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REVIEW

Whole-organism studies of adhesion in pad-bearing lizards: creative evolutionary solutions to functional problems

**Duncan J. Irschick · Anthony Herrel ·
Bieke Vanhooydonck**

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Abstract Understanding the evolution of complex functional traits is a challenge for evolutionary physiology. Here we investigate the evolution of subdigital toepads in lizards, which have arisen independently at least three times, although with subtle anatomical differences. Some designs (anole, gecko) appear functionally equivalent, whereas other designs (skink) are inferior. The functional equivalence of geckos and anoles highlights the creative aspect of the evolutionary process in that these two groups have arrived at the same functional endpoint along very different trajectories. However, this functional equivalence does not result in equivalence for performance at whole-organism tasks (e.g., running uphill), as the evolution of behavior (e.g., toe-furling) has enabled geckos to be superior climbers than anoles. We also show that adaptive increases in the toepad size within a closely related lizard genus (*Anolis*) has resulted in concomitant evolution of enhanced clinging ability and increased perch heights. A third insight is that pad-bearing geckos are capable of carrying tremendous loads (up to 250% of body weight) up smooth surfaces, and that the toepad itself does not appear limiting. This comparative and whole-organism approach to lizard toepads underscores how organisms can evolve multiple solutions to evolutionary problems.

Keywords Evolution · Toepad · Adhesion · Lizard · Performance

Introduction

Over the past 20 years, physiologists have become increasingly aware of the importance of examining functional traits from the perspective of the whole-organism (Huey and Bennett 1987; Bennett and Huey 1990; Lauder 1990; Wainwright 1994; Irschick and Garland 2001). Obviously, certain aspects of any complex physiological system (e.g., respiration in mammals) must be examined by first considering the constituent parts in detail. However, several syntheses have stressed that living organisms often exhibit emergent behaviors and functional abilities that might not be predictable from the constituent parts alone (Pough 1989; Irschick and Garland 2001). Examples of this phenomenon abound; dolphins routinely stay under the water for longer periods of time than predicted by biophysical models because they adopt an intermittent swimming style that conserves energy (Williams et al. 1999). Many jumping animals can produce far more mechanical power than predicted based on studies of single muscle fibers because of their ability to store elastic energy in tendons (e.g., see Aerts 1998). This lesson is especially important when considering complex functional abilities such as climbing, swimming, or vocalization, because animals often exhibit behaviors that can alter the predicted relationship between morphology and performance ability (Lauder and Reilly 1996; Garland and Losos 1994; Irschick 2003).

The ability of animals to adhere to surfaces offers an excellent opportunity to understand how a complex

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D. J. Irschick (✉)
Department of Ecology and Evolutionary Biology,
Tulane University, 310 Dinwiddie Hall,
New Orleans, LA, 70118, USA
e-mail: Irschick@tulane.edu

A. Herrel · B. Vanhooydonck
Department of Biology, University of Antwerp,
Universiteitsplein 1, 2610 Antwerpen, Belgium

functional trait can be examined from both reductionist and whole-organism approaches. Several vertebrate and invertebrate groups have evolved structures for adhering to surfaces that are used for climbing, mating, capturing prey, or for some other function (Ruibal and Ernst 1965; Williams and Peterson 1982; Dai et al. 2002; Arzt et al. 2003). Within lizards, three groups have independently evolved the ability to adhere to surfaces by means of specialized hair-like projections, or setae, on expanded portions (toepads) of their toes (Ruibal and Ernst 1965; Ernst and Ruibal 1967; Peterson and Williams 1981; Williams and Peterson 1982; Bauer and Good 1986; Bauer and Russell 1988; Losos 1990a; Irschick et al. 1996; Autumn et al. 2000, 2002). The toepads of these different lizard groups differ in setal density, size, and shape (Williams and Peterson 1982). For example, anoles have highly dense, unbranched setae whereas geckos have less dense, multi-branched setae (Williams and Peterson 1982). The most spectacular example of the adaptive value of toepads are geckos, which can climb smooth surfaces with agility, even with very large loads equaling at least 200% of their body weight (Irschick et al. 2002, 2003). This remarkable ability has been examined for pad-bearing lizards in terms of morphology, behavior, and function at both whole-organism (Irschick et al. 1996; Elstrott and Irschick 2004; Bloch and Irschick 2005; Vanhooydonck et al. 2005), and reductionist (Autumn et al. 2000, 2002) levels. Here, our goal is to highlight whole-organism studies of clinging ability in pad-bearing lizards and show how such studies can shed light on the evolution of the lizard toepad and clinging ability.

