The effect of perch diameter on escape behaviour of *Anolis* lizards: laboratory predictions and field tests

JONATHAN B. LOSOS & DUNCAN J. IRSCHICK
Department of Biology, Washington University

Abstract. This study investigated whether the escape behaviour of lizard species could be predicted by knowledge of their functional capabilities. In the laboratory, the effect of perch support diameter on sprinting and jumping ability was measured in five species of *Anolis* lizards. In all species, sprint speed declined with decreasing perch diameter, but decreased perch diameter had little effect on jumping ability. The escape behaviour of a lizard on a particular-sized support in nature was then evaluated as a function of the lizard's sprinting and jumping capabilities. As diameter decreased, lizards in all but one species tended to escape by jumping more frequently because jumping ability is less affected by diameter than is sprinting ability. It was also predicted that species in which running ability declines greatly as diameter decreases should switch to escape by jumping more often than species that experience less of a decline in running ability. This prediction was not confirmed. Consequently, functional capabilities play a role in determining escape behaviour in *Anolis* lizards, but other factors may be important as well.

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Physiological ecologists and evolutionary biologists have recently focused on studies of whole organism performance capability to understand whether and how organisms are adapted to their environment (e.g. Arnold 1983; Huey & Bennett 1986; Garland & Losos 1994). Implicit in this approach is the assumption that laboratory measures of performance are relevant to the behaviour of organisms in nature, but this assumption is rarely investigated.

Studies of the locomotor capabilities and escape behaviour of squamate reptiles, however, are an exception. Laboratory studies have demonstrated that the maximum sprinting capabilities of lizards and snakes are affected by a wide variety of factors, including body temperature, gravidity, tail loss and exhaustion (reviewed in Garland & Losos 1994). In turn, field studies have documented that when maximum locomotor ability is impaired, individuals alter their behaviour by fleeing at a greater distance as a predator approaches, relying more on crypsis or aggressively defending themselves (reviewed in Greene 1988; Garland &

Losos 1994). Many of these studies share a similar conceptual approach in studying, first, how changing conditions, either external (e.g. temperature) or internal (e.g. exhaustion), lead to decreased locomotor capabilities, and second, how organisms respond to these reduced capabilities by using a different escape strategy. None of these studies, however, has evaluated whether the effectiveness of the alternative strategy is also affected by changing conditions. Under such circumstances, one might expect the organism to use the strategy that is least compromised by conditions, but this hypothesis has never been tested.

In the present study, we investigated whether escape behaviour varies as a consequence of substrate characteristics. Lizard sprint speed, clinging ability and agility are affected by support diameter (Losos & Sinervo 1989; Sinervo & Losos 1991; Losos et al. 1993). We predicted that lizards should alter their escape behaviour as a function of support diameter. We simultaneously considered the effect of substrate on two methods of escape, running and jumping, and inquired whether lizards altered their escape behaviour to use the more effective means of escape.

This study was divided into three parts. First, laboratory studies investigated whether the

Correspondence: J. B. Losos, Department of Biology, Campus Box 1137, Washington University, St Louis, MO 63130-4899, U.S.A. (email: losos@biodec.wustl.edu).

Table I. Snout–vent length (SVL), residual limb length, perch height and perch diameter for each species

Species	SVL (mm) ($\bar{X} \pm$ SE)	Relative hind limb length*	Perch height† (m)	Perch diameter† (cm)
A. carolinensis	65.4 ± 0.6	-0.15	1.8	4.7
A. grahami	65.3 ± 1.5	0.04	2.5	17.7
A. gundlachi	61.1 ± 1.0	0.21	1.3	33.5
A. lineatopus	55.3 ± 1.3	0.13	1.0	26.0
A. sagrei	58.6 ± 0.6	0.06	0.4	15.4

*Residual of a regression of ln(hind limb length) on ln(snout–vent length) for 53 species (J. B. Losos, unpublished data).
†Data for *A. carolinensis* collected on various Bahamian islands (unpublished data); other data from Losos (1990a).

sprinting and jumping capabilities of *Anolis* lizards were affected by perch diameter (experiments 1 and 2). Second, based on the results of these experiments, we formulated predictions about how the species should differ in escape behaviour, assuming that escape behaviour is influenced by functional capabilities (discussion of experiments 1 and 2). Finally, we tested these predictions by measuring the effect of perch diameter on escape behaviour in nature of all five species (experiment 3).

