

# Effects of substrate structure on speed and acceleration capacity in climbing geckos

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We studied the effects of substrate structure on locomotor performance in a climbing gecko, *Hemidactylus garnoti*. We quantified three performance traits (acceleration capacity, instantaneous speed, and final speed) on three substrates: (i) smooth wood, (ii) a cloth surface, and (iii) a wire mesh. While acceleration capacity and instantaneous speed were highest on the wooden surface, final speed did not differ significantly among substrates. Using scanning electron microscopy (SEM) pictures, we estimated that 98% of the wooden surface is available for adhesion by the setae on the toepads, while this percentage is much lower for the mesh and cloth (41 and 37%, respectively). We suggest that when a gecko climbs up a gap-filled substrate, such as the wire mesh or cloth, adhesion will only happen between part of the toepad and the substrate, resulting in a diminished acceleration capacity. The higher acceleration capacity on the wooden substrate and the fact that the geckos tend to slip less often on this particular surface, may explain the difference in instantaneous speed. As for final speed, geckos might achieve similar final speeds on all three substrates by employing different locomotor strategies. Our results suggest that microhabitat use in nature might have a profound effect on locomotor performance and survival for climbing lizards such as geckos. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, 85, 385–393.

ADDITIONAL KEYWORDS: clinging surfaces – habitat use – *Hemidactylus* – locomotion – performance – toepads.

## INTRODUCTION

The ability of animals to move on a wide array of substrates may be critically important for various ecological tasks, such as escaping from predators, thermoregulation, or finding mates. Examples of the above phenomena are numerous; for instance, squirrels often move on both rough tree surfaces and the ground to find food, and ectotherms, such as lizards, often shift microhabitats depending on environmental temperatures (e.g. Castilla & Bauwens, 1991; Melville & Schulte, 2001). Consequently, biologists have studied the effects of several aspects of structural environmental variation on locomotor performance. For

instance, several authors have compared locomotion on horizontal vs. inclined or vertical surfaces (e.g. Huey & Hertz, 1982; Irschick & Jayne, 1998; Jayne & Irschick, 1999; Vanhooydonck & Van Damme, 2001; Zaaf *et al.*, 2001; Claussen *et al.*, 2002), or on surfaces of different widths (e.g. Losos & Sinervo, 1989; Sinervo & Losos, 1991; Losos & Irschick, 1996; Macrini & Irschick, 1998). The effects of more subtle substrate qualities on locomotor performance have also been quantified, but to a lesser extent. For instance, maximum speed is influenced by substrate firmness in turtles (Claussen *et al.*, 2002), crabs (Herreid & Full, 1986), and humans (Kerdok *et al.*, 2002), while substrate roughness and texture affect clinging performance in beetles (Stork, 1980; Dai, Gorb & Schwarz, 2002) and lizards (Zani, 2000). Except for these few examples, however, little is known about how, at a fine-grained level, substrate structure affects locomotor performance.

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Here, we test how substrate structure affects locomotor capacity in climbing geckos. We use climbing animals because we expect that the effects of substrate structure on vertical locomotor performance will be profound, as animals must generate substantial force when moving against gravity. In particular, we chose to work with *Hemidactylus garnoti*, because geckos are exceptional in their ability to move up vertical surfaces of varying textures. Geckos create adhesive force by means of their microscopic setae (i.e. keratinous hair-like structures on their toepads), which adhere to the substrate surface. Geckos have been the subject of many studies examining the functional properties of their toepads and the mechanism of adhesion (Ruibal & Ernst, 1965; Hiller, 1968; Maderson, 1970; Russell, 1975, 1986; Autumn *et al.*, 2000, 2002; and references therein). From an ecological perspective, *H. garnoti* is an appropriate study organism because this species uses a variety of different substrates in its natural habitat. *Hemidactylus garnoti* is documented as occurring on the walls of buildings, on trees, and on rocky outcrops (Manthey & Grossmann, 1997). Thus, understanding how substrate structure affects locomotor performance may shed light on patterns of habitat use in these lizards.

