Out on a limb: the differential effect of substrate diameter on acceleration capacity in *Anolis* lizards

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Summary

We investigated how substrate diameter affects acceleration performance in three *Anolis* lizard species (*A. sagrei*, *A. carolinensis* and *A. valencienni*), representing three different ecomorphs (trunk–ground, trunk–crown, and twig, respectively). We did so by measuring maximal acceleration capacity of the three species on a broad and narrow dowel. In addition to acceleration capacity, we quantified maximal sprint speed on both dowels. Both acceleration capacity and sprint speed are affected by substrate diameter, but the way in which they are, differs among species. Acceleration capacity in the trunk–ground anole, *A. sagrei*, was least affected by dowel diameter, whereas it was greatly reduced on the narrow dowel in the twig anole, *A. valencienni*. Sprint speed on the narrow dowel, however, was reduced to the greatest extent in the fastest running species, *A. sagrei*, whereas sprint speed was hardly affected by dowel diameter in the slow *A. valencienni*. The differential effect of dowel diameter on maximal acceleration capacity cannot be explained by differences in the timing of reaching maximal acceleration, but may be due to interspecific differences in the relative positioning of the limbs on the different dowels. The differential effect of dowel diameter on sprint speed, on the other hand, may be based on interspecific differences in the relative contribution of subsequent acceleratory bouts to maximal sprint speed on the broad and narrow dowel.

Key words: arboreal locomotion, ecomorphology, performance, interspecific differences.

Introduction

How animals manage to effectively move around in complex arboreal environments is intriguing. Not only may perch density and inter-perch distance vary dramatically, but when moving about on, or in between trees, animals will come across a wide range of substrates differing in inclination, texture and diameter. Since different structural elements within the arboreal habitat pose different functional demands on the locomotor system, arboreal habitats are typically regarded as complex environments that are difficult to exploit. A wide diversity of organisms, however, seems capable of doing so, and examples of arboreal species exist for most tetrapod taxa (e.g. amphibians, reptiles, birds, mammals), many of which show distinct morphological and/or behavioural specializations to an arboreal lifestyle, such as the prehensile tail in monkeys (Lemelin, 1995), toe pads in frogs (Hanna and Barnes, 1991) and geckos (e.g. Autumn and Peattie, 2002), or the walking gait and prehensile feet in chameleons (Peterson, 1984) and didelphids (e.g. Lemelin et al., 2003).

However, despite these specializations, locomotor performance will not be optimized on all substrates simultaneously. For instance, differences in inclination (e.g. Huey and Hertz, 1982; Huey and Hertz, 1984; Vilensky et al., 1994; Farley, 1997; Irschick and Jayne, 1998; Vanhooydonck and Van Damme, 2001), substrate width (e.g. Losos and Sinervo, 1989; Sinervo and Losos, 1991; Losos et al., 1993; Losos and Irschick, 1996; Bonser, 1999; Dunbar and Badam, 2000; Schmitt, 2003; Stevens, 2003; Lammers and Biknevicius, 2004; Demes et al., 2006) and texture (e.g. Zani, 2000; Claussen et al., 2002; Dai et al., 2002; Kerdok et al., 2002; Vanhooydonck et al., 2005) have all been shown to affect locomotor performance traits in a wide range of organisms. Even more so, some structural elements are known to mediate performance trade-offs. Substrate size, for instance, plays a mediating role in the trade-off between stability and speed. Whereas on broad surfaces (e.g. on the ground) high sprint speed can be attained without detrimentally affecting stability, on narrow surfaces (e.g. branches) high stability leads to decreased sprint performance (Peterson, 1984; Cartmill, 1985; Losos and Sinervo, 1989; Sinervo and Losos, 1991; Losos et

al., 1993; Losos and Irschick, 1996; Dunbar and Badam, 2000; Stevens, 2003). The trade-off between stability and speed on narrow substrates can be explained mechanistically as both performance traits pose conflicting demands on limb length. Whereas fast running animals benefit from having long limbs, short limbs prevent an animal from toppling sideways when moving on narrow surfaces by keeping the centre of mass close to the substrate (Cartmill, 1985; Losos and Sinervo, 1989; Sinervo and Losos, 1991; Macrini and Irschick, 1998).

Probably one of the best known examples of how substrate size affects locomotor performance occurs within the Caribbean *Anolis* radiation. Caribbean *Anolis* lizards include highly arboreal species that have evolved independently at least four times into distinct forms, called ecomorphs (Williams, 1983; Losos et al., 1998). Ecomorphs differ with respect to microhabitat use (i.e. perch height and diameter), morphology and locomotor behaviour. Surface diameter has been shown to affect speed in *Anolis* lizards, but the extent to which it does, differs among ecomorphs (Losos and Sinervo, 1989; Losos and Irschick, 1996). Whereas long-legged trunk–ground anoles are typically fast on broad surfaces, they are very unstable on narrower ones. Short-limbed twig anoles, on the contrary, are relatively slow on substrates of all diameters but they rarely stumble (Losos and Sinervo, 1989; Losos and Irschick, 1996).