Study Species

We studied the functional capabilities and escape behaviour of five species of *Anolis* lizards. Although similar in size, the species included in this study differ morphologically and ecologically (Table I); the relatively longer-limbed species use broad surfaces low to the ground (e.g. tree trunks), whereas species with shorter hind limbs perch higher and on thinner surfaces (Collette 1961; Losos 1990a; Losos et al. 1994).

LABORATORY MEASUREMENTS OF LOCOMOTOR CAPABILITIES

Experiment 1: Sprinting Ability

Methods

The effect of surface diameter on sprinting capabilities is known for *A. grahami*, *A. gundlachi*, *A. lineatopus* and *A. valencienni* (Losos & Sinervo 1989). We supplemented these data by measuring the sprinting capability of two additional species,

A. carolinensis and *A. sagrei* (owing to differences in racetrack design and laboratory settings, some aspects of the experimental protocol, such as precise rod sizes, deviate slightly from those in Losos & Sinervo 1989).

Lizards for this experiment came from Georgetown, Bahamas (*A. sagrei*) and La Place, Louisiana (*A. carolinensis*). We conducted sprint trials within 8 weeks of capture. Between trial days, lizards were maintained in laboratory rodent cages, misted once or twice daily and provided with crickets every 2–3 days. On trial days, we placed lizards in plastic cups within an environmental chamber set to 30°C (for field body temperatures for these species, see Clark & Kroll 1974; Huey & Webster 1976; Lister 1976).

We covered rods with fibreglass window screening (1.6 mm mesh) to provide good traction and measured sprint speed on rods of the following diameters (cm): 0.6, 1.6, 2.5, 5.1. As the lizard ran up the track (which was angled at 38°), it interrupted infrared light beams stationed at 0.25 m intervals. A computer connected to photocells then calculated sprint speed for each interval. We excluded trials in which the lizard ran at sub-maximal speed (recognized by running posture and gait). Lizards that jumped off the rod or noticeably stumbled were re-tested immediately. We ran lizards on each rod once per day, with at least 1 h separating trials.

We conducted four sets of trials with at least 4 days between trials. We randomized the order of supports between days such that no lizard ran on any support in the same position more than once (e.g. for each lizard, we used the largest support in

the first trial of the day only once). For each lizard, the fastest interval on a rod between the four trials was considered the maximum speed for that rod size. Some lizards produced no acceptable runs on some rod sizes, particularly the 0.6-cm rod.

For statistical analyses, we used each lizard's maximal sprint speed on each rod (assuming that the lizard had produced an acceptable trial on that rod size). We used two statistical tests to determine whether, within a species, rod diameter affected sprint performance. First, we ranked performance on the four dowels and used Kendall's test of rank concordance to evaluate whether the relative ranking of dowels was similar between individuals. Second, we compared whether more individuals ran faster on the largest versus the smallest diameter rod using Wilcoxon's signed-rank test (both analyses followed Siegel & Castellan 1988). Statistical tests were one-tailed because we predicted that sprinting ability would decline with decreasing perch diameter (e.g. Losos & Sinervo 1989; Sinervo & Losos 1991).

Previous work led to the hypothesis that the effect of diameter on sprinting ability is a function of hind limb length; longer-legged species appear to suffer greater reductions in sprint speed on narrow diameter supports than shorter-legged species (Losos & Sinervo 1989; see also Sinervo & Losos 1991). We statistically tested this hypothesis by combining our data for *A. carolinensis* and *A. sagrei* with previously collected data (Losos & Sinervo 1989). For each species, we calculated the slope of the regression of speed on support diameter. We then regressed this slope against relative hind limb length, which was calculated for each species as the residual of the regression of limb length on snout–vent length for 53 species of *Anolis* (J. B. Losos, unpublished data).

Comparative studies are statistically invalid unless information on the phylogenetic relationships of taxa are incorporated into the analysis (Felsenstein 1985; Losos & Miles 1994). Phylogenetic relationships of *Anolis* are currently unsettled (Cannatella & de Queiroz 1989; Williams 1989; Guyer & Savage 1986, 1992; Hass et al. 1993). Consequently, we conducted comparative analyses using the independent contrasts method (Felsenstein 1985; Garland et al. 1992) twice using two different hypotheses of relationships between the *Anolis* species included in this analysis.