We examined locomotor performance on three structurally different substrates (wood, metal wire mesh and cloth). We first measured how speed and acceleration differed among these different substrates. Next, in an attempt to understand why substrate structure affects locomotor performance, we quantified the underlying microstructure of these three materials. We accomplished this second goal by estimating the amount of surface area available for adhesion by the toepads of these geckos, using scanning electron microscopy (SEM; see Methods for a detailed description). Using this technique, we show that these surfaces differ in the frequency of 'gaps' or empty spaces, where no attachment between the setae and the surface likely can occur. However, our method did not assume any model of setal adhesion (e.g. Van der Waals' forces, interlocking), and only assumed that intimate contact between the surface and the setae – as required by all adhesive mechanisms – is necessary for generating force. Because locomotor performance in geckos should be affected at least partly by the amount of adhesive force generated by the toepads, we predicted that speed and acceleration would be higher on surfaces with more attachment area available for the setae. Because geckos also use claws to climb, we did not necessarily expect a 1 : 1 relationship between available surface area for attachment by setae and locomotor performance; nevertheless, we generally expected locomotor performance to be diminished on surfaces with smaller available surface area for setal adhesion.

We chose speed and acceleration as measures of performance for several reasons. First, locomotor speed has been widely studied in a variety of organisms, and is ecologically relevant for animals in a variety of circumstances (Garland & Losos, 1994; Irschick & Garland, 2001). We also quantified acceleration because the ability of animals to effectively capture prey or elude predators may depend largely upon the initial burst of acceleration (Huey & Hertz, 1982). Moreover, the ability of geckos to climb vertical surfaces depends on how much force the gecko is able to generate between its feet and the substrate. Thus, we asked the following specific questions: (1) do wood, cloth, and metal mesh differ in the amount of surface area available for contact with gecko setae?; and (2) do geckos exhibit higher speed and acceleration on surfaces with a greater amount of surface area available for contact with gecko setae?

## MATERIAL AND METHODS

### ANIMALS

We obtained seven adult *H. garnoti* individuals (average mass  $\pm$  SE =  $2.68 \pm 0.13$  g; *H. garnoti* is a unisexual species) from the pet trade (Glades Herp, Inc.). The lizards were housed in pairs or alone in plastic cages (15 cm  $\times$  25 cm  $\times$  20 cm) in a temperature-controlled room ( $29 \pm 2$  °C) illuminated 12 h a day. The geckos were fed live crickets, dusted with calcium and vitamins, three times a week and they were watered once daily. Only non-gravid individuals were used in the test trials.

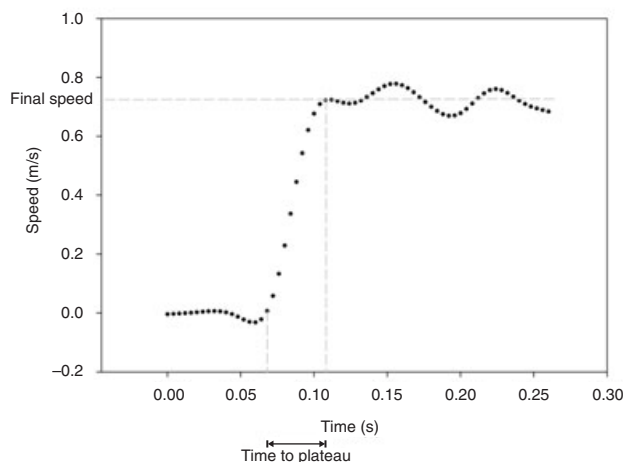
### LOCOMOTION TRIALS

In order to obtain measurements of speed and acceleration, we filmed the geckos with a high speed video camera (Redlake Motionscope PCI camera) at 250 fps while running up a custom-built racetrack placed at an angle of 90°, starting from a standstill. The racetrack consisted of a wooden base (13 cm wide, 150 cm long), to which different surfaces could be attached, with plexiglass walls (see also Irschick *et al.*, 2003). Only those trials in which the animal started from a complete standstill and moved in a straight line were used in analyses. All lizards were run on three structurally different substrates attached to the racetrack: (1) a smooth, wooden (plywood) surface; (2) a metal wire mesh (mesh width 1 mm); and (3) a cloth (canvas) surface. Each lizard was run at least ten times on each of the three substrates. We tested the animals on multiple, non-consecutive days on each substrate type. Prior to experimentation and in between trials, the lizards were placed in an incubator set at 30 °C for at least one hour.