In this study, we investigated whether and how substrate diameter affects acceleration capacity by quantifying maximal acceleration capacity on differently sized surfaces. We chose to investigate acceleration capacity for several reasons. First, in nature, *Anolis* lizards, and lizards in general, typically use short, explosive bursts of locomotion to escape predators and/or to capture prey. Although acceleration capacity seems ecologically relevant (sensu Huey and Stevenson, 1979), most studies have focused on steady-state locomotor performance traits, such as sprint speed (see Garland, Jr and Losos, 1994). To our knowledge, only a handful of data on the influence of substrate characteristics on acceleration capacity exist. Even more so, these studies investigated whether acceleration capacity is affected by incline or surface texture in terrestrial lizards and climbing geckos (Huey and Hertz, 1984; Irschick and Jayne, 1998; Vanhooydonck et al., 2005). Although the effect of substrate diameter on acceleration performance may be especially relevant in arboreal habitats, no such data are available to date.

In addition, it remains unclear whether acceleration capacity is similarly affected by surface characteristics as compared with steady-state locomotor performance such as sprint speed. Whereas sprint speed is typically defined as the average speed over a given distance (e.g. 0.25 cm), and reflects a (relatively) longer-duration performance trait, acceleration is usually defined as the instantaneous rate of change in speed (i.e. short duration). The scarce available data suggest that the effect of some surface characteristics such as inclination or texture on speed and acceleration are not necessarily similar (Huey and Hertz, 1982; Huey and Hertz, 1984; Irschick and Jayne, 1998; Vanhooydonck et al., 2005). For instance, acceleration capacity

in climbing geckos is greatly diminished on substrates with smaller available surface area for setal adhesion, whereas sprint speed is unaffected (Vanhooydonck et al., 2005). This seeming discrepancy has remained unexplained since it is unclear how differences in acceleration capacity translate into differences in sprint speed. Up till now, no empirical data exists on whether and how the variation in some aspects of the acceleration profile (i.e. number of acceleratory bursts, amplitude of these acceleration bursts) explain the variation in sprint speed within one running bout. Anecdotal data on human sprinters suggest that initial acceleration and maximum running speed are relatively unrelated to one another (Delecluse, 1997; Little and Williams, 2005), whereas Irschick and Jayne (Irschick and Jayne, 1998) suggested that differences in final maximal speeds in terrestrial lizards may be due to differences in the time over which lizards were able to accelerate.

Here, we quantify both sprint speed and acceleration capacity on broad and narrow surfaces in three species of *Anolis* lizards. The three species (*Anolis sagrei*, *A. carolinensis* and *A. valencienni*) represent three ecomorphs (trunk–ground, trunk–crown and twig, respectively), known to differ in microhabitat use, limb length, sprint speed and sprint sensitivity [i.e. relative decrease in sprint speed on narrower substrates (Losos and Sinervo, 1989; Losos and Irschick, 1996; Irschick and Losos, 1999)]. We first tested how substrate diameter affects maximal acceleration capacity in the three species. We did so by comparing maximal acceleration capacity on the narrow and broad dowel for each species. In addition, we quantified maximal sprint speed and compared the results to the results on acceleration capacity. To be able to explain the differential effect of substrate diameter on both locomotor performance traits we tested whether the timing of reaching maximal acceleration and maximal sprint speed within a running bout differs and whether acceleration profiles (i.e. number of acceleration peaks and acceleration amplitudes) differ among species and between dowels.

Materials and methods
Animals

Between November 2001 and February 2002, we captured 15 male *Anolis carolinensis* Voigt (mean snout–vent length (SVL) ± 1 s.e.m.=67.08±0.43 mm), 22 male *A. sagrei* Cocteau (mean SVL ± 1 s.e.m.=59.22±0.36 mm) and ten male *A. valencienni* Dumerial and Bibron (mean SVL ± 1 s.e.m.=67.95±1.44 mm) by hand or noose. Both *A. carolinensis* and *A. sagrei* individuals were captured on mainland USA (New Orleans, LA and Miami, FL, respectively). *A. valencienni* individuals were caught around the Discovery Bay field station in Jamaica.

All the animals were transported back to the laboratory at Tulane University, New Orleans, LA. Upon arrival in the lab, the lizards were housed in pairs in 40-l terraria lined with leaf litter and a dowel. Terraria were placed in a temperature controlled room (29±2°C) with a 12 h:12 h light:dark photoperiod. We fed the animals live crickets dusted with

calcium and vitamin supplements three times a week; lizards were sprayed with water daily.