We integrate findings from several previously published studies of whole-organism clinging in lizards to address several primary questions: First, has the independent evolution of toepad structures resulted in functionally equivalent phenotypes? Second, how has clinging performance evolved, and has it co-evolved with key morphological aspects of shape and habitat use? Third, which factors limit the ability of pad-bearing lizards to climb? Finally, we also consider several recent mechanistic studies that shed light on the ability of pad-bearing lizards to climb. We integrate findings addressing these above issues to understand how the complex morphological toepad structure may have evolved to facilitate climbing.

Has the independent evolution of toepad structures resulted in functionally equivalent phenotypes?

A persistent debate within both the physiological and evolutionary communities is the degree to which convergent structures are functionally equivalent (Schluter and Ricklefs 1993; Losos and Miles 1994 and references therein; Leal et al. 2002). In some cases, the answer would appear to be clearly not, as for example, in the case of flying in bats, birds, and insects, which fly in very different ways. However, such gross macroevolutionary comparisons are of limited value because such dramatically different groups may use their structures in very different ways. Indeed, comparisons within more closely related groups may be more informative because one can measure similar performance abilities for each phenotype. However, such comparative data are rare, and therefore the idea of functional equivalence remains largely untested.

The evolution of subdigital toepads in arboreal lizards offers an excellent possibility for addressing this idea because grossly similar, but nevertheless anatomically different, structures have evolved independently within geckos, anoles, and a small clade of skinks (Ruibal and Ernst 1965; Hiller 1976a, b; Williams and Peterson 1982; Irschick et al. 1996). These toepads are used for a similar function within each group (climbing), and species in all three groups share many similarities in body size (typically less than 20 g, with the exception of a few very large gecko species that reach body masses of over 50 g) and habitat use (highly arboreal). Thus, one can reasonably compare how each of these groups cling for understanding whether these convergent phenotypes are functionally equivalent.

Irschick et al. (1996) measured the clinging abilities of 14 species of pad-bearing lizards by including representatives of all three groups (four anole species, six gecko species, and four skink species, Fig. 1). Clinging ability in these lizards is easily measured by means of a force platform with a smooth substrate (an acetate sheet) that enables an accurate measure of clinging force independent of the effects of the claws (Irschick et al. 1996; Elstrott and Irschick 2004). Briefly, individual lizards are induced to place their two front feet on the acetate sheet that is in turn attached to a force platform. Each lizard is repeatedly dragged at a constant speed (i.e., lizards were not jerked) of approximately 5 cm/s, until a consistent measure of clinging force (N) is obtained for each individual.

An evolutionary analysis of how toepad area, clinging ability, and body mass change with size in these fourteen species reveals several points: First, all three groups (geckos, anoles, and skinks) fall on the same allometric line comparing toepad area versus body mass, indicating that the three groups share approximately similar toepad areas per unit body size (Fig. 2, Irschick et al. 1996, see this publication for details). We note that evolutionary analyses (independent con-

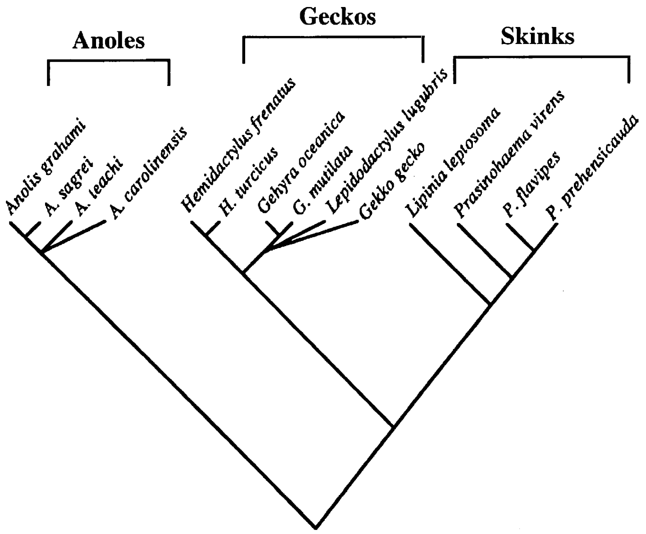

Fig. 1 Phylogenetic relationships among 14 gecko, anole, and skink species. Taken from Irschick et al. (1996)