We digitized the tip of the snout of the geckos in all locomotion trials at 250 Hz using MOTUS Peak Performance software. A sequence started 20 frames before the animal actually moved and lasted until the animal ran out of view or stopped. The data were smoothed using a Quintic Spline processor (MOTUS Peak Performance). Subsequently, instantaneous speed and instantaneous acceleration (i.e. per frame) were calculated with the MOTUS Peak Performance software.

As an estimate of an individual's maximum instantaneous speed and acceleration capacity on each substrate, we used the highest value of (instantaneous) speed and (instantaneous) acceleration attained in any sequence on that certain substrate.

Additionally, we included 'final speed' in the analyses. Final speed was defined as the mean speed the geckos attained after their first burst of locomotion (i.e. after acceleration ended) until the end of the trial. This corresponds to the average value of instantaneous speed taken over the whole plateau (see Fig. 1). Final speed, as measured here, can thus be regarded as analogous to speeds measured over a fixed distance on a racetrack (typically referred to as maximum speed). Only sequences in which the animals showed a clear plateau after an initial burst were used (see example in



**Figure 1.** Example of a scatterplot of instantaneous speed ( $\text{m s}^{-1}$ ) against time (s) for the climbing gecko *Hemidactylus garnoti*. Final speed was calculated as the mean speed the gecko attained after one locomotory burst. Only trials in which speed reached a clear plateau (as in this example) were used in the calculation of final speed. In total, for the seven individual geckos in this study, 48 out of 223 sequences fit this criterion. Final speed was calculated as the average of instantaneous speed (i.e. speed per frame) once the plateau was reached until the end of the trial. Time needed to reach the plateau was calculated as the time interval between the first movement of the animal and the first frame it reached the plateau.

Fig. 1). We made this selection based on graphical representations of instantaneous speed vs. time.

#### SCANNING ELECTRON MICROSCOPY

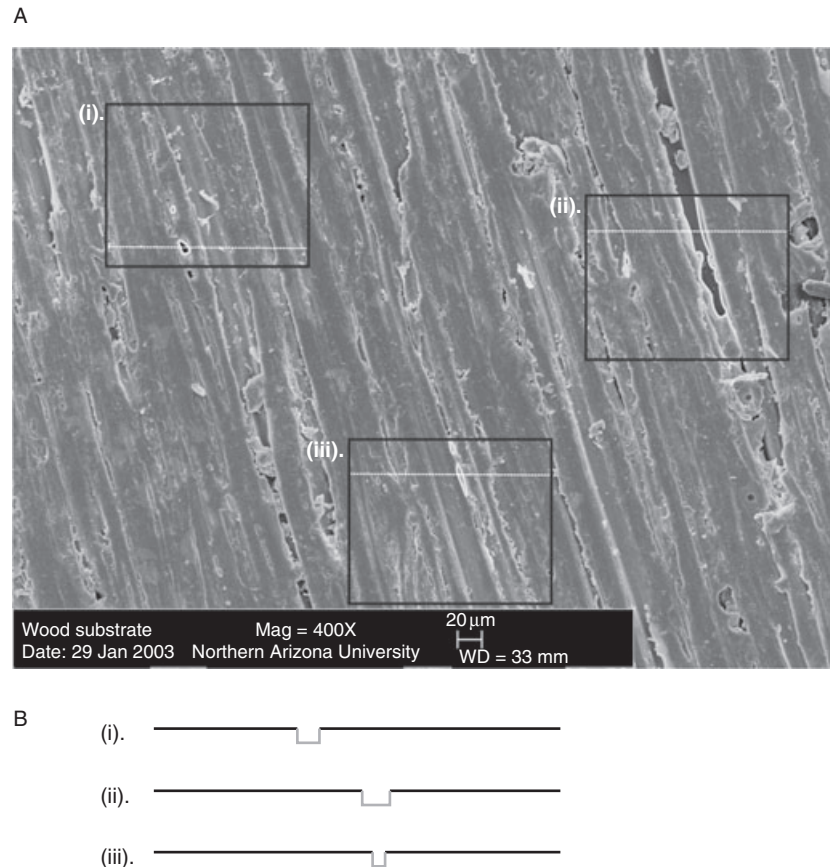
Pieces of each substrate ( $0.01 \text{ m} \times 0.01 \text{ m}$ ) were mounted on an aluminium stub, and sputter-coated with gold. Pictures of each substrate were taken using a LEO 435VP scanning electron microscope at 15 kV. For further analyses we used digital pictures at a magnification of 400 $\times$ , 27 $\times$ , and 100 $\times$  for the wood, mesh, and cloth substrate, respectively. For each substrate we demarcated three arbitrary areas on the picture [black boxes (i) (ii) and (iii) on Figs 2, 3, 4]. We then used Scion Image for Windows (v.4.0.2; Scion Corporation, 2000) to quantify the potentially available surface area to which the toepads could adhere (see Figs 2, 3, 4) and the total surface area within the demarcated areas.