Both phylogenetic hypotheses are consistent with those in Losos (1990a, b). In the first analysis, *A. carolinensis*, which was not included in the phylogeny presented in Losos (1990a, b), is placed as the sister taxon relative to the other species in this analysis with a branch length of 28 (based on Shochat & Dessauer 1981). In the second analysis, *A. carolinensis* is placed as the sister taxon to the three Jamaican anoles, with *A. gundlachi* the sister taxon to all four (following Guyer & Savage 1986). Because this phylogeny is inconsistent with the distances generated in immunological studies (Shochat & Dessauer 1981; Hass et al. 1993), we could not assign branch lengths. Thus, this analysis assumed a speciational mode of character evolution in which the expected change on all branches of the phylogeny is equal (Garland et al. 1992). For the first phylogeny, the effectiveness of standardization of the contrasts was verified following Garland et al. (1992); the speciational mode of evolution assumed in the second phylogeny does not require this diagnostic test (Garland et al. 1992). Because of the uncertainties concerning anole phylogeny, we present the results of both phylogenetic and non-phylogenetic analyses. The former are evaluated using regression through the origin (Garland et al. 1992) and the latter using Spearman's rank correlation test. Ideally, we also would have calculated the residuals of hind limb length versus snout–vent length using contrasts (cf. Losos 1990b). This was not possible, however, because a robust phylogenetic hypothesis for the entire genus *Anolis* does not exist.

Results

In both *A. carolinensis* and *A. sagrei*, sprint speed declined moderately between 5.1- and 1.6-cm dowels and then dropped sharply on the 0.6-cm dowel (Fig. 1; *A. sagrei*: signed-rank test, $z=2.67$, $N=9$, $P<0.005$; Kendall's $W=0.51$, $N=7$, $P<0.025$; *A. carolinensis*: $z=2.03$, $N=7$, $P<0.025$; $W=0.63$, $N=5$, $P<0.05$). For the six species of *Anolis* studied to date, analysis of covariance indicates that heterogeneity exists in the effect of diameter on sprint speed ($F_{1,5}=5.20$, $P<0.01$). Between these species, a strong positive correlation exists between relative limb length and the effect of diameter on sprint speed (Fig. 2; Spearman $r_S=0.94$, $P<0.005$; phylogeny 1: $r^2=0.85$, $P<0.01$; phylogeny 2: $r^2=0.86$, $P<0.01$).
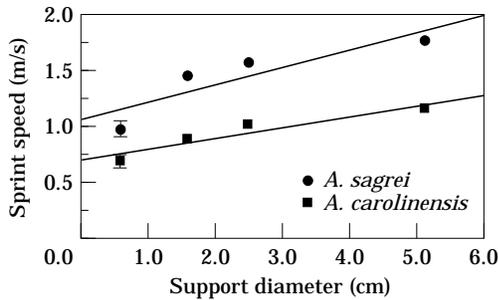
Figure 1. Sprint speed ($\pm$ SE) versus support diameter for *A. sagrei* (N=9, 16, 16, 17, from smallest to largest rod) and *A. carolinensis* (N=6, 17, 18, 22).

Figure 2. Relative hind limb length versus slope of sprint speed on support diameter for six *Anolis* species. Relative hind limb lengths are residuals of the regression of ln(hind limb length) onto ln(snout–vent length) for 53 species of *Anolis*. Slope of sprint speed on support diameter is the regression slope, as in Fig. 1 for *A. sagrei* and *A. carolinensis*.

Experiment 2: Jumping Ability

Methods

Studies on jumping ability initially focused on *A. carolinensis* and *A. sagrei*. Lizards in these studies came from Sarasota, Florida (*A. sagrei*) and Oahu, Hawaii (*A. carolinensis*). We conducted all jumping trials within 4 weeks of capture. Between trial days, lizards were housed individually in plastic shoe boxes, provided with two crickets, and misted with water. We placed lizards into plastic cups and moved them to the experimental room the night before trials; room temperature was $28.5 \pm 1.5°$C.