trasts, see Felsenstein 1985) are crucial in this case, because values from the species in Fig. 1 are not statistically independent. The same analysis of clinging ability suggests that the evolutionary transition from geckos to skinks resulted in a concomitant reduction in clinging performance (Fig. 2). The most relevant measure of comparable clinging force among these groups is the ratio of clinging ability divided by toepad area (N/mm^2). This measure takes into account variation in body size because both the numerator and denominator increase with body size. Furthermore, this variable has intrinsic ecological relevance to the animal, and to the hypothesis of functional equivalence, because it describes how much force is produced per unit toepad area. While such ratios are controversial, recent reviews (Smith 1999) show that they are appropriate as long as one does not plot ratios against one another. Figure 3 shows a bar chart of mean ratios of clinging force per unit toepad area for the three groups. A phylogenetically-corrected ANOVA (conducted in the computer program PDAP using the phylogeny in Fig. 1, 1,000 simulations, see Garland et al. 1993 for details) shows a significant difference in the three groups, with anoles and geckos showing similar force/toepad area ratios, and skinks being substantially poorer clingers (one-way ANOVA, $P < 0.05$). A phylogenetic ANOVA conducts a standard ANOVA by taking the phylogenetic relationships of the study species into account (Garland et al. 1993). Accordingly, this above result suggests that the toepad designs of geckos and anoles are largely functionally equivalent, but that the toepad design of pad-bearing skinks is clearly inferior.

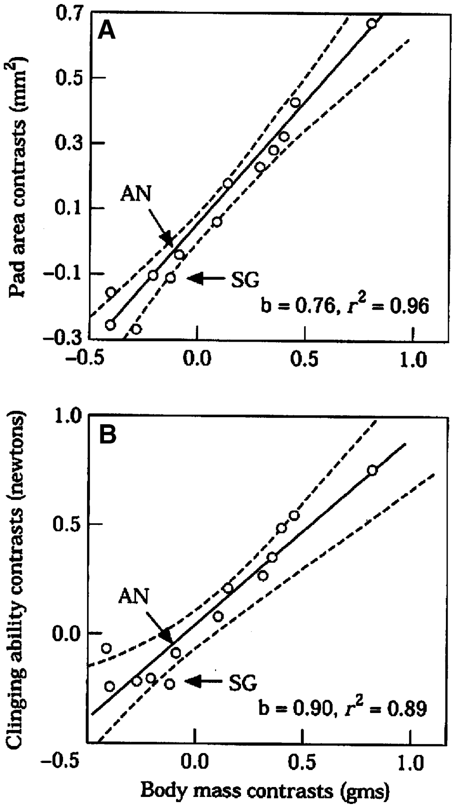

Fig. 2 Scatterplots of independent contrasts of body mass (x-axis) versus toepad area (y-axis, **a**), and clinging ability (y-axis, **b**) for the 14 pad-bearing lizard species shown in Fig. 1. Independent contrasts represent units of evolutionary change that are independent of the confounding effects of phylogeny (see Felsenstein 1985 for calculations). *SG* represents the evolutionary transition between geckos and skinks, whereas *AN* represents the evolutionary transition between anoles and the ancestor of all other lizards. Note that for clinging ability (**b**), skinks have evolved an usually low clinging ability per unit body mass. Taken from Irschick et al. (1996)