Experimental setup

We induced lizards to run up a plastic dowel covered with metal wire mesh (mesh width 1 mm) by clapping our hands or tapping the lizards slightly on the base of their tail. All lizards were tested on both a broad and a narrow dowel (diameters of 0.08 m and 0.01 m, respectively). Both dowels were 2 m long and placed against the wall at an angle of 45°. Lizards were filmed in lateral view over a distance of 1 m using a high speed video camera (Redlake Motionscope PCI camera) set at 250 frames s^{-1}. Filming at this frame rate has been shown to be sufficiently accurate (cf. Walker, 1998), particularly for accelerations and velocities observed in this study. We placed the lizards on the dowel so that the lizard was just in view. We performed between five and ten trials per individual on each dowel. Trials were conducted on several non-consecutive days with trials on the broad and narrow dowel alternated among days. Prior to experimentation and in between trials, the lizards were placed in an incubator set at 32°C for at least 1 h to allow the lizards to attain body temperatures similar to their preferred field body temperatures (see also Toro et al., 2003).

After filming, we selected all 'good' sequences per individual. A 'good' sequence was defined as a sequence in which the lizard started from a complete standstill, ran non-stop over a distance of at least 0.20 m, and ran on top of the dowel, in a straight line. For these sequences, the tip of the snout was digitized at 250 frames s^{-1} using Peak Performance MOTUS software. At the beginning of each sequence, we digitized four points a known distance apart on the reference grid. We started the frame by frame digitization 20 frames before the first movement (i.e. lizard sitting still) and we stopped when the lizard stopped running or ran out of view. The x,y coordinates obtained from the digitizations were then smoothed using the Quintic Spline Processor (QSP) implemented in the MOTUS software. The routine fits the 5th degree polynomial to the displacement data and smoothes them based on an estimate of the error variance. The error variance depends on the nature of the data and is estimated for each sequence that is analyzed. We chose to use the QSP because in this routine the derivatives are computed directly from the spline coefficients, and instantaneous velocity and acceleration are subsequently calculated (see also Bergmann and Irschick, 2006; Vanhooydonck et al., 2006). The QSP method, however, consistently underestimates maximal acceleration (Walker, 1998).

We subsequently inspected all acceleration profiles visually, and only included those sequences for which the profile showed a smooth and continuous pattern. An example of such a sequence is shown in Fig. 1. In addition, we noted the amplitudes of the first five consecutive acceleration peaks of all acceleration profiles (see Fig. 1).

Based on the instantaneous displacement data, we calculated, for each sequence, the average speed over 0.20-m intervals using a custom written QBasic program. In this
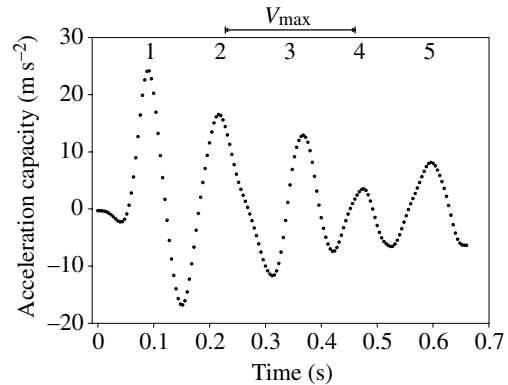

Fig. 1. Acceleration profile of an *Anolis carolinensis* individual running on the narrow dowel. Five acceleration peaks are present. Amplitude of peak 1=24.15 m s^{-2}, amplitude of peak 2=16.53 m s^{-2}, amplitude of peak 3=12.88 m s^{-2}, amplitude of peak 4=3.51 m s^{-2}, and amplitude of peak 5=8.13 m s^{-2}. The part of the run that contains the highest speed over an interval of 0.20 m is indicated (v_{max}).

program, the time it takes a lizard to cover any 0.20 m interval out of the total distance of 1 m over which we filmed, is calculated. Sprint speed is subsequently calculated by dividing 0.20 m by the time it takes the lizard to cover this distance. This estimate of sprint speed is similar to measurements of sprint speed using electronic racetracks (cf. Huey et al., 1981; Garland and Losos, 1994) and represents a measure of average sprint speed over a given distance.

Statistical analyses

To test whether dowel diameter differentially affects maximal performance in the three *Anolis* species, we selected maximal acceleration and sprint speed for each individual. As an estimate of an individual's maximal acceleration capacity, we used the highest instantaneous acceleration attained by that individual in any of the trials. However, if the highest acceleration out of all trials for a given individual equalled or was greater than 200% of the second highest acceleration for that individual we discarded the former estimate and used the latter in further analyses. As an estimate of an individual's maximal sprint speed, we used the highest speed attained over any 0.20 m interval in any trial for that individual.

Both performance values were logarithmically transformed (log_{10}) prior to statistical analyses. Subsequently, we performed a repeated-measures ANOVA with 'dowel' as the within-subject factor, 'species' as the between-subject factor and either performance trait (i.e. maximal acceleration capacity or maximal sprint speed) as the within-subject variable (GLM procedure SPSS 12.0). Data on 12 *A. carolinensis* individuals, 16 *A. sagrei* individuals, and eight *A. valencienni* individuals were used in the repeated-measures ANOVA on maximal acceleration; in the repeated-measures ANOVA on sprint speed, data on 11 *A. carolinensis*, 17 *A. sagrei* and seven *A. valencienni* individuals were used.

