzSimons 1943; Bauer 1999; Johnson, Russell & Bauer 2005) and is the most distinctive and derived member of its genus (all members of which are diurnal), in terms of both morphology and biology. It differs qualitatively from its congeners in its preference for horizontal sheet rock as a substrate (Bauer, Russell & Powell 1996). It is an accomplished cursor and may run, often for tens of metres, across relatively level terrain, before stopping (Odendaal 1979). Relative to its congeners, *R. afer* exhibits a reduction in the size of its adhesive apparatus and is characterized by elongation of the crus, metatarsals and proximal phalanges of the pedal digits (Higham & Russell 2010). During horizontal sprints, it runs with its adhesive pads hyperextended, with the ventral aspect of the metapodium and the proximal ends of the digits providing contact with the substratum and imparting locomotor thrust. For *Rhoptropus*, therefore, *R. afer* presents a situation for which habitat structure constitutes a compromise between a secondarily cursorial escape style, similar to that of other lizards, and the retention of a functional, albeit reduced, adhesive system (Johnson & Russell 2009).

We quantified the structural composition of the habitat, habitat use during escape, and morphology for four

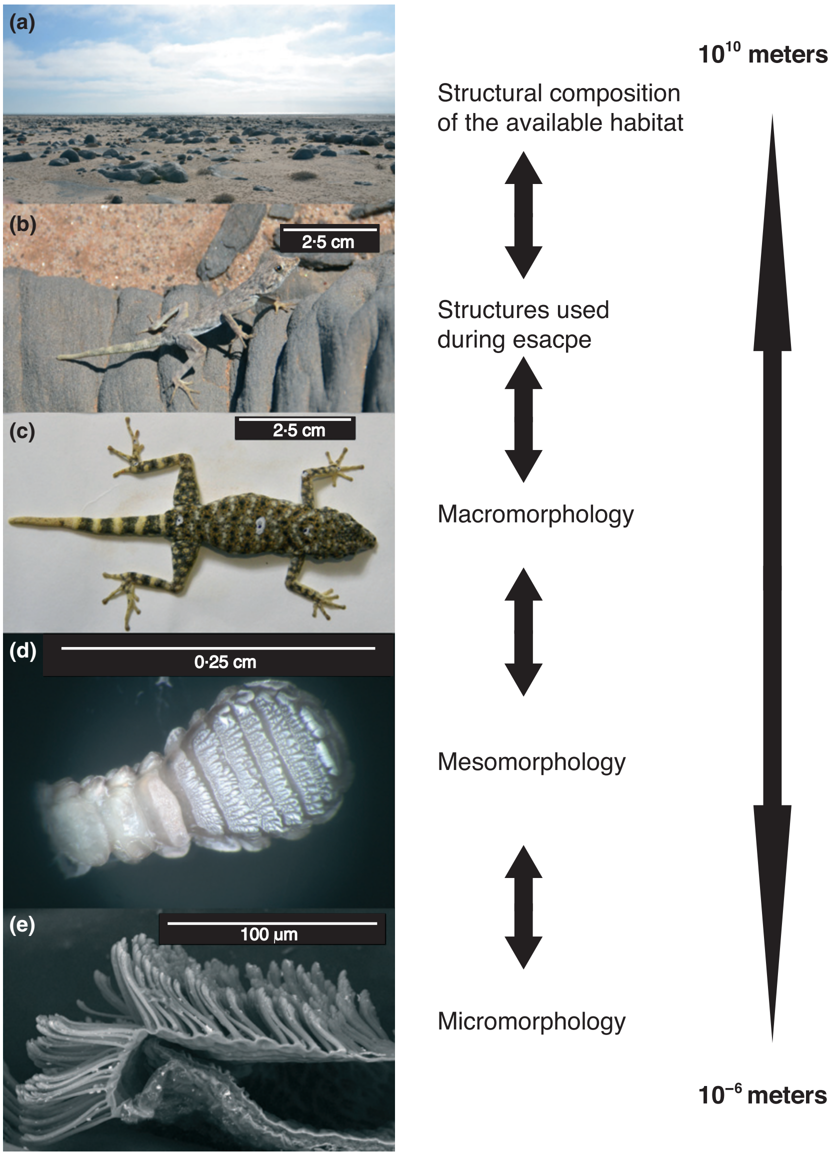

Fig. 1. The 8 orders of magnitude spanned by this study. From top: (a) structural composition of the available habitat, (b) structural composition of each locality that was used by an individual during an escape manoeuver, (c) gross locomotor morphology, (d) subdigital pad area and (e) setal morphology.

populations of *R. afer* that occupied habitats that appeared to differ in structure (Figs 1 and 2). If natural selection favours the reduction of the adhesive system in relatively flat habitats, where it would be counterproductive to locomotion, then geckos that use relatively flat terrain during predator evasion should have a relatively smaller adhesive system. We test the hypothesis that the adhesive system exhibits the greatest degree of reduction in populations that rely on the flattest terrain, and therefore escape trajectories, employed. Our study integrates the structural composition of the available habitat, the specific structural components of habitat used during escape, and morphology, providing a vehicle for exploring how morphology may respond to, and reflect, environmental demands (Fig. 1).