In the case of the wooden substrate, we considered the surface area suitable for adhesion as the smooth, regular surface (see Fig. 2B for a schematic representation). For the wire mesh substrate, we assumed that the surface area suitable for adhesion is the actual metal grid (see Fig. 3B for a schematic representation). As the single strands of the cloth fibres are round, we only considered the mid-sections of the single strands as surface area available for adhesion (see Fig. 4B for a schematic representation). Thus our estimates of surface area available for setal adhesion are based on the interpretation of a 2D representation of the substrate and must be considered crude estimates only. However, based on these measurements we can at least get a first indication of the magnitude of the structural differences among the surfaces. To quantify the microstructure of the surface more precisely 3D reconstructions of the substrate would be needed. As an estimate of the available surface area per substrate, we used the mean (over the three demarcated areas of each substrate) surface area available for adhesion divided by the total surface area.

#### STATISTICAL ANALYSES

Prior to statistical analyses, all data were logarithmically ( $\log_{10}$ ) transformed.

We analysed data for maximum instantaneous speed and maximum instantaneous acceleration separately, using a repeated-measures ANOVA (GLM procedure, SPSS v.10.05). In order to test whether the sphericity assumption was met (i.e. variance-covariance matrix is circular), we also performed a Mauchly's test of sphericity. Individual was entered as subject factor, substrate type as the within-subject factor, and each performance trait as the dependent variable.



**Figure 2.** A, SEM pictures of the smooth wooden substrate at magnification 400 $\times$ . We demarcated three areas at random, represented by black boxes (i–iii), and calculated the proportion of surface area available for adhesion by the toepads in each area. We outlined the gaps in the substrate in grey. B, schematic drawings (side view) of a cross section of each area at the white dotted line in panel (A). Grey lines represent places inaccessible for the setae on the toepads (i.e. gaps); black lines represent places accessible for the setae. 98% of the wooden surface appeared to be suitable for adhesion by the toepads.

Data on final speed were analysed using a univariate one-way ANOVA (SPSS v.10.05) because we were unable to gather data on final speed for all seven individuals on all three substrates. We entered substrate as factor and final speed as dependent variable in the analyses.

## RESULTS

### LOCOMOTION TRIALS

Mauchly's test of sphericity proved non-significant for both maximum instantaneous acceleration (Mauchly's  $W_2 = 0.47$ ,  $P = 0.15$ ) and maximum instantaneous speed (Mauchly's  $W_2 = 0.87$ ,  $P = 0.71$ ). Therefore, we did not have to adjust the degrees of freedom in the repeated-measures ANOVA output.