To be able to test whether the differential effect of dowel diameter on maximal acceleration capacity is due to differences in the timing of maximal acceleration capacity, we noted whether the first or one of the subsequent acceleration peaks was the maximal one within one sequence. We only used the maximal acceleration sequences, i.e. those sequences used in the repeated-measures ANOVA as described above. Since the number of individuals per species differed greatly, we subsequently performed a Loglinear analysis per species (SPSS 12.0). By entering 'dowel' as factor in the analysis, we tested whether the timing of maximal acceleration differed between dowels.

In a next step, we tested whether and how the different acceleration peaks contributed to sprint speed. We did so by regressing the amplitudes of the first five acceleration peaks against sprint speed for all digitized sequences (backward method, SPSS 12.0). In total, 210 sequences were used in the regression analysis. To test subsequently whether the differences in maximal performance between dowels and species can be explained by differences in the acceleration profiles (i.e. amplitude of different acceleration peaks and number of acceleration peaks) we performed two additional analyses. In both these analyses we only included those variables that were significant in the overall regression model and data from the maximal sprint sequence for each individual. Maximal sprint speed and peak amplitudes were logarithmically transformed ($\log_{10}$) prior to statistical analyses. Firstly, we performed a repeated-measures ANOVA with 'acceleration peak number' as the within-subject factor, 'species' and 'dowel' as the between-subject factors, and 'peak amplitude' as dependent (i.e. within-subject) variable. Secondly, we counted how many acceleration peaks were present before reaching maximal sprint speed for each sequence. Since the number of individuals differed greatly among species, we performed a loglinear analysis (SPSS 12.0) for each species separately. By entering 'dowel' as factor, we tested whether maximal sprint speed was reached after a different number of acceleration peaks on the broad and narrow dowel.

In all statistical analyses, the significance level at which the null hypotheses of 'no difference' or 'no relationship' was rejected equals 0.05. However, since we were dealing with relatively small sample sizes, we described results as 'tendencies' if P values ranged between 0.05 and 0.10.

Results

Effect of dowel diameter on maximal performance

Maximal acceleration capacity differed significantly between dowels (repeated-measures ANOVA, $F_{1,33}=9.65$, $P=0.004$) and among species ($F_{2,33}=11.17$, $P<0.0001$). The dowel×species interaction effect, however, was marginally non-significant ($F_{2,33}=2.77$, $P=0.078$). On both dowels, A. sagrei was the fastest accelerator of the three species; A. valencienni was the slowest and A. carolinensis performed intermediately with regard to acceleration capacity (Fig. 2A).
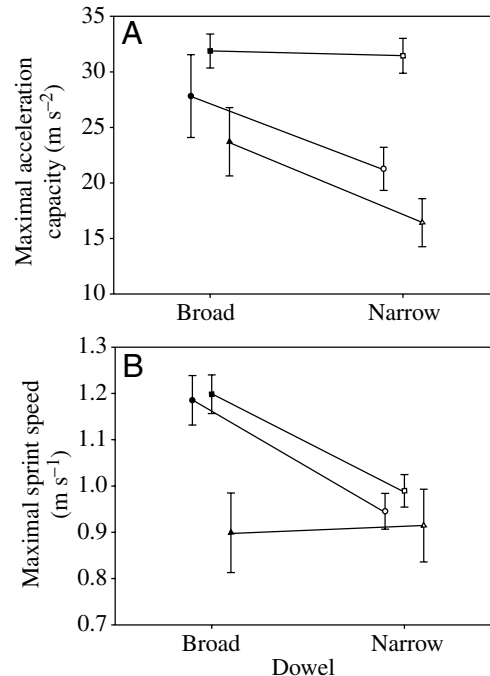

Fig. 2. Plot of maximal performance of *A. sagrei*, *A. carolinensis* and *A. valencienni* on the broad and narrow dowel. Data are the means per species ± s.e.m. (bars). (A) Maximal acceleration capacity and (B) maximal sprint speed. Symbols: squares, *A. sagrei*; circles, *A. carolinensis*; triangles, *A. valencienni*. Solid symbols, on broad dowel; open symbols, on narrow dowel. Points are offset for each dowel diameter so that standard error bars do not overlap.

However, acceleration capacity tends to be affected by dowel diameter to a lesser degree in *A. sagrei* as compared to *A. carolinensis* and *A. valencienni*. Whereas acceleration capacity on the narrow dowel equalled 99% of the acceleration capacity on the broad dowel in *A. sagrei*, acceleration capacity was greatly reduced on the narrow dowel in both other species (76% in *A. carolinensis* and 69% in *A. valencienni*).