We measured jumping ability by placing a lizard on a dowel covered with 1.5 mm fibreglass mesh 28 cm above the floor; we chose this height to correspond with previous studies of anole jumping (Losos 1990b). Lizards were oriented perpendicular to the dowel, directed towards a refuge (pile of sticks in a dark box laid on its side in the corner of the room) that was just beyond jumping distance, and induced to jump by taps to the base of the tail. We then measured the horizontal distance of the jump. Some lizards did not make an acceptable first jump; for example, they were not balanced on the dowel, did not jump perpendicular to the dowel, did not adopt a good jumping posture (cf. Bels & Theys 1989), or made an obviously short jump. These lizards were immediately induced to jump a second time. We tested each lizard 12 times with three jumps on each of four dowel sizes: 0.4, 1.0, 1.6, 2.7 cm. We conducted two trials per day with a minimum of 6 h between trials. Lizards received 1–2 days of rest after every 2 days of testing. Each lizard jumped once off each dowel size in each 2-day
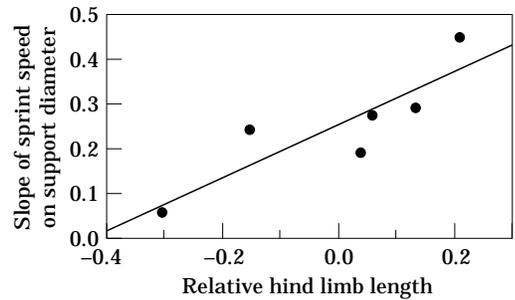
set of trials, but the order of presentation was randomized between individuals within sets of trials and between sets of trials.

Subsequent to these studies, we decided to measure jumping ability in three of the four species included in Losos & Sinervo's (1989) study of sprinting ability: *A. grahami*, *A. gundlachi*, and *A. lineatopus* (the fourth species, *A. valencienni*, was not available in sufficient numbers). Based on the relatively slight effect of perch diameter on jumping ability detected for *A. carolinensis* and *A. sagrei* (see below), we only used the largest and smallest dowels in these experiments. Because these studies were conducted at field sites, we modified our experimental protocol in several ways. Lizards were captured and immediately placed into plastic cups. We conducted jumping trials on the subsequent 3 days. On each day, each lizard was jumped once on the large and once on the small dowel (order randomized between individuals) with a minimum of 5 h between trials. We conducted trials at room temperatures of $30.0 \pm 2.5°$C.

Statistical analyses were the same as those used in the sprinting experiment.

Results

There was no significant effect of dowel diameter on jump performance in *A. carolinensis* (comparison between largest and smallest dowels, Wilcoxon signed-rank test: z=0.83, N=17, P<0.25; Kendall's coefficient of concordance:
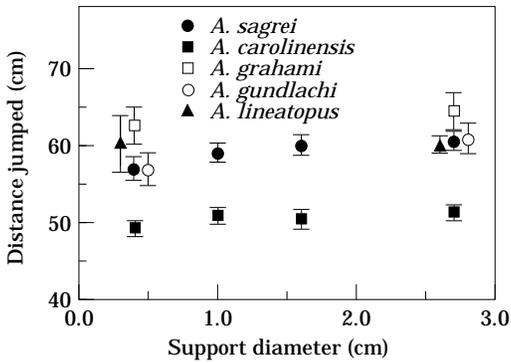
Figure 3. Jump distance ($\pm$ SE) versus support diameter for five *Anolis* species. We collected jumping data for *Anolis grahami*, *A. gundlachi* and *A. lineatopus* only on the largest and smallest diameter rods. Points are offset for 0.4- and 2.7-cm rods for visual clarity. Sample sizes (from smallest to largest rod): *A. sagrei* (13, 14, 13, 17), *A. carolinensis* (18, 17, 16, 19), *A. grahami* (8, 8), *A. gundlachi* (13, 13), *A. lineatopus* (7, 7).

$W=0.03$, $N=14$, $P<0.40$), *A. grahami* ($z=0.63$, $N=8$, $P<0.30$) and *A. lineatopus* ($z=0.09$, $N=7$, $P<0.95$; Fig. 3). By contrast, two species jumped further on larger diameter supports, although the difference was relatively slight: *A. gundlachi* (Fig. 3; $z=2.23$, $N=13$, $P<0.02$) and *A. sagrei* (comparison of largest and smallest dowel: $z=2.10$, $N=13$, $P<0.025$; rank concordance: $W=0.12$, $N=11$, $P<0.15$).