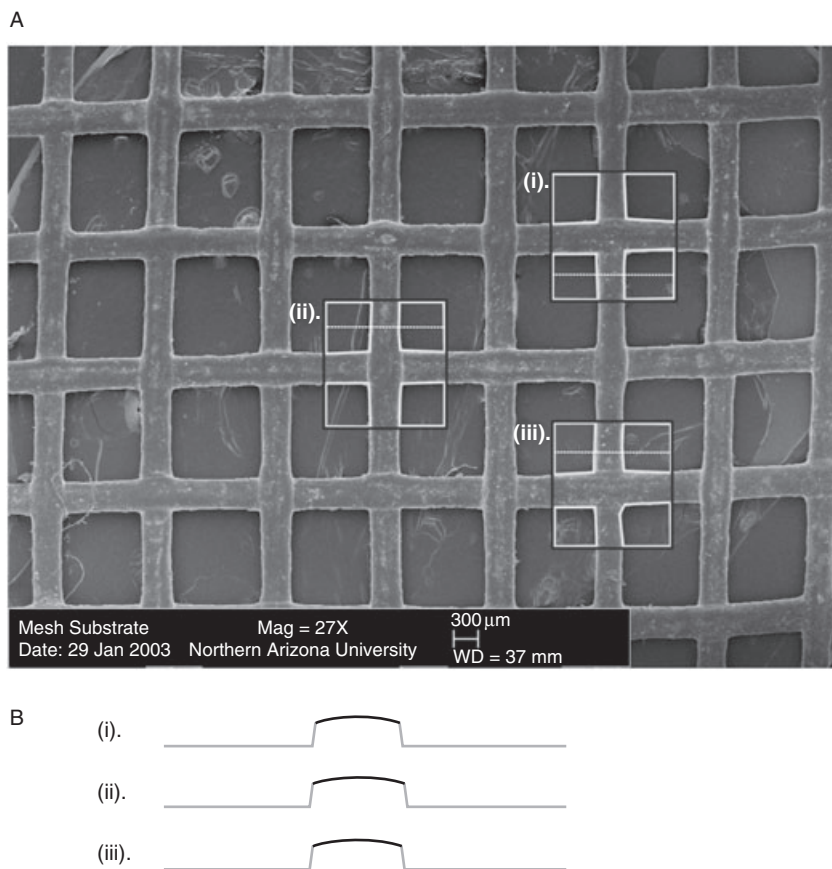
Repeated-measures ANOVA showed that instantaneous acceleration differed significantly among substrates ( $F_{2,12} = 5.38$ ,  $P = 0.02$ ) and among individuals

( $F_{1,6} = 330.93$ ,  $P < 0.001$ ). Instantaneous acceleration was highest on the smooth, wooden surface, and substantially lower on both the wire mesh and the cloth substrates (Fig. 5A). The differences among substrates in maximum instantaneous speed were marginally non-significant ( $F_{2,12} = 3.72$ ,  $P = 0.06$ ), although the individuals differed significantly ( $F_{1,6} = 375.24$ ,  $P < 0.001$ ). Maximum instantaneous speed was also highest on the smooth wooden surface (Fig. 5B).

A univariate one-way ANOVA showed that final speed did not differ significantly among substrates ( $F_{2,13} = 1.42$ ,  $P = 0.27$ ). Thus, lizards appear capable of achieving similar final speeds on different substrates after accelerating (Fig. 5C).

### SCANNING ELECTRON MICROSCOPY

The SEM pictures show that the three substrates differ substantially from a structural perspective. After



**Figure 3.** A, SEM pictures of the metal wire mesh at magnification 27 $\times$ . B, schematic drawings (side view) of a cross section of each area at the white dotted line in panel (A). Details as for Fig. 2. 41% of the wire mesh appeared to be suitable for adhesion by the toepads.

digitization of the SEM pictures, we found that  $98\% \pm 1.8\%$  (mean  $\pm$  SE) of the wooden substrate is available for adhesion by the toepads. The surface area suitable for adhesion of both the wire mesh and cloth substrate constituted a much smaller proportion of the total surface area ( $41\% \pm 1.1\%$  and  $37\% \pm 3.4\%$ , respectively). The claws, however, will probably be used more effectively on the latter surfaces as they need larger irregularities on the substrate to generate friction.