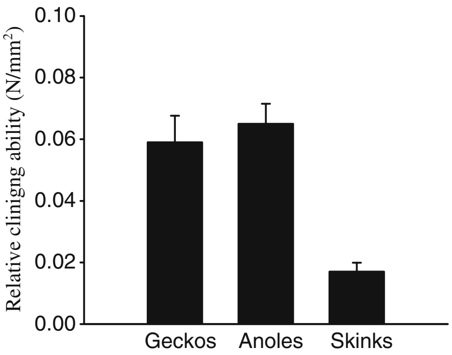

Fig. 3 Mean ratios (+ 1 SE) of clinging ability (N) divided by toepad area (mm^2) for a sample of 14 gecko, anole, and skink species shown in Fig. 1 (data taken from Irschick et al. 1996). Note that the ratios are similar for geckos and anoles, but much lower for skinks, indicating that while the two former groups are equivalent clingers, the toepads of skinks are inferior

Two factors are key in explaining the differences in relative clinging ability among pad-bearing lizard groups. First, morphological differences among groups in toepad design may be important. Several trends emerge from Williams and Peterson (1982), who provided detailed SEM photographs and morphological measurements for representative geckos, anoles, and skinks. First, geckos possess relatively large and multi-branched setae, whereas anoles possess relatively small unbranched setae. Interestingly, anoles appear to compensate for this difference by exhibiting a substantially higher density of setae overall, resulting in approximately similar total areas of attachment via setae (Williams and Peterson 1982). This represents a clear example of how two groups can arise at the same functional endpoint via evolution of distinct morphological designs. By comparison, the setae of the representative skink species is thicker than those of anoles, and also single-stalked, yet still much smaller than for geckos. The total available areas of attachment for this skink are accordingly much lower than for anoles and geckos (Williams and Peterson 1982), which may explain the difference in relative clinging force (Fig. 3).

A second factor is behavior. The fact that geckos and anoles apparently exhibit similar maximum clinging capacities on a smooth force platform (Fig. 3), yet differ dramatically in their ability to climb smooth vertical and overhanging surfaces in nature suggests that functional considerations alone are insufficient. Indeed, the force plate design is not intended to measure the clinging ability of pad-bearing lizards under normal locomotor conditions, but is designed to remove the effects of such behaviors, and measure clinging ability in a standardized fashion. One behavior unique to geckos that could play a role in enhancing adhesion on smooth surfaces is their habit of curling and uncurling their toepads, which apparently facilitates rapid toepad placement and removal. Anoles do not exhibit this behavior (Russell and Bels 2001, and although no data are available for skinks, casual observations suggest that they also do not curl their toepads (D. Irschick, personal observation). Therefore, although the force platform clinging data suggest that the gecko toepad is not necessarily superior per se, emergent behaviors at the level of the whole organism may enable geckos to be much more proficient climbers than anoles. A final consideration is the effects of the relatively poor clinging abilities of skinks on their microhabitat use. Little is known of the ecology of skinks with setal structures, but casual observations indicate that they can climb trees proficiently (Brown and Fehlman 1958; Austin and Jessing 1994; Austin 1995). Indeed, like many arboreal lizards that do not possess toepads (e.g., *Sceloporus* lizards), the use of claws appears to overcome non-existing, or poor toepad designs, again underscoring how multiple morphological evolutionary "solutions" can enable different animal groups to occupy the same arboreal niche.

How has clinging ability co-evolved with toepad shape and habitat use in pad-bearing lizards?

Comparative approaches in evolutionary biology have provided a unique window into understanding the adaptive process. If interspecific variation in morphology, performance, and habitat use are evolutionarily correlated, then this is at least partial evidence for adaptation via the mechanism of natural selection (Baum and Larson 1991). Caribbean *Anolis* lizards offer an excellent opportunity for addressing this issue in regards to toepad morphology and clinging ability, because different anole species exhibit distinct preferences for different perch heights, which can range from being largely terrestrial, to perches more than 3 m high in the forest canopy (Williams 1983; Losos 1990b; Irschick et al. 1997; Losos et al. 1998). More broadly, within each of the Greater Antillean islands of Jamaica, Puerto Rico, Hispaniola, and Cuba, *Anolis* lizards have independently evolved into a series of "ecomorphs", which occupy distinct microhabitats (reviewed in Williams 1983; Losos 1994; Roughgarden 1995). For example, trunk-ground anoles typically occur close to the ground and on broad surfaces, such as on tree trunks or logs, whereas trunk-crown anoles usually occur much higher in the canopy, and on somewhat narrower surfaces. Thus, studying the evolution of toepad area and clinging ability could shed light on the adaptive diversification of *Anolis* species because of the dimensions along which anole species partition their habitat use.

