



Variation in morphology, gait characteristics and speed of locomotion in two populations of lizards

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Received 1 July 1997; accepted for publication 27 October 1997

Locomotor behaviour varies between two subspecies of the Spanish wall lizard *Podarcis hispanica*. One subspecies inhabits the Columbretes islands, the other lives on the Spanish mainland. Size standardized voluntary speeds (as measured in unrestrained laboratory conditions) are lower in the island population (*P. h. atrata*) than in the mainland population (*P. h. hispanica*). Maximal running performance (when chased) is much higher in the mainland population than in the island population. High speed video recordings show that subspecies differ in gait characteristics: individuals from the mainland modulate running velocity primarily by modifying stride length, individuals from the island primarily by altering stride frequency. *P. h. hispanica*'s strategy for modulating speed probably allows this mainland subspecies to attain higher maximal speeds than the island subspecies *P. h. atrata*. Theoretical considerations suggest that at high speeds, *P. h. hispanica*'s running style is energetically more favourable, but this hypothesis awaits experimental verification. We suggest that the differences in locomotion efficiency between the subspecies result from differences in predation pressure between the mainland and the island. The mainland study site has a higher predator diversity and offers less hiding opportunities to the lizards.

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ADDITIONAL KEY WORDS:—Ecomorphology – locomotion – performance – gait characteristics – lizards – intraspecific variation.

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INTRODUCTION

Lizard locomotion has been the topic of many ecological, ecomorphological and ecophysiological studies. There are several good reasons for this: (1) locomotor abilities are considered to be crucial for capturing prey, escaping from predators and during social interactions in many lizard species; locomotion is therefore an ‘ecologically relevant’ function (Arnold, 1983; Losos 1990a,b; Garland, Hankins & Huey, 1990; Jayne & Bennett, 1990; Garland, 1994); (2) variation in locomotor performance (speed, stamina, etc.) can be assessed with relative ease in the laboratory; (3) the candidate morphological and physiological origins of this performance variation have been identified (review in Garland & Losos, 1994) and (4) inter-individual variation in locomotor capacities is repeatable over long time periods and genetically based, and therefore bears the potential for evolution by natural selection (Huey & Dunham, 1987; Van Berkum & Tsuji, 1987; Tsuji *et al.*, 1989).

While many studies have explored causes and consequences of variation in locomotor performance within populations and among species, differences between conspecific populations have received far less attention. This is surprising, because interpopulational differences are essential to evolutionary analyses. Geographic variation is the smallest amount of evolution that can be detected in nature unless populations are followed through time (Arnold, 1981; Garland & Adolph, 1991; Garland & Losos, 1994). The few studies that have compared locomotor capacities among populations obtained promising results. Crowley (1985a,b) suggested that differences in sprint speed between populations of *Sceloporus undulatus* from Colorado and New Mexico may correlate with differences in predator density between both localities. Snell *et al.* (1988) compared sprint capacities of *Tropidurus albemarlensis* from sparsely and heavily vegetated areas of Isla Plaza Sur (Galápagos). Males, but not females, from the exposed habitat are faster than their conspecifics from the covered areas. The authors suggest that sexual selection for territorial defence favours short approach distances in males, and leads to natural selection for higher speed in the open habitat. Huey & Dunham (1987) and Huey *et al.* (1990) found differences in sprint speed between two Texas populations of *Sceloporus merriami* to be consistent across years. Remarkably, the lizards from the area with the highest rate of predation were slower than those from the area with low predation rate. Sinervo and Losos (1991) showed how an evolutionary trade-off between speed and ‘sure-footedness’ resulted in interpopulational variation in arboreal locomotor performance in *Sceloporus occidentalis*. In this species, more terrestrial populations run faster on thick rods, but slower on thin rods than did lizards from more arboreal populations.

Differences in locomotor performance between populations can be analysed in mechanistic and evolutionary terms (Huey *et al.*, 1990). In the studies mentioned above,

the mechanical causes for the observed differences in speed remained unclear. Even simple biomechanical predictions (e.g. longer-legged lizards should be able to run faster)—although corroborated by interspecific comparisons—do not seem to hold when populations are compared. Possibly, interpopulational differences in ‘design’ (morphology, physiology, biochemistry) are subtle and difficult to demonstrate, especially with small sample sizes. Recent ecomorphological analyses (e.g. Moreno & Carrascal, 1993; Miles, 1994) have shown that minor morphological changes may have important consequences for performance. Also, the studies may have centred on the wrong design parameters. The quantification of design is typically restricted to measuring hind limb lengths, but locomotor performance is the outcome of a complex interaction between various morphological, physiological and biochemical traits, all of which may vary between populations (Garland, 1994). Variation in motivation is an additional potentially confounding factor. Differences in maximal sprinting speed between populations (as measured on a race track) may reflect differences in responsiveness towards human ‘harassment’ rather than divergence in physical abilities. No studies have tested whether lizards that show high maximal sprinting performance when chased along a race track, also move fast in unrestrained conditions.