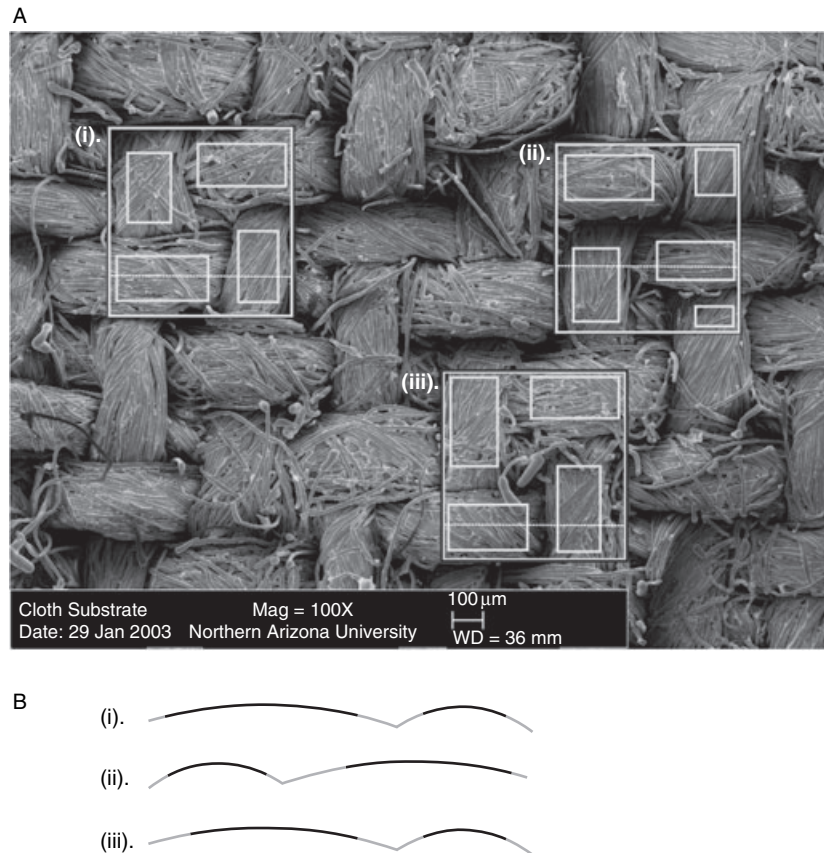
## DISCUSSION

### EFFECT ON LOCOMOTOR PERFORMANCE

We showed that the three surfaces examined (wood, cloth, and metal mesh) differ substantially in the estimated available surface area for attachment by gecko setae. Furthermore, our prediction that acceleration capacity should be positively related to available attachment area for the toepads was confirmed. Acceleration capacity in *H. garnoti* is highest on the sub-

strate with the highest proportion of surface area available for the toepads to adhere (wood), and lower on the substrates with less surface area suitable for adhesion (metal mesh and canvas cloth). This result is consistent with studies showing that vertical pulling forces exerted through beetles' setae are higher on smooth than on rough surfaces (see Betz, 2002 and references therein). Our results on maximum instantaneous speed show a similar, but marginally non-significant, trend: geckos attain higher maximum instantaneous speeds on the wood surface than on metal or cloth surfaces. Thus, substrate type affects instantaneous acceleration and maximum instantaneous speed in a similar fashion. The fact that geckos can attain higher maximum instantaneous speeds on the wood substrate might simply be a consequence of the higher acceleration capacity on that substrate, and of the fact that geckos tend to slip less frequently (see below).

Final speed, or the speed the geckos attained after accelerating, on the other hand, does not differ sig-