Materials and methods

We conducted our field study in November 2012 and May 2013 in the Namib-Naukluft and Dorob National Parks, and the Gobabeb Research and Training Centre in Namibia. *R. afer* is a small (3·15–5·2 cm, ±4 SE), diurnal, terrestrial gecko that occurs from (−20·900833°, 13·533611°) to (−23·557551°, 15·044396°) in the coastal range of Namibia (FitzSimons 1943).

STRUCTURAL COMPOSITION OF THE AVAILABLE HABITAT

We quantified the structural composition of the available habitat for each population ($n = 4$) by conducting 2 × 50 metre transects. We defined the structural composition of the available habitat as the structural composition of the locality that each population occupied. The beginning point of each transect was determined randomly and each 50-m transect was then directed north. For each transect, substrate type (rock outcrop, gravel or sand) and the incline of the substrate in degrees were determined. Each 50-m transect was subdivided into 10-m segments, demarcated at each end by a vertical indicator. A digital protractor (PRO 360 Digital Protractor™; Mitutoyo, Aurora, IL, USA) was levelled at the mid-point of each segment, and each 10-m segment was photographed (Pentax K-x DSLR; Ricoh Imaging Americas Corp, Denver, CO, USA or Nikon D7000 DSLR; Nikon Inc., Melville, NY, USA) from an orthogonal angle with the angle finder in the centre of the photograph and the camera lens parallel to the 10-m transect segment.

From the photographs, all inclines (±1°), and the linear distance of the segment occupied by that incline, were measured along the entire transect using IMAGEJ (version 1·46r) (Rasband 1997). The inclinations of the substrate were calibrated and measured in ImageJ using a straight line drawn across the top of the angle finder that represented the 0° horizon.

Two estimates of habitat variability were derived from the absolute values of inclines measured in each photograph: the number of changes >5° for each 10-metre segment and the difference in slope between each successive pair of inclines.

HABITAT USE: PREDATOR SIMULATIONS AND ESCAPE OBSERVATIONS

Habitat use was defined as the structural composition of each locality that was used by an individual during an escape manoeuver. For each focal locality, random transects were walked by two to three observers. We employed human-simulated predation because of our ability to observe the geckos during their escape movements and to retain consistency with previous studies (e.g. Cooper 1997a,b). Upon sighting an individual ($n = 10$ per population), predation events were simulated by one observer (CEC, APR, or TEH) facing the animal and walking directly towards it at a steady speed of *c*. 1 ms^{-1}. When the lizard began fleeing, the pursuer stopped and all observers watched it as it ran. This was repeated twice more for each individual in order to fully

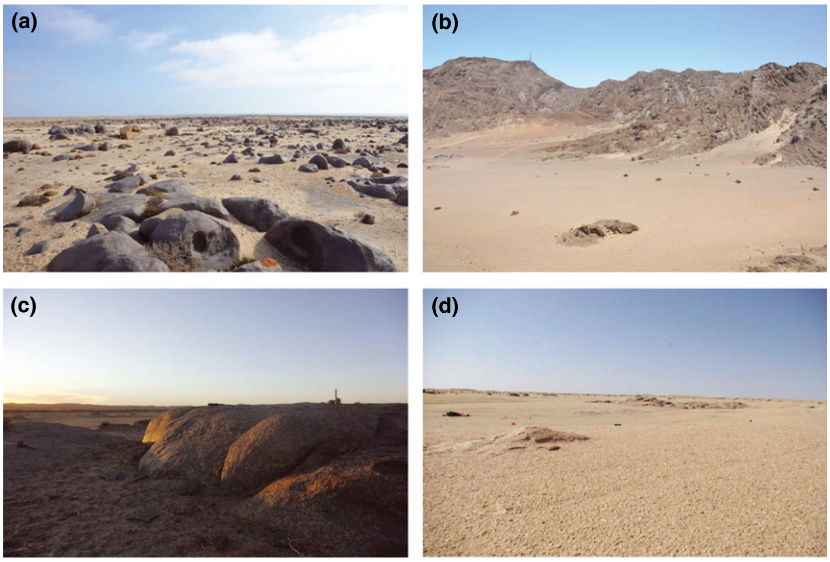

Fig. 2. Depictions of localities of *R. afer* examined in this study. (a) The Beach & Boulders locality is located on the Atlantic coast of Namibia and is characterized by sand and gravel with larger boulder outcrops strewn throughout. (b) The Granite Mountain habitat is located adjacent to Rössing Mountain and consists of large granite outcrops adjacent to sandy substrata, either as isolated patches (foreground) or as the lower reaches (midground) of more continuous granitic outcrops of greater elevation (background). (c) The Gravel Plains habitat is located east of the Gobabeb Research and Training Centre and consists of low-lying, but undulating gravelly substrata interspersed among low-elevation rock outcrops. (d) The Sheetrocks habitat located northeast of Dune 7 in the Namib-Naukluft Park consists of sandy substrate interspersed with low-lying sheetrock outcrops.