Elstrott and Irschick (2004) examined how toepad area, clinging ability, and habitat use (perch height) co-evolved in 12 species of Caribbean anoles. This group is composed of six ecomorphs (trunk-ground, trunk-crown, twig, crown-giant, trunk, and grass-bush), several of which have evolved multiple times. Thus, this group is ideal for phylogenetic comparisons because of the large number of independent evolutionary events, which provides high levels of statistical power. Elstrott and Irschick (2004) tested two primary predictions: (1) Relative clinging ability and relative toepad area should be correlated evolutionarily. In other words, anole species with large size-adjusted clinging capacities should possess large size-adjusted toepads. (2) Perch height should be correlated evolutionarily with relative clinging ability. In other words, anole species that perch high in the canopy (either on an absolute scale, or relative to their size) should have relatively greater clinging abilities compared to species that perch low in the canopy. In all of the below comparisons that deal with "size-adjusted" values, we are specifically referring to residuals of the relevant variable (e.g., clinging ability) based on regressions with body mass (see Elstrott and Irschick 2004 for details).

The comparative data confirm these two predictions. As predicted, *Anolis* lizard species with relatively larger (i.e., adjusted for size) toepads exhibit relatively greater clinging abilities (Fig. 4). Thus, relative clinging ability appears to be a direct consequence of relative toepad area. *Anolis* species that perch high in the canopy (either on an absolute scale, or relative to body size) have relatively larger toepads and clinging capacities compared to species that perch relatively low in the canopy. Taken together, these data provide indirect comparative evidence that the evolution of increased toepad size in some anole species is adaptive, by facilitating the occupation of perches high in the canopy. As a caveat, many anole and gecko species possess prominent claws that also play an important role in climbing, particularly on rough surfaces (see e.g., Zani 2000, 2001), and hence future studies that integrate (and preferably isolate) the effects of toepads and claws on adhesion would be welcome.

Limiting factors on vertical climbing

Geckos are renowned for their ability to run uphill (or upside down), even on smooth vertical surfaces. At a broad level, locomotion in pad-bearing lizards on such smooth vertical and overhanging surfaces is influenced by both the ability of toepads to adhere, and the properties of the underlying properties of limb muscles. A key goal has been to understand the relative roles of these two characteristics in determining the ability of pad-bearing lizards to climb on such smooth surfaces.

Loading studies with pad-bearing lizards are ideal for testing the factors that limit locomotion because, relative to unloaded locomotion, moving with loads increases the amount of work expended to move a given distance for a given speed, and therefore must increase total power output. Further, many organisms in nature move with large loads, such as when females carry large eggs (Vitt and Congdon 1978; Bauwens and Thoen 1981), or when animals eat large meals (Garland and Arnold 1983). Therefore, studying how loading affects locomotor performance is ecologically important (see Aerts 1990; Vanhooydonck and Van Damme 1999).