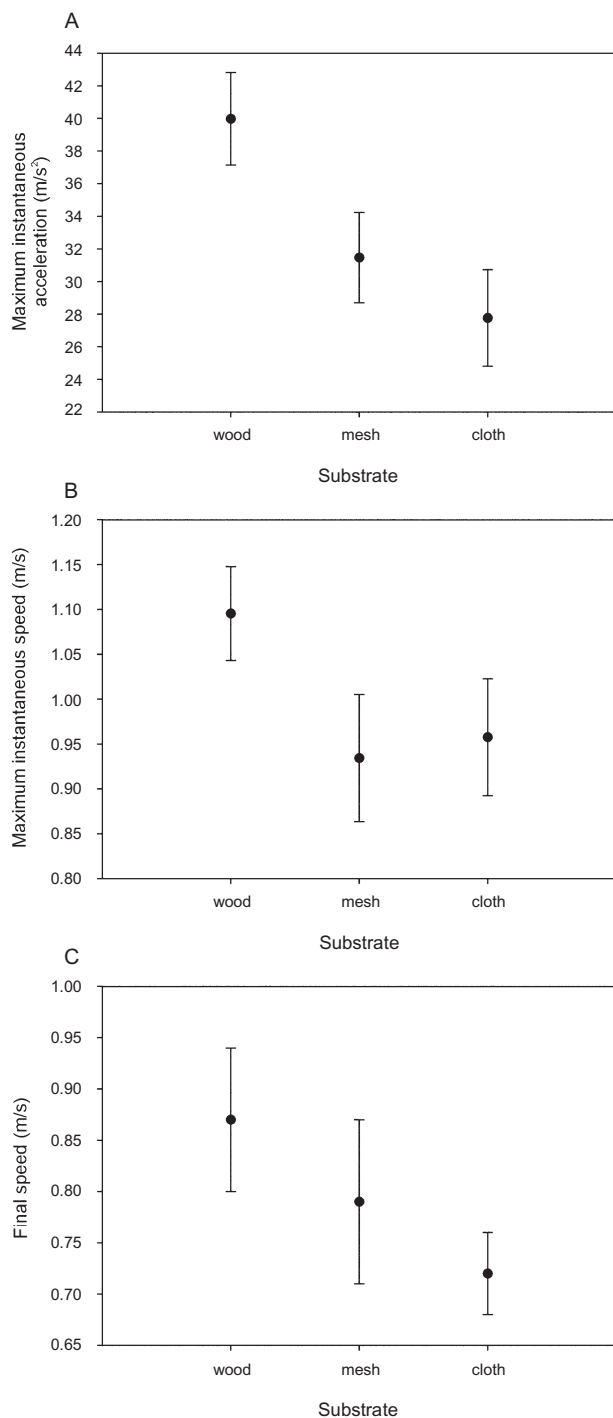


**Figure 4.** A, SEM pictures of the cloth substrate at magnification 100 $\times$ . B, schematic drawings (side view) of a cross section of each area at the white dotted line in panel (A). Details as for Fig. 2. 37% of the cloth substrate appeared to be suitable for adhesion by the toepads.

nificantly among substrates. The lack of substrate effect on final speed suggests that while geckos achieve similar final velocities on all substrates, they might do so by employing different strategies. *Callisaurus draconoides* and *Uma scoparia* accelerate over different time periods on inclined and horizontal surfaces to achieve different final speeds (Irschick & Jayne, 1998). In an analogous fashion, geckos may reach similar final speeds by accelerating over different time periods. However, when we compared the time needed to reach the plateau on the speed curve (see Fig. 1 for example) on the three substrates, geckos took as long to reach the plateau on the wire mesh and cloth as on the wood surface (one-way ANOVA,  $F_{2,13} = 0.90$ ,  $P = 0.40$ ). We may have been unable to detect significant differences in final speed (and/or time period) because of the low sample size (7 individuals, 48 sequences in total). While mean final speed declines on the cloth and, to a lesser extent, mesh surfaces (see Fig. 5C), the difference among substrates is not statistically significant. Clearly, more data are needed to elucidate this situation.

#### MECHANISM OF VERTICAL LOCOMOTION

We manipulated the surface area suitable for adhesion by using substrates differing in the density of 'gaps' (see Figs 2, 3, 4). In this study, the gaps correspond to the empty spaces between the wire and cloth strands. At these so-called gaps, we assume that no intimate contact between the toepads and the surface occurs. This means that when a gecko climbs up a gap-filled substrate, adhesion will only happen between a small portion of the toepad and the substrate, resulting in a diminished accelerating capacity. It was also evident that geckos cling poorly on gap-filled substrates such as wire mesh and cloth based on observations that on these substrates lizards often slipped when starting from a standstill (B. Vanhooydonck & A. Herrel, pers. observ.). Because we were unable to gain data on acceleration and maximum speed in those trials, we were forced to discard them from further statistical analyses. However, the high occurrence of slipping on the metal and cloth surfaces suggests that the geckos are unable to generate the forces needed to attain similar levels of acceleration as on the wooden surface.