characterize the structural habitat features used by the geckos during escape. In many instances, the lizard in question ran from an exposed position and took refuge under a rock flake. If this happened, the rock flake was lifted and the distance and trajectory run by the lizard to its next stopping point was observed.

After each escape event, the same methods for measuring structural habitat for the transects (see above) were employed to quantify the features of the terrain used along the escape path. When possible, individuals that were observed in this way in the field were captured. Flagging tape was used to mark each original sighting location and its GPS coordinates recorded. This accomplished three tasks – it: (i) ensured that the same individual was not pursued twice, (ii) allowed us to bring the animals into a laboratory setting laboratory to measure morphology and (iii) allowed the individuals that were not used in further analyses to be released at their original locations.

MORPHOLOGICAL MEASUREMENTS

A subset of five individuals from each locality were euthanized, fixed in 10% neutral buffered formalin and preserved in 70% ethanol. These were transported to the University of California, Riverside, and the following standard morphological measurements recorded using digital calipers accurate to the nearest 0·01 mm: snout to vent length (SVL), intergirdle distance (from shoulder to hip), femur (from hip to knee) length, shank (from knee to ankle) length and pes length (from ankle to the tip of the longest toe).

The toe pad on the ventral side of the longest digit of the right or left pes was photographed using a Leica MA FlII SPOT Pursuit camera attached to Leica MZIII Pursuit Stereo Scope. From the resulting image, the total pad area was measured using ImageJ. As in other studies (Russell & Johnson 2007, 2013; Johnson & Russell 2009), the scansors (bearing setae) were included in the measurements of pad area, but the more proximal lamellae were not.

Subsequently, the tip of each digit for which pad area was recorded was removed and sectioned sagittally under a dissecting microscope. The two resulting sections, with their cut face uppermost, were affixed using double stick, electrically conductive carbon tape, to a stub that was secured into the custom tilt stage of a Hitachi TM-1000 Tabletop Scanning Electron Microscope (in the Institute for Integrative Genome Biology at UCR) and viewed at a 90° angle. Each complete section and each scansor were photographed, saved and opened in ImageJ, from which the following measurements were taken: setal length, setal diameter and setal density. Setal length was measured along the midline of each seta from its base to its tip. Setal diameter was measured at a height of *c.* 5–15 μm from its base. Setal density was calculated by first counting the number of setae along a 32 μm length of each scansor, squaring this number and then multiplying by 1000 to obtain a setal density per mm^2 (Russell & Johnson 2007, 2013; Johnson & Russell 2009).

STATISTICAL ANALYSIS

A series of discriminant function analyses (DFA) were used to characterize the relationships between structural habitat composition and habitat use during escape and to explore differences among the localities in escape and behaviour. First, the variables for structural habitat composition were entered into a DFA, with each locality serving as an independent variable. Secondly, the structural habitat composition variables from each locality were pooled and compared to the habitat structures used during escape by entering all variables into a DFA with ‘availability’ and ‘use’ set as independent variables. Thirdly, a DFA was used to explore the differences among populations in habitat use patterns during escape. Then, a DFA was used to characterize and describe the differences among populations in the suite of morphological traits measured for each individual. Because all but one of the morphological variables measured were predicted by body size ($P < 0{\cdot}05$), prior to analysis, they were regressed against SVL, and the residuals were used as size-free morphological components in subsequent analyses. Wilks’ Lamda, relative eigenvalues, and the misclassification rate were used to determine the power of each DFA to discriminate between the indicated independent variables. We interpreted the canonical loadings by comparing the positive and negative values to the raw data for each locality.

Post hoc comparisons were made for the strongest DFA independent variables to elucidate the differences among populations, as follows: *t*-tests between the percentage of upslope vs. downslope escapes; a one-way analysis of variance (ANOVA) on the percentage of habitat exhibiting a pitch of >10° for each population; a one-way ANOVA on the first set of canonical axis scores derived from the morphological DFA; finally, a two-way ANOVA on the size-corrected raw morphological data that were most informative in separating the groups in the DFA. All statistical analysis was conducted using JMP® (Version 10 for Mac. SAS Institute Inc., Cary, NC, USA, 1989–2007).