For maximal sprint speed, however, both the main effects as well as the dowel × species interaction effect were significant (repeated-measures ANOVA, dowel: $F_{1,32}=34.72$, $P<0.0001$; species: $F_{2,32}=4.43$, $P=0.020$; dowel × species: $F_{2,32}=9.71$, $P=0.001$). Whereas sprint speed was greatly reduced on the narrow dowel in both *A. sagrei* and *A. carolinensis*, and equalled 83% and 80%, respectively, of the sprint speed attained on the broad dowel, it was similar on both dowels in *A. valencienni* (100%; Fig. 2B).

Timing of maximal acceleration

In neither of the three species did the timing of reaching maximal acceleration differ between dowels (loglinear analysis: all $\chi^2_1<1.19$, all $P>0.28$). In all three species and on both dowels, maximum acceleration capacity was reached at the first peak at least 75% of the time (Fig. 3).
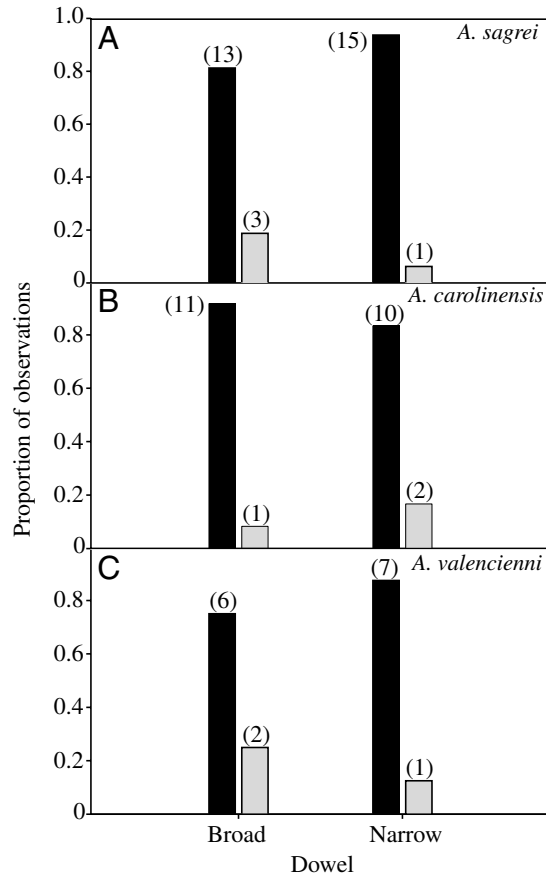
Fig. 3. Proportion of observations of reaching maximal acceleration capacity at the first peak and at subsequent peaks in *A. sagrei*, *A. carolinensis* and *A. valencienni* on broad and narrow dowel. (A) *A. sagrei*, (B) *A. carolinensis* and (C) *A. valencienni*. Black bars, maximal acceleration at the first peak; grey bars, maximal acceleration at a subsequent peak. The actual number of observations per group is indicated in brackets.

Interrelationships between acceleration profiles and sprint speed

The multiple regression in which sprint speed is entered as the dependent variable and the amplitudes of the first five acceleration peaks are entered as independent variables resulted in a significant model (r=0.55, $F_{2,208}$=46.04, P<0.0001). However, only the variation in the first two acceleration peaks contributed significantly to the variation in sprint speed across all trials (acceleration peak 1: r_{part}=8.06, P<0.0001; acceleration peak 2: r_{part}=3.79, P<0.0001).

The subsequent repeated-measures ANOVA with the amplitudes of acceleration peak 1 and 2 as within-subject variables, only including data for the maximal sprint speed sequences, shows that the amplitude of peak 1 and 2 differ significantly from one another ($F_{1,63}$=67.08, P<0.0001). This pattern (i.e. amplitude of peak 1 greater than amplitude of peak 2) does not differ between dowels ($F_{1,63}$=2.22, P=0.14), or among species ($F_{2,63}$=0.43, P=0.65). The three way interaction effect (peak number×dowel×species) is non-significant

($F_{2,63}$=0.67, P=0.52). On both dowels, and in all three species, acceleration peak 2 was significantly lower than acceleration peak 1 (Table 1; Fig. 4).

With regards to the between-subject effects, the mean amplitude of the first two acceleration peaks (i.e. both acceleration peaks taken together) differed significantly among species ($F_{2,63}$=6.53, P=0.003). The effect of dowel on peak amplitude was marginally non-significant ($F_{1,63}$=3.00, P=0.088). The dowel × species interaction is non-significant ($F_{2,63}$=0.15, P=0.86). The mean amplitude was greatest in *A. sagrei*, smallest in *A. valencienni* and intermediate in *A. carolinensis* and it tended to be greater on the broad compared to the narrow dowel (Fig. 4).