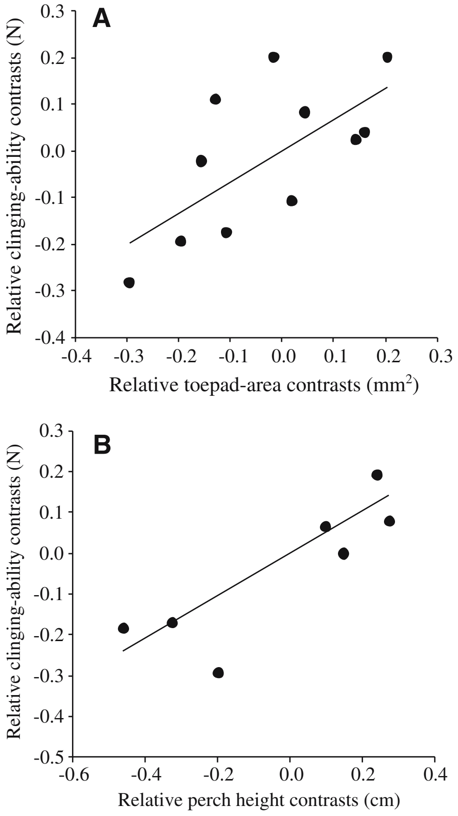

Fig. 4 Scatterplots of independent contrasts for a group of anole species showing **a** a positive evolutionary relationship between relative clinging ability and relative toepad area, and **b** a positive evolutionary relationship between relative clinging ability and relative perch height. Therefore, anole species that have relatively larger toepads tend to be both relatively better clingers, and also tend to perch relatively high in the forest. Because the axes in units of independent contrasts, and for different sets of individuals, the axes do not match. Further, the number of independent contrasts differs between the two plots because the ecological analysis (**b**) represents eight species (for which habitat data were available), whereas the analysis comparing relative clinging ability versus relative toepad area (**a**) examined 12 species. Taken from Elstrott and Irschick (2004)

Irschick et al. (2003) induced two gecko species of greatly differing size [a small gecko, *Hemidactylus garnoti* (2–4 g), a large gecko, *Gekko gecko* (30–60 g)] to run vertically on a smooth substrate with varying loads (unloaded to 200% body weight). Two key results are apparent from this study. First, both gecko species are capable of carrying extremely large loads up smooth vertical surfaces; the small gecko was capable of carrying loads up to 200% body weight, with a few individuals even carrying 250% body weight, whereas the large gecko species could reliably carry loads up to 100% of body weight. Second, power output showed a general pattern of increase from running with no loads to running with a very large load (200% body weight for *H. garnoti*), but after this initial increase, power output reaches a plateau quickly, resulting is similar power outputs for moving with a 100, 150, and 200% body weight load (Fig. 5). This finding strongly suggests that power output limits vertical loaded locomotion in these geckos (Irschick et al. 2003).

Do toepads limit the ability of these geckos to climb uphill with loads? Answering this question is challenging because locomotion is a dynamic process, and applying estimates of adhesion, either from single setae (Autumn et al. 2000, 2002), or from whole organisms (Irschick et al. 1996). One unresolved issue is exactly how much force a gecko can produce in a dynamic locomotor situation. When dragged across a force platform under steady-state conditions, Irschick et al. (1996) found estimates of clinging about 10× lower than studies of single setae (e.g., *G. gecko*, Autumn et al. 2000). The disparity between these measures may result from the likelihood that all setae will adhere simultaneously, even during conditions of maximal adhesion. Certainly, based on the higher estimates of Autumn et al. (2000), clinging ability clearly cannot limit the ability of geckos to climb with loads. Determining whether clinging ability limits load-carrying ability based on the estimates of Irschick et al. (1996) is difficult because these force plate studies were conducted under steady-state conditions, whereas geckos clearly run dynamically when moving uphill. More data on the exact adhesive forces of gecko toepads during uphill climbing with loads is clearly needed to resolve this issue.