Results

Our initial observation that the four localities varied in incline and steepness was verified by examining plots of the percentage of habitat with a pitch of >10° available within each locality *vs.* that which was used during escape (Fig. 3). A *t*-test indicated that lizards constituting the Beach & Boulders population (Fig. 2a), but no others, used 10° inclines significantly less than would be expected relative to their availability ($P < 0{\cdot}05$) (Fig. 3).

DIFFERENCES BETWEEN STRUCTURAL HABITAT COMPOSITION AND HABITAT USE

The DFA successfully distinguished between the habitat structures used during escape and the availability of habitat structures as measured in transects. The habitat variables that best distinguished between use and availability data for each locality were differences between successive inclines and the percentage of distance with a pitch >10° incline (Table 1). The overall misclassification rate was *c.* 22%. For each locality, *R. afer* consistently used substrates during escapes that traced flatter and less heterogeneous courses than would be predicted from the average lie of the terrain.

DIFFERENCES AMONG LOCALITIES IN HABITAT STRUCTURAL COMPOSITION AND HABITAT USE

The DFA for the structural habitat composition of each locality revealed differences in the structural composition of available habitat at each locality. The features that best distinguished among habitats along canonical axis one were the percentage of habitat pitched at >10° incline, habitat variability and the rockiness of each habitat (Table 2, Fig. 4a). The second canonical function accounted for

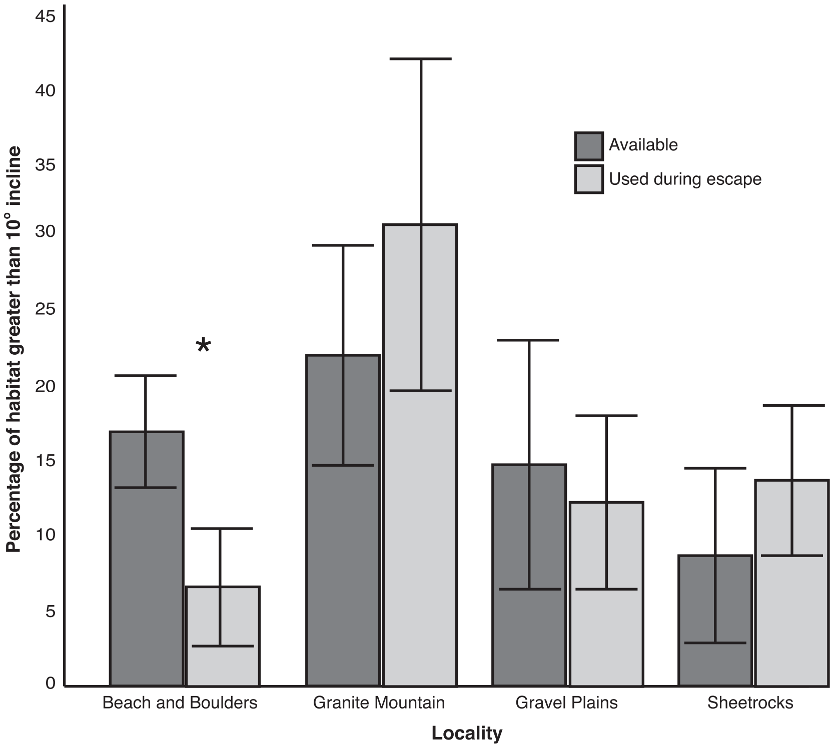

Fig. 3. Bar graph representing the percentage of habitat with a pitch of >10° supports the initial observation that the each locality varied in its structural habitat composition. An asterisk indicates a significant difference between the structural composition of available habitat and habitat use (*t*-test, $P < 0{\cdot}05$). The *R. afer* at the Beach & Boulders locality used significantly fewer 10° inclines relative to the terrain available to it compared to *R. afer* examined at other localities.

Table 1. Summary of discriminant function analyses of structural habitat features used during escape and available at each locality. Standardized canonical coefficients >0·8 are boldfaced

Canonical axis	Eigenvalue	%	Total	Approx. *F* =	*P*-values	>10	Max incline	Avg. difference	Max difference
1	0·46	100	100	6·48	0·0001	**0·86**	−0·48	**1·64**	**−0·71**

Table 2. Summary of discriminant function analyses of structural habitat features available by locality. Standardized canonical coefficients >0·8 are boldfaced

Canonical axis	Eigen value	%	Total	Approx. *F* =	*P*-values	>10	Max incline	Avg. difference	Max difference	%rock
1	1·84	80	80	3·22	0·0001	**0·92**	0·39	**−1·76**	**1·47**	**1·45**
2	0·45	19	99	1·36	0·22	0·02	**1·18**	**−1·77**	**1·35**	−0·41
3	0·01	1	100	0·12	0·97	−0·19	−0·41	2·03	−0·88	−0·04

19% of the data, and the most powerful variables were habitat variability and maximum incline (Table 2, Fig. 4a). The structural composition of the Granite Mountain (Fig. 2b) locality exhibited the rockiest, most variable, and most inclined structural habitat composition relative to the other three localities ($P < 0{\cdot}001$) (Table 2, Fig. 4a). The Beach & Boulders (Fig. 2a) locality exhibited relatively horizontal and less variable substrates ($P < 0{\cdot}001$) (Table 2, Fig. 4a). The Gravel Plain (Fig. 2c) locality was misclassified as Sheetrock (Fig. 2d) at a rate of *c.* 50%, thus we infer that these two localities were similar in their structural composition (Fig. 4a).