In addition, the loglinear analyses on the number of times maximal sprint speed is attained after acceleration peak 1 and after acceleration peak 2 showed differences between dowels for two out of the three species (Fig. 5). In *A. sagrei* maximal sprint speed was reached after the second acceleration peak on the broad dowel, but it was already reached after the initial acceleration peak on the narrow dowel (χ^2_1=6.23, P=0.013; Fig. 5A). The difference between dowels is marginally non-significant in *A. carolinensis* (χ^2_1=2.95, P=0.086; Fig. 5B), but a similar trend is present. In *A. valencienni*, on the contrary, there was no difference in when maximal sprint speed is reached on the broad and narrow dowel (χ^2_1=0.11, P=0.74; Fig. 5C); on both dowels, maximal sprint speed was reached in similar proportions after the first and second acceleration peak.

Discussion
Effect of substrate diameter on acceleration capacity

Acceleration capacity is generally reduced on the narrow, compared to the broad dowel. However, acceleration capacity does not seem to be affected to the same extent in the trunk–ground anole, *A. sagrei*, as in the trunk–crown and twig anole. In *A. carolinensis* and *A. valencienni* acceleration capacity on the narrow dowel was reduced to about 76% and 69%, respectively, of the original value on the broad dowel, whereas in *A. sagrei* acceleration capacity was hardly affected by dowel diameter. Thus, the trunk–ground anole *A. sagrei* was the fastest accelerator and its maximal acceleration was least affected by dowel diameter, whereas the twig anole *A.*

Table 1. *Mean amplitude of acceleration peak 1 and 2 per species and dowel*

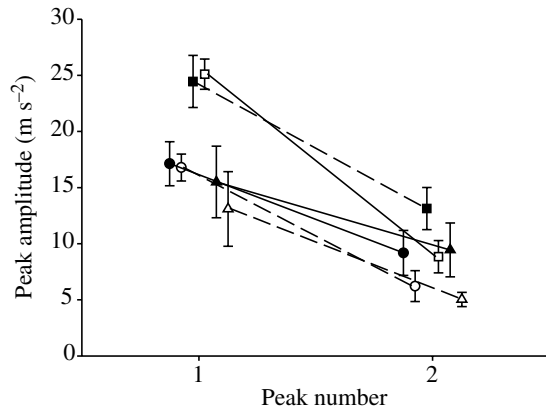| Species	Dowel	Amplitude peak 1	Amplitude peak 2
A. sagrei	Broad	24.46±2.32	13.13±1.88
	Narrow	25.11±1.35	8.84±1.44
A. carolinensis	Broad	17.13±1.96	9.18±2.00
	Narrow	16.80±1.20	6.21±1.38
A. valencienni	Broad	15.50±3.19	9.44±2.40
	Narrow	13.09±3.32	5.03±0.64

Values are means ± s.e.m.

Fig. 4. Plot of amplitude of acceleration peaks 1 and 2 for maximal sprint sequences of *A. sagrei*, *A. carolinensis* and *A. valencienni* on the broad and narrow dowel. Data are the means ± standard errors (bars) per species, dowel and peak. Symbols: squares, *A. sagrei*; circles, *A. carolinensis*; triangles, *A. valencienni*. Solid symbols, on broad dowel; open symbols, on narrow dowel. Full lines connect species means on the broad dowel; dashed lines connect species means on the narrow dowel. Points are offset for peak 1 and peak 2 so that standard error bars do not overlap.
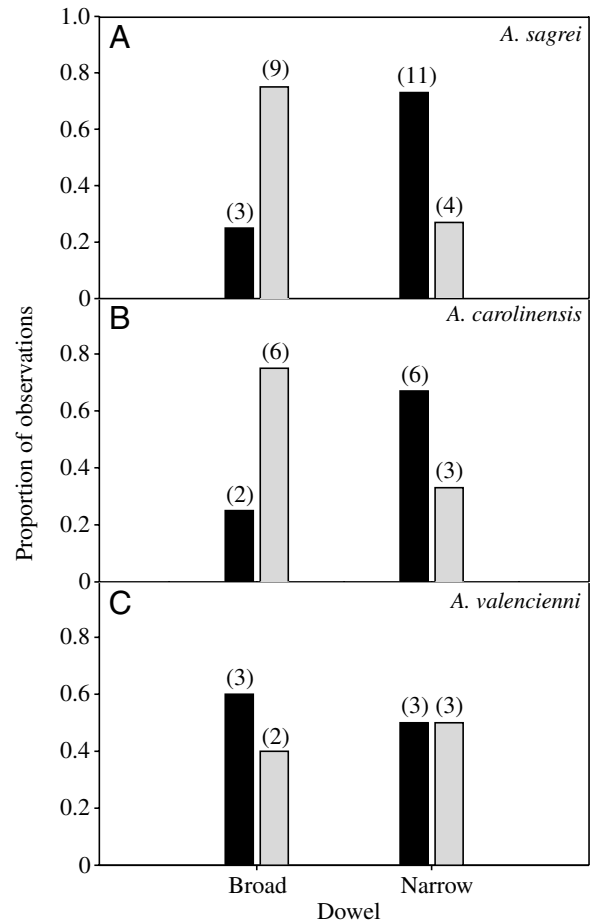