**Figure 5.** Mean and SE bars of the three locomotor traits per substrate for seven individuals of *H. garnoti*. A, acceleration capacity; B, maximum instantaneous speed; C, final speed.

We note, however, that toepads are not the only structures generating adhesive force in geckos. Like many climbing organisms, geckos have well-developed claws. While they are not able to use their

claws effectively on a smooth surface (i.e. the wood substrate), we observed the lizards using their claws on both the mesh and cloth substrates. Previous studies have shown that while toepads appear to be specialized for clinging to smooth surfaces, claws are more important when clinging to rough surfaces (see Stork, 1980; Zani, 2000; Betz, 2002; Dai *et al.*, 2002). In this study, it is plausible that the loss of adhesive force on the cloth and metal mesh surfaces is, at least partly, compensated for by the use of the geckos' claws.

Moreover, our estimates of available contact area on the mesh and cloth substrate might be too conservative; probably toepads come into closer contact with a larger surface area than demarcated on the SEM pictures (see Figs 2, 3, 4). Toepads as a whole are not rigid structures. Instead, it seems plausible that they can curl around the edges of the metal wire or cloth strands. Moreover, in case of the metal mesh, some setae might come into close contact with the underlying substrate (we pinned the wire mesh in the experimental set-up to a wooden substrate). The substrates, on the other hand, are probably not rigid either. Soft substrates might deform to enable intimate contact over a relatively large contact area (Gay & Leibler, 1999; Autumn *et al.*, 2000). Clearly, more detailed studies examining intimate contact of setae to different surfaces would be useful. Finally, one must consider that these three surfaces are not made of the same material, and hence likely may show differing levels of attraction (at a microscopic level) to setae, particularly if Van der Waals' forces are used (Autumn *et al.*, 2000). In this regard, it would be useful to conduct similar experiments using the same material, but with differing amounts of available surface area for setal adhesion.

#### ECOLOGICAL RELEVANCE

Based on our results, we can predict that microhabitat use in nature will have a profound effect on locomotor performance in *H. garnoti*. Both acceleration capacity and instantaneous (maximum) speed should be highest on smooth surfaces, such as smooth bark or leaves, and substantially lower on rougher substrates (e.g. bark or rocks). Final (average) speed, on the contrary, does not seem to be affected by microhabitat use. If natural selection acts on acceleration capacity (e.g. if being able to accelerate fast is important when escaping from predators, or capturing prey), substrate choice could influence fitness. Thus, being on the wrong substrate at the wrong time might have a disastrous effect. Anecdotal observations suggest that this possibility may occur in certain situations; for example, geckos will sometimes fall to the ground when chasing prey or one another on certain substrates (e.g.

walls; A. Herrel, pers. observ.). Given that acceleration capacity is an important part of the locomotor repertoire of geckos, then one would expect climbing geckos to have a preference for surfaces that enable high degrees of setal adhesion. However, if final speed is more important than acceleration capacity, then substrate use may not have a large impact on the geckos' survival, and one would expect geckos to use a broad range of substrates. In this regard, further ecological studies that quantify how much time geckos spend on different substrates would be useful.

Our results may also offer a partial explanation to why the toe pads of geckos are seemingly overbuilt (Irschick *et al.*, 1996; Autumn *et al.*, 2000). For example, by extrapolation from studies on single setae, one predicts that a single gecko foot can produce 100 N of adhesive force (Autumn *et al.*, 2000), although whole-organism clinging studies show that they produce far less than this amount (Irschick *et al.*, 1996). The majority of substrates that geckos will encounter in nature are likely to have an irregular microstructure. Consequently, geckos may frequently occupy surfaces in which only a small number of setae can effectively adhere. Thus, having an overabundance of setae may provide an additional 'safety factor' during movement on particularly challenging surfaces.

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