The structural habitat features used during escape varied among localities. A DFA on habitat use successfully classified *R. afer* populations at a rate of 68%. The first canonical axis accounts for 74% of the variation between localities and the most powerful predictors were the percentage of habitat pitched at >10° incline, and the percentage of habitat composed of rock outcrops (Table 3, Fig. 4b). Canonical axis two accounts for 24% of the variation between localities, with the most powerful predictors

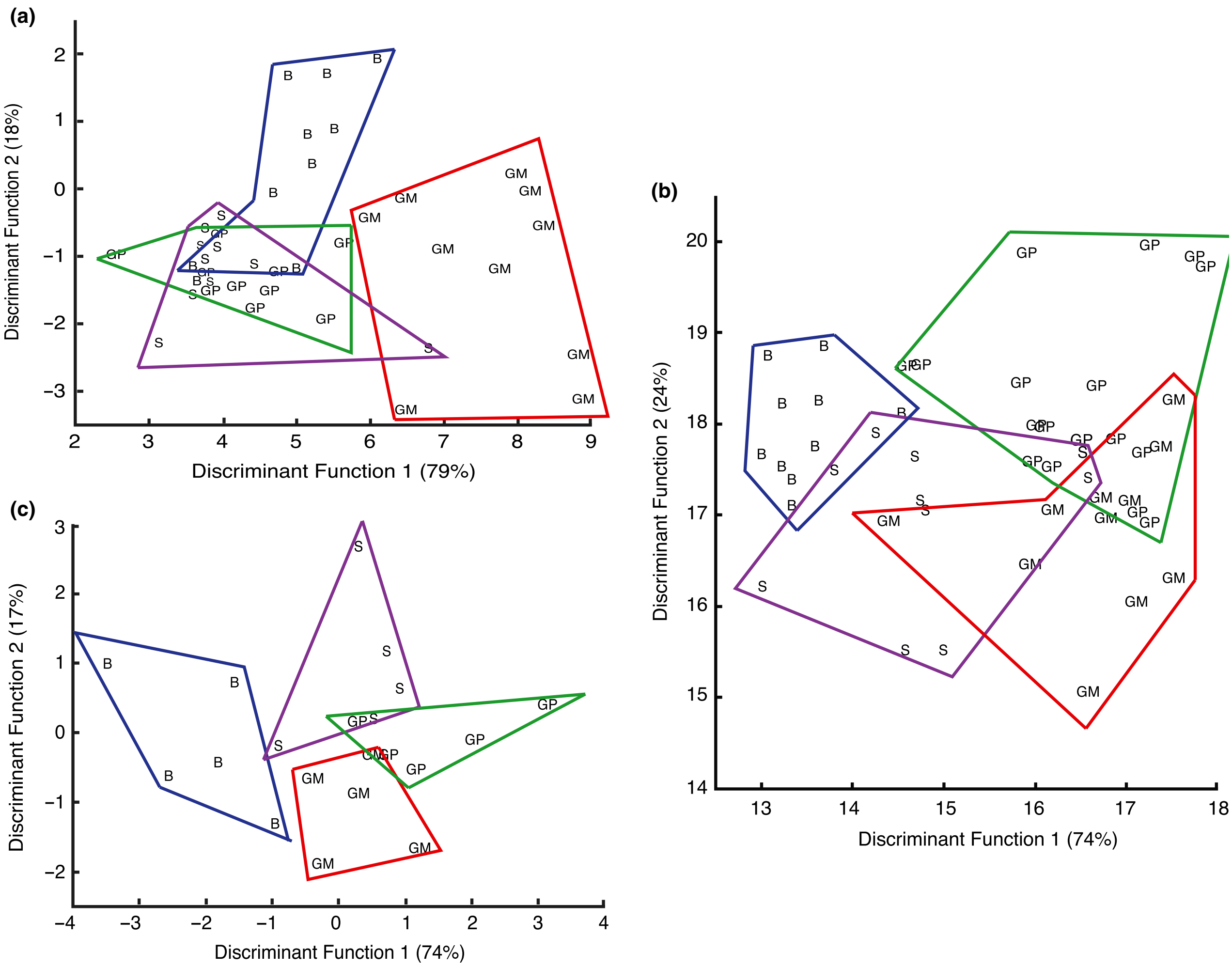

Fig. 4. (a) Discriminant function plot of scores from transects through each locality indicating differences among populations in the structural habitat features available. Positive loadings on canonical axis one describe rockier, more inclined substrata and large differences between successive incline changes. Positive loadings on canonical axis two describe more inclined substrata and large differences between successive incline changes. (b) Discriminant function plot of scores from the habitat structures used during escape by each population of *R. afer*. Positive loadings on canonical axis one describe rockier and more inclined substrata. Positive loadings on canonical axis two describe more horizontal habitats. (c) Discriminant function plot of scores from morphological measurements indicate separation among populations in two directions. Positive loadings on canonical axis one indicate greater toe-pad area and longer pes. There were no loadings equal to or >0·80 on canonical axis two but the strongest, seta length, indicated that positive loadings on canonical axis two described longer setae. Abbreviations: B – Beach & Boulders; GP – Gravel Plains; GM – Granite Mountains; S – Sheetrocks.

Table 3. Summary of discriminant function analyses of habitat used during escape by locality. Standardized canonical coefficients >0·8 are boldfaced in the far right column

Canonical axis	Eigen value	%	Total	Approx. *F* =	*P* > *F*	>10	Max incline	Max rise	AvgDiff prev	MaxDiff prev	%rock
1	1·70	75	75	2·48	0·0021	**2·83**	0·19	0·05	−0·32	0·20	**1·00**
2	0·55	24	99	1·24	0·28	**3·03**	0·23	0·48	0·37	0·43	−0·07
3	0·03	1	100	0·19	0·96	2·69	−0·54	0·49	0·65	−0·38	0·18

being the percentage of habitat pitched at >10° incline, and habitat variability (Table 3, Fig. 4b). *R. afer* at the Beach & Boulders locality were subject to the least misclassification – only one individual was misclassified from this locality, whereas 2–7 individuals were misclassified from other habitats.