Fig. 5. Proportion of observations of reaching maximal sprint speed after first and after second acceleration peak in *A. sagrei*, *A. carolinensis* and *A. valencienni* on broad and narrow dowel. (A) *A. sagrei*, (B) *A. carolinensis* and (C) *A. valencienni*. Black bars, maximal acceleration after the first peak; grey bars, maximal acceleration after a subsequent peak. Only those sequences in which maximal sprint speed was attained after the first or second acceleration peak were used in the analyses. The actual number of observations per group is indicated in brackets.

valencienni was the slowest and its acceleration capacity was greatly reduced on the narrow compared to the broad dowel (Fig. 2A). How can we explain the interspecific difference in acceleration sensitivity to surface diameter in the three species under study here? We hypothesize that species may differ in the timing of reaching maximal acceleration and/or in the relative positioning of the limbs on differently sized substrates.

If species differ with respect to whether maximal acceleration is attained early (within first stride) or late (in subsequent strides) in a running sequence we might expect a differential effect of substrate diameter on acceleration capacity. Since we were particularly interested in 'starts from standstill', lizards were given time to position themselves properly on the dowel, which may allow them to adjust to surface diameter (see also below) prior to starting to run. If animals attain maximal acceleration within the first bout (i.e. immediately after starting from standstill), dowel diameter may not affect acceleration capacity to a great extent. By contrast, if animals only attain maximal acceleration capacity in subsequent bouts (i.e. while they are already on the move) they will be unable to re-position themselves on the dowel, possibly resulting in a greater effect on maximal acceleration capacity. In an analogous fashion, Losos and Irschick (Losos and Irschick, 1996) explained the differential effect of substrate diameter on speed and jumping distance in *Anolis* lizards. Our results show that in all three species and on both dowels maximal acceleration capacity is reached early (i.e. first peak) within a running bout at least 75% of the time (Fig. 3). If our reasoning as outlined above is correct, we would not expect dowel diameter to affect acceleration capacity in any of the species. Our data, therefore, do not seem to support the

hypothesis that interspecific differences in the timing of reaching maximal acceleration may explain interspecific differences in substrate sensitivity. It is unclear whether similar results would be obtained under natural conditions. When attacked or pursued by a predator, lizards may have less time to prepare themselves than in an experimental setup. In such situation, the lizard's ability to position itself properly before moving on narrow substrates may well differ among species (see also Pounds, 1988; Losos and Irschick, 1996).

As referred to above, the ability of animals to position themselves properly on substrates may be of crucial importance. Recently, it has been suggested that the less favourable positioning of the limbs and limb segments on narrow substrates is responsible for a large decline in sprint speed in the trunk–ground anole, *A. sagrei* (Spezzano and

Jayne, 2004). Detailed hind limb kinematics of *A. sagrei* moving at a constant speed on various substrate diameters show that the long axis of the foot is oriented perpendicularly with respect to the direction of travel on the narrowest surfaces (Spezzano and Jayne, 2004). Because of this perpendicular orientation of the foot, the ability to use plantar flexion is reduced (Spezzano and Jayne, 2004). A reduction in plantar flexion, in turn, may impair the generation of high ground reaction forces and/or reduces the period of time during which force can be applied to the surface (Irschick and Jayne, 1999; Spezzano and Jayne, 2004), resulting in a decrease in sprint speed. If the placement of the foot prior to take-off (i.e. at standstill) is similarly affected, this may result in a decline in acceleration capacity on the narrow dowel. Moreover, if species differ in the degree to which the foot is oriented perpendicular to the direction of travel on the narrow dowel compared to the broad dowel, this may explain why surface diameter differentially affects acceleration performance. If our reasoning is correct, we would expect this shift in foot orientation to be greater in *A. carolinensis* and *A. valencienni* than in *A. sagrei*. At the moment, however, we cannot explicitly test this hypothesis as detailed hind limb kinematics of *Anolis* running from standstill on differently sized dowels is lacking.

Acceleration versus speed

Contrary to the results on acceleration capacity and sensitivity, maximal sprint speed was reduced to the greatest extent in *A. sagrei* whereas sprint speed in *A. valencienni* was least affected (Fig. 2B). This result is in accordance with results from previous studies in which it has been shown that maximal sprint speed in twig anoles is less sensitive to changes in dowel diameter than maximal sprint speed in trunk–ground or trunk–crown anoles in general (Losos and Sinervo, 1989; Losos and Irschick, 1996). However, on all dowels, twig anoles are slower than the other ecomorphs and surefootedness appears to come at the cost of speed (Losos and Sinervo, 1989; Sinervo and Losos, 1991; Losos and Irschick, 1996; Macrini and Irschick, 1998).