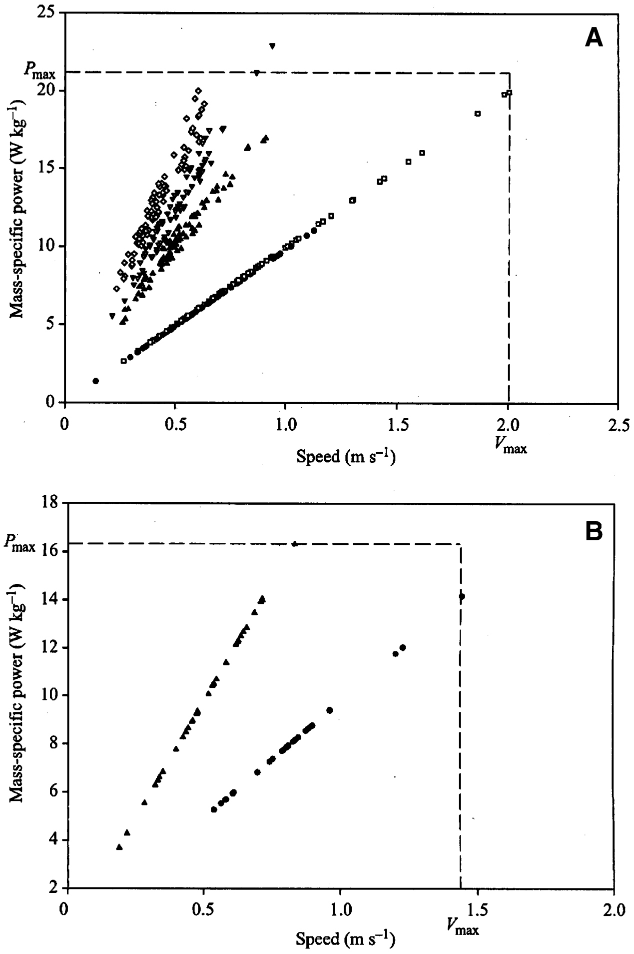

Fig. 5 The relationship between power output (y-axis) and locomotor speed (x-axis) for an **a** small species of gecko (*Hemidactylus garnoti*), and **b** a large species of gecko (*G. gecko*). For **a** *filled circles* unloaded, *open squares* 2% body mass (*BM*), *filled triangles* 100% BM, *grey inverted triangles* 150% BM, *grey diamonds* 200% BM. For panel **b** *filled circles* unloaded, *filled triangles* 100% BM. For both species, most of the loading conditions tend to level off near P_{max} (Maximum power output), supporting the hypothesis that mass-specific power output limits speed. Taken from Irschick et al. (2003)

One relevant question is why the gecko species discussed here, and pad-bearing lizards in general, have so much more clinging capacity (especially based on force estimates from single setae) than they need for everyday activities. Vanhooydonck et al. (2005) showed that acceleration capacity is greatly affected by substrate structure in the gecko *H. garnoti*: geckos can accelerate more rapidly on smooth surfaces as compared to more irregular surfaces (i.e. wood or cloth). This substrate effect potentially occurs because on the smooth surface, more surface area is available for attachment by setae, whereas on rough surfaces, there is less available surface area due to the presence of ‘gaps’ on which setae likely cannot adhere. However, in nature, the majority of surfaces geckos will encounter are likely to have an irregular microstructure. Consequently, geckos may frequently occupy surfaces on which only a small fraction of the total number of setae can effectively adhere. Thus, possessing overbuilt toepads may provide an additional ‘safety factor’ during movement on particularly challenging surfaces (Vanhooydonck et al. 2005).

Mechanistic insights into adhesion

Two recent studies may shed light on some of the mechanistic factors underlying the evolution of toepad function in pad-bearing lizards. Bloch and Irschick (2005) examined the influence of toe-clipping on the clinging ability of a pad-bearing *Anolis* lizard (*A. carolinensis*). Toe-clipping is a commonly-used, and permanent marking technique for small lizards in which the claw is removed (usually by using scissors or nail-clippers) (see Dodd 1993; Dunham et al. 1994). Bloch and Irschick (2005) found that removal of only two claws (one per each forefoot) dramatically diminished (40%)

clinging ability on a smooth surface, whereas removal of four claws on the forefeet (two claws/foot) resulted in a 60% decline in clinging ability. The implications of these data for the ecology of pad-bearing lizards are profound. Ecological studies show that toe loss in lizards is common (e.g., Hudson 1996), due to either fights with conspecifics, or confrontations with predators, and these clinging data indicate that loss of even a few toes can dramatically diminish overall clinging capacity. This study might also explain why pad-bearing lizards possess far more clinging capacity than they need for everyday activities; while a gecko with a full set of toes might seem to have excessive clinging ability, if that same lizard were to lose just two toes, its clinging ability would be dramatically diminished. The reason for the decline in clinging ability is not obvious, but likely relates to the severing of a tendon that lies at the juncture between the toepad and the base of the claw, which apparently dramatically reduces toepad function (A. Russell, personal communication).