A *t*-test revealed that at the Granite Mountain locality, the majority of *R. afer* escapes occurred on upslope substrates, rather than downslope or level ones ($P < 0{\cdot}01$). Additionally, the percentage of escapes at this locality pitched at greater than a 10° incline was greater than would be predicted based upon the average availability of

Table 4. Summary of discriminant function analyses of morphology. Standardized canonical coefficients >0·8 are boldfaced in the appropriate column

Canonical axis	Eigen value	%	Total	Approx. F =	*P*-values	Pad area	Intergirdle	Femur	Shank	Foot	Setae length	Setal width
1	1·85	74	74	1·05	0·44	**0·80**	−0·57	0·68	−0·74	**1·16**	−0·60	−0·22
2	0·44	17	91	0·60	0·81	0·45	0·24	−0·33	0·58	−0·22	0·61	0·23
3	0·22	9	100	0·54	0·74	−0·78	0·31	0·21	0·63	0·02	−0·12	0·36

Table 5. Summary of one-way ANOVA on size-corrected toe-pad area (left) including and Tukey–Kramer multiple post hoc comparisons (right). Localities connected by the same letter are not significantly different. Mean and standard error (SE) reported for each locality

Source	DF	SS	MS	*F*	*P*-value	Locality	SE	Mean	Letters report
Model	3	0·68	0·23	6·3		Beaches & Boulder	0·08	−0·31	A
Error	16	0·57	0·03			Sheetrocks	0·08	0·08	B
Total	19	1·28			0·0050	Granite Mtn	0·10	0·10	B
						Gravel Plains	0·07	0·07	B

habitat pitched at greater than a 10° incline, although this was not statistically significant. For all other localities, there were no statistical differences between upslope vs. downslope escape trajectories.

MORPHOLOGY

The DFA for the morphological measurements revealed no significant differences (Wilks' Lambda, $P = 0{\cdot}4$). However, a 25% misclassification rate indicated that this DFA, although not statistically significant, performed moderately well and indicated important distinctions between each population (Fig. 4c). Canonical axis one accounted for 74% of the variation among populations and discriminated among groups, with the strongest coefficients being for pad area and foot length. Canonical axis two accounted for 19% of the variation among populations and most strongly discriminated among populations for maximum seta length and shank length (Table 4, Fig. 4c). The Beach & Boulders population was not misclassified, yet all of the other populations exhibited at least one misclassification.

Because trends in morphological differentiation were evident in the DFA, a two-way ANOVA with Tukey–Kramer post hoc tests on size-corrected subdigital pad area ($P < 0{\cdot}02$) and pes length ($P = 0{\cdot}06$) was used to clarify the differences among populations. The Beach & Boulders population exhibited smaller toe pads relative to the other three populations (Table 5, Fig. 5).