Discussion

In summary, sprint speed declined strongly with decreasing diameter in the species tested. By contrast, jumping ability declined only slightly, if at all, with decreasing diameter. This differential effect of support diameter on sprinting and jumping abilities suggests that lizards may alter their behaviour depending on their location to maximize their locomotor capabilities.

Based on this observation, we formulated two predictions about the effect of functional capabilities on escape behaviour. First, we predicted that within species, the frequency with which lizards escape by jumping should increase with decreasing diameter. This prediction follows from the observation that jumping ability is less affected than sprinting ability by narrow support diameters.

Second, we predicted that between species, the relative difference in effect of diameter on the two performance abilities should be proportional to the corresponding change in escape behaviour as diameter changes. To calculate the relative change in jumping versus sprinting ability as a function of diameter, we first calculated by interpolation the sprint speeds expected for *A. carolinensis* and *A. sagrei* on the largest and smallest diameters used in Losos & Sinervo (1989) to account for the different rod sizes used in the two experiments. We then calculated for each species the ratio of performance on the smallest versus largest diameter rod for both sprinting and jumping. Finally, to assess the change in relative performance capability (sprinting versus jumping) as diameter decreases, we calculated the ratio of these two ratios.

This ratio thus represents the extent to which, as diameter decreases, running capabilities decline relative to jumping abilities. For all species, the ratio is less than 1.0, which indicates that running ability decreases more than jumping ability as diameter decreases. The ratio was lowest for *A. gundlachi* (0.63), followed by *A. lineatopus* (0.69), *A. carolinensis* (0.74), *A. sagrei* (0.78) and *A. grahami* (0.80). We thus predicted the same ordering in the effect of diameter on escape behaviour in nature, with *A. gundlachi* expected to show the largest increase in jump frequency as diameter decreases and *A. grahami* expected to show the least effect.

Experiment 3: Escape Behaviour in Nature

Methods

We collected data at the following times and places: *A. carolinensis* and *A. sagrei*: 1–26 April 1992 on various islands in the Bahamas, most of which were inhabited by both species (Losos et al. 1994); *A. grahami* and *A. lineatopus*: 28 June–11 July 1994 at various localities in Jamaica (the same localities as in Losos 1990b, except Southfield); *A. gundlachi*: 18–26 June and 12–27 July 1994 at the El Verde Field Station, Luquillo Mountains, Puerto Rico.

We approached adult male lizards in a consistent manner and at a constant pace (approximately 30 m/min) until they fled (for the purposes of this study, we equated fleeing with escape behaviour). Escape behaviour was scored as run or jump

(cases in which a lizard ran a few steps before jumping were scored as jumps). We only collected data between 0900 and 1730 hours on warm days in which lizards had the opportunity to thermoregulate at preferred body temperatures. We searched in a given area only once to avoid repeatedly testing the same animal and only included lizards that were stationary when first observed. The diameter of the surface that the lizard initially occupied was subsequently measured; lizards on the ground were not included.

Differences in the availability of nearby structures as a function of perch diameter could confound a relationship between escape behaviour and diameter (e.g. lizards might jump more frequently from narrow perches if such perches tended to be closer to other objects to which they could jump). To investigate this possibility, we measured the habitat matrix (i.e. the ensemble of structures of varying dimensions and positions in the vicinity of a lizard; Moermond 1979; Pounds 1988) for three species: *A. grahami*, *A. gundlachi* and *A. lineatopus*. For each lizard, we measured the distance from its original position to the nearest structure in each of the following classes (following Pounds 1988; Losos 1990a): (1) branches and stems 0.2–1.0 cm in diameter, as well as leaves; (2) branches and stems 1.0–1.5 cm; (3) branches, stems and rocks larger than 1.5 cm. In addition, we measured perch height for all five species.

All habitat measurements were ln-transformed for statistical analysis. We used linear regression to investigate whether frequency of escape by jumping is a function of perch diameter. Jumps were coded as 1 and non-jumps as 0. Analyses using the non-parametric Kolomogorov–Smirnov test yielded similar conclusions for each species and are not presented.