A second study (Bergmann and Irschick 2005) examined the effect of varying temperature on the whole-organism clinging capacities of a diurnal gecko (*Phelsuma dubia*). Previous work (Losos 1990a) found that clinging ability (based on the angle of slippage on a smooth glass surface) was temperature dependent in the gecko *G. gecko*, with maximum values occurring at relatively low temperatures (17°C). In *P. dubia*, by contrast, temperature exerted no significant effect on maximum clinging ability when lizards were pulled across a force platform (Bergmann and Irschick 2005). Given the similarity of the setal morphology of *G. gecko* and *P. dubia*, the contrast between these results may result from the method of measuring clinging ability; under "submaximal" conditions (Losos 1990), temperature influences clinging ability, compared to "maximum" conditions, in which the setal system appears temperature independent (Bergmann and Irschick 2005). This difference implies that muscular control may be relevant for subtle adjustment of the toepad during submaximal conditions, but unimportant for maximal conditions. Indeed, the findings of Bergmann and Irschick (2005) stands largely in agreement with recent work emphasizing the dominant role of Van der Waals forces in determining clinging ability (Autumn et al. 2000, 2002).

Synthesis

The evolution of complex functional traits has proved an enduring problem for evolutionary physiology. Our primary thesis in this paper is that whole-organism studies can provide insight into the evolution of complex functional traits, such as the toepads of lizards. Some surprising insights from the discussed whole-organism studies include: not all toepad designs are functionally equivalent. Some designs (anole, gecko) appear approximately equivalent, whereas other designs (skink) are inferior. The functional equivalence of geckos and anoles highlights the creative aspect of the evolutionary process in that these two groups have arrived at the same functional endpoint along very different trajectories. However, this functional equivalence does not result in equivalence for performance at whole-organism tasks, such as climbing vertical smooth surfaces, as the evolution of behavior (e.g., toe-curling and uncurling) has enabled geckos to be superior climbers than anoles. A second insight is that evolutionary diversification in toepad shape appears correlated with diversification in clinging ability and habitat use in a closely related group of pad-bearing lizards. Therefore, evolutionary diversity in toepad shape and structure affects habitat use at both broader (e.g., independent evolution of setae among lizard families) and finer macroevolutionary (e.g., within a single lizard genus) levels, and thus holds tremendous explanatory power for understanding how species invade new habitats. A third insight is that pad-bearing geckos are capable of carrying tremendous loads (up to 200% of body weight) up smooth surfaces, and that the toepad itself does not appear limiting. Studies of both acceleration on different substrates, and also toe-clipping suggest that excess clinging capacity may have evolved both because of the potential for toe loss or damage, and/or the need to move on substrates of varying textures.

New and exciting vistas remain for the study of adhesion in lizards and other organisms (e.g., invertebrates). Most glaringly, no studies have linked microevolutionary variation in toepad shape among individuals with variation in clinging ability and fitness. Such a study might bear fruit, as some work (Hecht 1952) shows that selection favors large numbers of lamellae (scales composing the lizard toepad) in *Aristelliger* geckos. Because of the strong link between relative toepad area and relative lamellae number among anole species (Macrini et al. 2003), one might therefore predict a positive relationship between relative lamellae number and clinging ability in *Aristelliger*, as well as in other pad-bearing lizards. If such a correlation exists, one could examine the relationship between lamellae number and fitness within lizard populations. Most obviously, more research is needed to understand the mechanism of clinging in lizards at the whole-organism level. Studies of the mechanics of single setae (Autumn et al. 2000, 2002; Dai et al. 2002; Arzt et al. 2003) have shed considerable light on the underlying mechanism of adhesion, but we lack equivalent data for clinging at the whole-organism level. Although some studies have shown that clinging in one species of diurnal gecko is temperature independent (Bergmann and Irschick 2005), qualitative observations of clinging in anoles suggests that they can slowly increase clinging force, suggesting a sequential recruitment of muscle fibers used to press the toepad onto the surface. If true, this would also suggest that clinging is not a passive all-or-none response, and may be analogous to the subtle hand motions of humans attempting to apply gradual force to a musical instrument. Prior detailed research has already been conducted on the anatomy of the toepad and associated limb structures (e.g., Russell 1975, 1979; Bauer and Good 1986; Russell and Bauer 1989), and therefore, studies that link anatomy and muscle function (e.g., EMG, sonomicrometery) during clinging would be useful for testing this possibility.

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