The differential effect of dowel diameter on speed and acceleration capacity seems contradictory at first sight. Whereas in human athletes, acceleration and maximum speed are specific qualities and relatively unrelated (Delecluse, 1997; Little and Williams, 2005), in these lizards, ultimate sprint speed in general (i.e. across all recorded sequences and speeds) is determined by the amplitude of the first two acceleration peaks. Whereas sprint speed was greatly reduced on the narrow dowel in *A. sagrei*, acceleration capacity was not. The opposite is true for *A. valencienni*. In *A. carolinensis*, both speed and acceleration capacity were affected by dowel diameter. Even more so, a comparison of the acceleration profiles shows that the profiles are similar with regards to the amplitudes of the first two peaks on both dowels and for all three species: the amplitude of the first acceleration peak was always greater than that of the second peak (Fig. 4). We believe that the timing of reaching maximal sprint speed may be crucial in explaining the apparent discrepancy between the speed and acceleration results.

Our results suggest that consecutive acceleration peaks do not always contribute equally to maximal sprint speed (Fig. 5). Whereas maximal speed was usually reached after the first two acceleration peaks on the broad dowel in all three species, the second acceleration peak did not seem to contribute to maximal speed on the narrow dowel in *A. sagrei* and *A. carolinensis*. This may result in the observed decline in final maximal sprint speed on the narrow dowel in both of these species. In *A. valencienni*, on the other hand, maximal speed was reached after the second acceleration peak on both surfaces, thus translating into similar sprint speeds on both the broad and narrow dowel. In an analogous fashion, Irschick and Jayne (Irschick and Jayne, 1998) argued that differences in final maximal speeds in *Callisaurus draconoides* and *Uma scoparia* might be explained by differences in the period of time over which the lizards were able to accelerate.

As mentioned earlier, of the three species under study here *A. valencienni* remained the slowest sprinter on both dowels. In the past, this contradictory combination of a decreased sensitivity, with regards to sprint speed, to changes in surface diameter, and an overall reduced sprint capacity in twig anoles, has been observed but remained unexplained (see Losos and Sinervo, 1989; Spezzano and Jayne, 2004). Our acceleration data, however, provide a potential answer to the riddle. In *A. valencienni*, although consecutive acceleration peaks contribute to final maximal speed on both broad and narrow substrates, the amplitudes of these peaks are still much lower compared to those of *A. sagrei* and *A. carolinensis*. Since the amplitude of the acceleration peaks determine maximal final speed, *A. valencienni*, although the most stable, is the slowest sprinter of the three. Maximal acceleration capacity, in turn, is determined by the morphological and physiological properties of the limb muscles [e.g. muscle mass (Curtin et al., 2005; Vanhooydonck et al., 2006)]. The absence of massive limb muscles in twig anoles as compared to other ecomorphs, thus explains *A. valencienni*'s diminished acceleration capacities (Vanhooydonck et al., 2006).

Ecological implications

Our results show that acceleration capacity in *A. sagrei*, a trunk–ground anole specialized in the use of broad surfaces, is least affected by perch size; it is capable of accelerating as fast on narrow (e.g. twigs) as on broad substrates (e.g. ground). Acceleration capacity in *A. valencienni*, a twig anole specialized in the use of narrow perches, however, is greatly reduced on narrow substrates. This raises important questions with respect to the ecological relevance of acceleration performance in *Anolis* lizards. In general, locomotor performance is assumed to be a crucial determinant of organismal fitness (see LeGalliard et al., 2004; Miles, 2004), but surprisingly few data exist on the ecological relevance of different locomotor performance traits. It remains largely unknown how often animals actually use their maximal locomotor abilities under natural conditions. One of the few studies addressing this issue (Irschick and Losos, 1998) showed that *Anolis* lizards typically only sprint at their maximal

capacity when escaping from predators, whereas sprint performance during feeding bouts and during undisturbed activity is lower. Even more so, jump performance in the same lizards is always submaximal under natural conditions (Irschick and Losos, 1998). To date, no data on the use of maximal acceleration capacity in the field are available. However, it seems plausible that different locomotor performance traits (e.g. speed, acceleration, stability) are ecologically relevant and selected for in different ecological (e.g. different substrates) and behavioural (e.g. escaping predators *versus* capturing prey) contexts. To complicate matters even further, the ecological relevance of different locomotor performance traits may vary among species. Quantifying field locomotor performance in different contexts and long-term studies on survival, and fitness in general, and its performance correlates in different ecomorphs are crucial to address this issue.

In conclusion, our data show that sprint speed and acceleration capacity are differentially affected by substrate diameter in three *Anolis* species representing different ecomorphs. Whereas sprint speed is reduced to the greatest extent in the fastest species, the opposite is true for acceleration capacity. Moreover, our data show important differences in the contribution of different acceleration peaks to sprint speed in the three species examined here. Whereas *A. valencienni* is able to perform and make use of multiple acceleratory bursts on all substrates, *A. sagrei* can only utilise one acceleratory burst on the narrowest substrate, resulting in a concomitant decrease in overall sprint speed. Thus, our data show the importance of investigating multiple performance traits to understand better the relationships between substrate diameter and the evolution of locomotor strategies in arboreal lizards.

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