Discussion

Adhesion is an evolutionary innovation that enables some geckos to exploit a variety of substrata, including inverted surfaces, that are not generally accessible to other tetrapods (Ruibal & Ernst 1965; Autumn *et al.* 2006; Russell & Johnson 2007, 2013). Our findings suggest that the deployment of the adhesive apparatus is inefficient for locomotion on relatively horizontal surfaces and may thus be counterproductive to the evasion of predators in such situations. The geckos in our study used habitat topography in non-random ways when assessed against availability among and within each locality. In escape sprints, *R. afer* avoided steep inclines and declines and also heterogeneous substrates, thus selecting escape routes that were circuitous rather than direct. Avoiding steep inclines was the principal mode of differentiation between structural composition of the available habitat and escape trajectory in the Beach & Boulders population. *R. afer* in this locality also exhibited reduction of the area and structure of the adhesive toe pads beyond that which typifies the species as a whole (Johnson & Russell 2009) and relative to the patterns shown by conspecifics at the other locations examined in this study. Thus, our study directly associates variation in morphology with variation in the habitat structures used during escape, something not previously observed for geckos. Our study also reinforces the idea that information about morphological variation should be combined with escape behaviour to understand the ways in which species are adapted to local habitat structures (Vitt *et al.* 1997; Herrel, Meyers & Vanhooydonck 2001; Kaliontzopoulou, Carretero & Llorente 2010).

Effectively evading predators often includes accelerating and sprinting at high velocities (Arnold 1983; Zehr & Sale 1994; Irschick & Losos 1998; Miles 2004; Dayton *et al.* 2005; Husak 2006; Calsbeek & Irschick 2007). Greater velocity is achieved through increasing stride length, increasing stride frequency or a combination of both. Relative to its congeners, *R. afer* exhibits much longer hindlimbs and toes, and these have evolved in concert with a cursorial lifestyle (Higham & Russell 2010). Hence, greater stride length is achieved through morphological modification (Johnson, Russell & Bauer 2005; Higham & Russell 2010). Increasing stride frequency is complex and involves

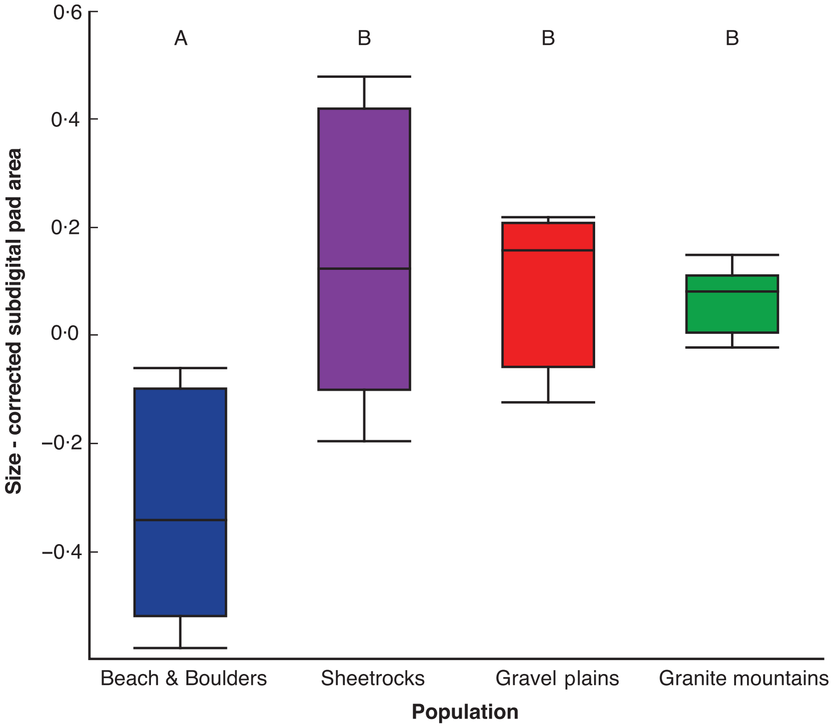

Fig. 5. Box & whiskers plot showing the morphological differences between populations of *R. afer*. The Beach & Boulders population exhibited significantly smaller subdigital pad area than the other three populations ($P = 0{\cdot}005$). Localities connected by the same letter are not significantly different.

many integrated suites of physiological and morphological traits, such as greater muscle contraction rates and mass reduction in distal limb elements (Biewener 1989; Fieler & Jayne 1998; McElroy & Reilly 2009). Stride frequency in pad-bearing geckos is further limited by the time it takes to deploy and detach the adhesive system (Autumn *et al.* 2006; Russell & Higham 2009). Deployment of the adhesive system is triggered at inclines of about 10° (Russell & Higham 2009), and it is not recruited on horizontal surfaces. This is important because sprint speed becomes limited on inclined surfaces above 10^{o} as a result of the time taken to insert the attachment and detachment phases of adhesion into the step cycle. This response is reflexive and is seemingly controlled by feedback from the vestibular system (Russell & Higham 2009). Furthermore, the relative (and absolute) size of the adhesive apparatus will influence the absolute amount of time taken to engage and disengage setae during the step cycle, thereby increasing stride frequency through morphological modification. Thus, we suggest that the adhesive apparatus of geckos is both morphologically and behaviourally phenotypically plastic and that it is responsive to the demands of habitat topography and heterogeneity encountered during escape. We have shown that this is the case for localized populations within the confines of a single species. However, common garden experiments are necessary to rule out genetic differences as opposed to phenotypic plasticity between populations.