To examine the habitat matrix data, we separately analysed the data for each species and took two approaches. First, we used discriminant functional analysis (DFA) to investigate whether jumpers could be distinguished from non-jumpers on the basis of habitat matrix. Second, we conducted a principal components analysis (PCA) to reduce the dimensionality of the data and remove collinearity of variables. We then asked whether the position on each PCA axis differed between jumpers and non-jumpers. We found only one significant difference between the position of

jumpers and non-jumpers on any of the PCA axes (PCA I for *A. gundlachi*; see below). To factor out the effect of habitat matrix (as represented by PCA I) on escape behaviour in *A. gundlachi*, we calculated the residuals of the regression of perch diameter on habitat matrix. We then tested whether a relationship existed between relative perch diameter (i.e. the size of a perch relative to that expected given the habitat in which it occurs) and escape behaviour.

Results

In all species, jumping was a relatively infrequent means of escape from perches greater than 5 cm in diameter (<15%), but increased in frequency with decreasing diameter to greater than 50% in some species (Fig. 4). This increased jumping frequency with decreasing diameter was significant for four species and non-significant, but in the same direction for *A. carolinensis* (Table II). Analysis of covariance indicated that the rate of increase in jumping frequency with decreasing diameter differed between species (heterogeneity of slopes, $F_{4,668}=4.64$, $P<0.002$). Post-hoc analyses on subsets of the data indicate that two groups of species exist with respect to these differences. The effect of changing diameter did not differ between *A. grahami*, *A. gundlachi* and *A. lineatopus* (heterogeneity of slopes, $F_{2,268}=0.97$, $P<1.0$; difference in intercepts, $F_{2,270}=1.46$, $P<0.25$), nor between *A. carolinensis* and *A. sagrei* (heterogeneity of slopes, $F_{1,400}=0.59$, $P<0.45$; difference in intercepts, $F_{1,401}=0.38$, $P<0.55$).

We tested our performance-based predictions by calculating the slope of escape behaviour on perch diameter (Fig. 4). We predicted that a relationship should exist between this slope and the ratio in performance decline of running versus jumping. The highest (i.e. most negative, because jumping was scored as 1 and running as 0) slope was displayed by *A. grahami* (−0.228), exactly opposite to our predictions, followed by *A. lineatopus* (−0.215), *A. gundlachi* (−0.211), *A. sagrei* (−0.091) and *A. carolinensis* (−0.056). We found no relationship between relative performance decrement (as calculated in the Discussion of Laboratory Measurements of Performance Capability) and slope of escape behaviour ($r_S=−0.20$, $P>0.50$; phylogeny 1: $r^2=0.00$, $P>>0.50$; phylogeny 2: $r^2=0.18$, $P>0.40$).

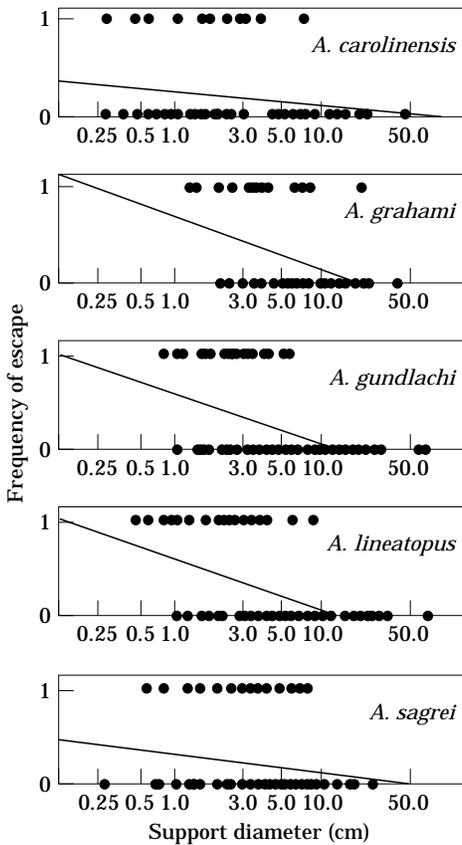The habitat of jumpers could not be distinguished from that of non-jumpers in the

Figure 4. Frequency of escape by jumping as a function of support diameter. Escapes by jumping scored as 1, non-jump escapes scored as 0. Slopes are the linear regression of escape on diameter.