The evolutionary causes of geographical variation in locomotor performance may be even more difficult to assess. Variation in predation pressure is often considered a likely candidate (Crowley, 1985a,b; Snell *et al.*, 1988; but see Huey *et al.*, 1990), but it is difficult to assess.

In a previous paper (Van Damme, Aerts & Vanhooydonck, 1997), we reported substantial differences in sprint speed between two subspecies of the lizard *Podarcis hispanica*. Lizards from a population of *P. h. hispanica* on the eastern coast of Spain are on average smaller than those from the island subspecies *P. h. atrata*, but sprint much faster when chased along an experimental track. This is true regardless of the inclination of the track; there was no trade-off between sprinting on a flat surface and climbing on a slope. The proximate causes for the observed differences in maximal locomotor speed remained unclear.

In this paper, we extend our measurements on the locomotor speed of *P. hispanica* and include observations from lizards in unrestrained conditions. We explore the potential causes for the observed differences in maximal sprinting capacity between both populations of lizards. Rather than assess various morphological, physiological and biochemical traits directly, we opted to study different gait characteristics (i.e. step length, stride length, stride frequency and duty factor) in a number of lizards from the two populations. This approach is less time-consuming, but is still likely to produce information on helping to assess which design parameters can be relevant. Studying the gait characteristics can thus be seen as a convenient intermediate step between design and performance in the study of the performance gradient (Arnold, 1983; White & Anderson, 1994). Finally, we speculate on the evolutionary origins of the interpopulational differences in locomotor speed.

MATERIAL AND METHODS

Study animals

We studied the same populations of *Podarcis h. hispanica* and *P. h. atrata* as described in Van Damme *et al.* (1997). *P. h. hispanica* lizards, from a population near the town

of Castellón, Spain, correspond to the image of typical European wall lizards. They are relatively small (adult snout–vent length 40–55 mm), agile and wary animals that are most often seen on or near vertical stone structures (garden walls in the case of the Castellón population). Individuals on the island are larger (adult svl 50–70 mm) and appear to be more stocky than individuals on the mainland. They bask on walls and rocks, but spend most of their time on the ground. *P. h. atrata* is endemic to the Columbretes archipelago, which is situated 50 km from the coast of Castellón. We chose these two populations because we were struck by the apparent difference in locomotor behaviour between them. In their natural surroundings, the mainland lizards seem to move at much higher speeds than the island lizards.

Predation risk in natural environments

Reliable estimates of predation pressure are hard to obtain. Ideally, one would want to have information on mortality rates and causes of death in both populations. It was not possible to gather sufficient data on these topics within the time frame of this study. Instead, we have scanned the literature for records on potential predators for *P. hispanica* and their occurrence at both sites. We also compared the exposure to potential predators at both sites by estimating the availability of hides in the immediate surrounding. Like most lacertids, *Podarcis hispanica* lizards allow potential predators to approach to a certain distance and then dash away in the direction of cover, which may consist of a patch of vegetation, fallen leaves or a crevice in or beneath a rock or wall. We determined the distances between each of 27 (Columbretes) and 30 (Castellón) spots where lizards were seen and the nearest potential hide. In addition, we selected 30 random points in each habitat and for each determined the distance to the closest refuge. The behavioural observations were made on bright days, between 10.00–13.00 and 15.00–17.00 h (MET).

Morphological measurements

Between 14 and 28 September 1994, we captured 64 *P. h. atrata* and 35 *P. h. hispanica* by noose or baited noose and measured the following characteristics to the nearest 0.01 mm using electronic calipers: snout–vent length (SVL), tail length, distance between front and hind limbs, maximal body width and height, length and maximal diameter of the upper and lower front and hind legs, hind and front foot length, length of the fourth toe of the hind foot and the second toe of the front foot. We determined body mass to the nearest 0.01 g on a portable electronic balance (Kern 444-33). After measurement, lizards were released at the site of capture. We used multiple analysis of variance to assess differences between subspecies and sexes in body dimensions, introducing SVL as a covariate. Differences in particular traits were examined using univariate *F*-tests. We checked for isometry by regressing trait values against SVL (both \log_{10} -transformed) and testing whether the resulting slope differed from unity. Because external assessment of morphological features in the field may go with substantial measuring errors (Miles, 1994), we double-checked

our in situ measurements of lengths of hind-limb segments on a subset of 25 lizards using X-rays (Siemens Tridoros-Optimatic 880, 35 kV, 400mas).