The adhesive apparatus is reduced via subdigital pad area reduction where flatter escape trajectories are used. In addition to reducing the time taken for setal attachment and detachment, reduced subdigital pad area is also advantageous in this context because it allows for more toe area to be dedicated to generating friction during escape (Russell & Bels 2001; Russell & Higham 2009). Because longer digits confer sprint speed and stability advantages, exhibiting a reduced adhesive system would allow the *R. afer* from the Beaches & Boulder site to use a longer toe to increase its running speed while carrying less of the digit in a hyperextended state (Russell & Bels 2001; Russell & Higham 2009). The proximal components of the pedal digits are relatively elongated in *R. afer* (Bauer, Russell & Powell 1996), demonstrating that there is a trade-off between proximal and distal digit length associated with the reduction of the adhesive system in this taxon. Future work detailing the mechanics of locomotion will reveal whether this advantage leads to more effective force transmission.

The sizes and shapes of gecko toe pads and setae vary tremendously between species, and this variation is tenuously linked to the occupancy of different structural habitats (Russell 1975, 1979; Carillo de Espinoza, Daniel Salas & Yehuda Werner 1990; Bauer & Russell 1991; Autumn & Peattie 2002; Harmon & Gibson 2006; Lamb & Bauer 2006; Gamble *et al.* 2008, 2011; Johnson & Russell 2009; Sistrom *et al.* 2012). It is possible that the differences in subdigital pad area in *R. afer* represent intraspecific adaptive phenotypic plasticity because *R. afer* sprints away from potential predators (FitzSimons 1943;

Johnson & Russell 2009; Higham & Russell 2010). Hence, relaxation of the physical constrains requiring adhesion and avoidance of inclines of >10°, that would trigger its deployment, may lead to further reduction of the size of the adhesive apparatus through the decrease of subdigital toe-pad area. This suggests that the reduction of adhesive capacity, long considered a key innovation, may be beneficial for the enhancement of cursoriality in geckos.

Competition is an important driver of habitat partitioning, structural niche realization, and speciation (Schluter 1994, 2001; Stamps, Losos & Andrews 1997). *Anolis* lizards in the Caribbean likely radiated to occupy their ecomorphological niches as a result of increased competition typical of insular ecosystems (Losos 1990, 1992; Irschick *et al.* 1997; Beuttell & Losos 1999; Glor *et al.* 2004). In cases in which phenotypic plasticity is evident, character displacement may occur as a result of competitive exclusion. Given a three-dimensional structural habitat available to a population (species A), a competitor (species B) that occupies an exclusive part of this habitat would relegate species A to a smaller realized niche (Schluter 1994, 2001). *R. afer* is syntopic with the closely related *R. bradfieldi* at the Beach & Boulders locality and may compete with it. *Rhoprtopus bradfieldi* exclusively occupies the large boulders, which are the principal sources of inclination at this locality. Although the ecological mechanics of the potential competition between these two species is unknown, it may have been a causal factor in driving the more horizontal escape trajectories used by *R. afer*. If this is the case, then competition may have provided the impetus for the adaptive phenotypic plasticity observed in the adhesive system. In other localities included in this study, *R. afer* is the only diurnal gecko present.

Despite the possession of reduced toe-pad size in the Beach & Boulders population of *R. afer*, the carriage of the digits in a hyperextended posture during horizontal sprinting imposes a physical disadvantage – reduced traction through a lessened area of contact. Epidermal spinules just proximal to the seta-bearing scanors on the subdigital pads of *R. afer* may enhance friction (Russell 2002; Russell, Johnson & Delannoy 2007) on level surfaces, while the digits are carried in hyperextension (Russell 2002). Because *Rhoptropus* is characterized as being pad-bearing but clawless, it is likely that the epidermal spinules enhance frictional interactions with the substratum during level locomotion (Lamb & Bauer 2001; Johnson, Russell & Bauer 2005; Johnson & Russell 2009). The relatively elongated proximal portions of the pedal digits in *R. afer* would provide for increased area for frictional interactions. Future experiments should characterize the role of the spinules and setae in ground-dwelling geckos (Khannoon *et al.* 2014), as well as internal morphological features such as tendon and muscular patterns that may enhance or constrain context – dependent performance (Abdala *et al.* 2009).

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Data accessibility

Data deposited in the Dryad repository: http://doi.org/10·5061/dryad.r20tr. (Collins, Russell & Higham 2015).

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