Table II. Effect of perch diameter on jump frequency

Species	r^2	F	df	P
A. carolinensis	0.015	2.02	1,64	<0.17
A. grahami	0.151	10.75	1,54	<0.005
A. gundlachi	0.263	40.69	1,110	<0.001
A. lineatopus	0.220	30.58	1,104	<0.001
A. sagrei	0.049	18.31	1,336	<0.001

discriminant functional analysis for either *A. grahami* (Wilks' $\lambda=0.907$, $F_{4,20}=0.51$, $P>0.70$) or *A. lineatopus* ($\lambda=0.96$, $F_{4,62}=0.61$, $P>0.65$). By contrast, for *A. gundlachi*, the discriminant function was significant ($\lambda=0.85$, $F_{4,105}=4.57$, $P<0.002$) and correctly classified 78.2% of the lizards as jumpers or non-jumpers.

Table III. Principal component analyses of habitat matrix data

	Principal components axis		
	I	II	III
A. grahami			
Height	0.68	0.51	0.46
Nearest small perch	0.84	0.19	−0.13
Nearest medium-sized perch	0.44	−0.82	0.37
Nearest large perch	0.80	−0.19	−0.34
% Variance explained	50.4	25.0	14.4
A. gundlachi			
Height	−0.01	0.97	0.24
Nearest small perch	0.78	0.20	−0.36
Nearest medium-sized perch	0.82	−0.02	−0.21
Nearest large perch	0.59	−0.21	0.77
% Variance explained	40.8	25.5	20.6
A. lineatopus			
Height	0.12	−0.95	0.28
Nearest small perch	0.75	−0.11	−0.27
Nearest medium-sized perch	0.74	0.05	0.56
Nearest large perch	0.60	0.32	0.04
% Variance explained	37.3	25.5	20.3

These results were confirmed by PCA. Patterns of loadings of habitat variables on PCA axes were similar for *A. gundlachi* and *A. lineatopus*, both of which differed from *A. grahami* (Table III). The habitat matrix for jumpers did not differ from that of non-jumpers for any of the PCA axes for either *A. grahami* or *A. lineatopus* (*t*-test: $P>0.15$ in all cases). By contrast, in *A. gundlachi* jumpers scored lower than non-jumpers on PCA I ($t=3.35$, $df=108$, $P<0.001$), which indicates that lizards jumped more frequently in habitats where potential targets to jump to were closer. Thus, jumping frequency of *A. gundlachi* was related to both perch diameter and habitat matrix, which suggests that the two variables may be confounded. Indeed, a relationship existed for *A. gundlachi* between habitat matrix (as defined by PCA I) and perch diameter ($r^2=0.069$, $P<0.005$; Fig. 5). With this confounding effect removed by using residuals (see Methods), however, a negative relationship still existed between jump frequency and relative perch diameter ($r^2=0.18$, $P<0.001$).

Only perch height data were available for *A. carolinensis* and *A. sagrei*. In *A. carolinensis*, jumpers and non-jumpers did not differ in perch height ($t=0.83$, $df=72$, two-tailed $P<0.45$). By contrast, in *A. sagrei* jumpers had lower perches than non-jumpers ($t=3.06$, $df=361$, $P<0.002$).
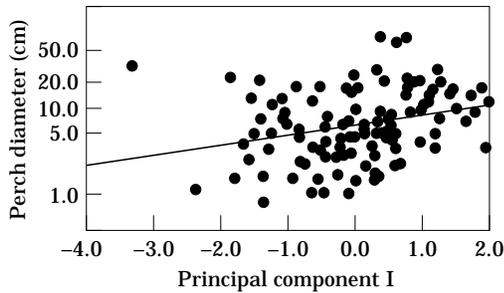
Figure 5. Relationship between habitat matrix (as represented by PCA I) and perch diameter for *A. gundlachi*. Lizards in habitats in which the nearest object to which they could jump was nearby (i.e. negative score on PCA I) tend to occur on relatively narrow perches. To factor out the confounding effect of habitat matrix on perch diameter, residuals of this regression were calculated.

For *A. sagrei*, however, perch height and diameter were not correlated ($r=0.089$, $df=344$, $P<0.15$) and a multiple regression ($r^2=0.07$, $P<0.001$) indicated significant effects for both perch diameter ($P<0.001$) and perch height ($P<0.001$) on jumping frequency. We thus concluded that the relationship between jumping frequency and perch diameter was not confounded by correlations with other aspects of the habitat matrix.

GENERAL DISCUSSION

Mechanistic approaches provide the opportunity to understand how differences in organismal attributes lead to interspecific variation in behaviour and ecology (Moermond 1986; Price 1986; Schoener 1986). Here we have applied this approach to understand one of the most critical aspects of an animal's life, its escape behaviour. In particular, we used studies of performance capability to predict how five species of lizards should alter their escape behaviour as a function of support diameter. We then conducted field studies that demonstrated that lizard behaviour conforms to some, but not all, of these predictions.

Performance, Predictions and Field Behaviour

The results support our hypothesis that within species, the effect of perch diameter on escape behaviour can be predicted from knowledge of how diameter affects differences in locomotor

capacities. Our laboratory studies revealed a difference in the effect of perch diameter on jumping and sprinting abilities. Jumping ability was barely affected, if at all (decreases of 0–7%), by decreasing perch diameter, whereas sprinting ability declined markedly (23–44%) with perch diameter in the five *Anolis* species examined (*A. valencienni*, for which we have no data on jumping or escape behaviour, does not show such a decline in sprinting ability; Losos & Sinervo 1989).

Because running capabilities decline more than jumping abilities with decreasing diameter, we predicted that all species would increasingly rely on jumping for escape as perch diameter declined. This hypothesis was verified for all species except *A. carolinensis*, for which the relationship was non-significant, but tending in the same direction.

A more quantitative prediction was not confirmed, however; no relationship was found between the relative effect of diameter on running versus jumping and the degree to which behaviour is affected by perch diameter. The failure of this prediction indicates that other factors (e.g. predator type, climate, light, social status, time of day, season) may affect escape behaviour. We conclude that it is not possible to base mechanistic explanations of the behaviour of these lizards solely on their own capabilities and ecological circumstances.

The Insensitivity of Jumping Ability to Support Diameter

All studies to date of the habitat-dependence of locomotor performance in small animals have shown that ecologically relevant variation in substrate affects locomotion (sprinting: Huey & Hertz 1982; Carothers 1986; Losos & Sinervo 1989; Sinervo & Losos 1991; Blumstein 1992; Losos et al. 1993; clinging: Losos et al. 1993; climbing: Thompson 1990). This study is the first of which we are aware to examine the effect of variation in substrate on jumping performance. A priori, one might expect support diameter to greatly affect jumping ability. On narrow supports, lizards might have difficulty maintaining balance and adopting jumping posture.

Our results do not meet these expectations. Although our data suggest that jump distance may decline slightly on narrow supports, this decrease may be biologically inconsequential: the maximum decrease in jumping ability from the

0.4- to 2.7-cm perches was 6.7% in *A. gundlachi*;
by contrast, no decline at all was evident in
A. lineatopus.

Lizards in nature, particularly when attacked or
pursued, may have less time to prepare to jump
than lizards had in these experiments (Pounds
1988). In such situations, the ability to position
itself properly for jumping may well be affected by
perch diameter. Similarly, the bending and sway-
ing of structural supports (which was prevented in
the experiment) may also affect locomotor per-
formance (Cartmill 1985; Alexander 1991). Anole
species vary in muscular and osteological speciali-
zations of the pectoral girdle for manoeuvring
through a three-dimensional matrix composed of
small and irregular supports (Peterson 1972).
More detailed studies may yet reveal interspecific
differences in the effect of perch diameter on some
aspects of jumping performance.

Biomechanical considerations may explain why
running ability is affected by perch diameter but
jumping ability is not. The flexibility and grasping
ability of anoles allows them to support them-
selves on perches on which more terrestrial lizards
would immediately fall (cf. Sinervo & Losos
1991). These capabilities appear to be sufficiently
developed in all anoles (few anoles are more
terrestrial than *A. sagrei*) that jumping ability is
not compromised on even very narrow supports.
In contrast to the stationary position of a jumping
lizard, a running lizard constantly raises and
lowers its legs, shifts its centre of balance, and
grasps and releases the substrate. These actions
are likely to be affected by perch diameter,
although more detailed biomechanical analyses
are needed.

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