Animal maintenance in the lab

Fifteen adult specimens of both subspecies were transported to the laboratory in Antwerp, Belgium for detailed analysis of their locomotor patterns. We selected individuals such that the SVL ranges of both subspecies overlapped (*P. h. hispanica*: 42.8–52.4 mm; *P. h. atrata*: 49.6–68.0 mm). Outside experimentation, lizards were kept in five 100 × 50 cm glass terraria. Two 150 W light bulbs at both sides of the terraria provided light and heat for 10 h/day. Temperature within the terraria ranged from 45°C to room temperature, allowing lizards to thermoregulate. The animals were daily fed abundant amounts of live crickets and mealworms, dusted with vitamins. Water was always available.

Behavioural observations: voluntary and fleeing speed

We videotaped eight *P. h. atrata* (SVL: 49.7–68.0 mm; mass: 2.39–6.27 g) and *P. h. hispanica* (SVL: 47.6–52.4 mm; mass: 2.04–3.29 g) moving freely in a 77.5 × 58 cm terrarium with a substrate of sand and schists. Two 150 W bulbs suspended 20 cm above the substrate at opposite corners of the terrarium provided light and heat during the recordings, so lizards were able to regulate their body temperature within the normal activity range. The animals were filmed with a Canovision EX1Hi 8 mm video camera (50 Hz; = 25 frames/s), 1.5 m above the test-box. The two subspecies were tested in groups of four individuals, with subspecies kept apart. Each specimen was given an individual dot code on its back (non-toxic white make-up creme). Recordings started shortly after introduction of the lizards into the terrarium and lasted 1 hour. After this hour, one of us entered the room, performing abrupt movements above the terrarium to frighten the lizards and to evoke escape responses. We thus obtained recordings of locomotion in unrestrained conditions ('voluntary movements', no observers or other potentially alarming stimuli present) and in a distressing situation ('fleeing').

The Super-8 tapes were copied to VHS-format and provided with a digital time code (Panasonic 7450 with time code generator and computer interface). This allowed precise playback in still mode at a prescribed frame interval. The positions of the lizards were digitized interactively by means of a NAC-400 XY-co-ordinator, connected to the video and the computer.

For the movements under unrestrained conditions ('voluntary locomotion'), we digitized positions of lizards at 10 frame intervals (0.4 s) for a total period of 15 s. Four sequences, taken randomly from the 1 hour recording period, were analysed for each individual lizard. Voluntary speeds were calculated from the distance moved within each 0.4 s interval (total of 2304 samples).

For the movements in distressing conditions ('fleeing'), we selected sequences showing fleeing lizards and digitized positions of the animals frame by frame (0.04 s intervals) during a 1 s period. We digitized five escape sequences for each individual lizard. Fleeing speed was defined as the maximal velocity (over 0.04 s) attained during each escape sequence.

*Gait analysis**Set-up*

We videotaped (NAC-1000 High Speed video; 500 frames/s; illumination 2.4kW Tri-Lite) lizards in dorsal view running on a motorized moving belt to study the different gait characteristics. To facilitate subsequent digitization of the images, we put small white dots (of a non-toxic make-up creme) mid-dorsally on the lizards' pelvis, and on the dorsal and ventral side of the right foot (distally on the metatarsus). After marking, lizards were placed in an incubator at 35°C for at least 1 h prior to experimentation. If it had a body temperature between 33 and 37°C, the lizard was put on the belt and was induced to run by a gentle stroke on the tail base. Typically, lizards would not run at the speed of the moving belt (0.23 m/s), but rather tended to sprint towards the end of the 0.5 m belt. We thus obtained video sequences of lizards running at velocities ranging from 0.18 to 1.37 m/s.

Image analysis

In a first screening, the approximate velocity attained during each recorded running bout was assessed by digitizing (with a NAC-1000 XY coordinator) a marker on the belt (as a reference) and the pelvic marker on the first and last frame of useful sequences. This allowed us to select, per individual, five sequences evenly spread throughout the range of velocities for further detailed analysis. On these sequences, we digitized the dot markings on the belt, the pelvis and right foot for every 0.006 s interval (i.e., every third frame). Only sequences for which the displacement of the pelvic marker against time was linear (i.e. during which lizards were running at a constant velocity) were retained. We were able to obtain a velocity range for 16 individual lizards (8 *P. h. atrata*, SVL : 49.6–62.2 mm; mass: 2.39–7.51 g; 8 *P. h. hispanica*, SVL: 42.8–52.4; mass: 1.58–4.27).

Estimating gait characteristics

As trotting was the only type of gait observed, description of the movement patterns of a single foot sufficed to describe all variables relevant to this study (called gait characteristics further on). We opted to digitize a hind foot because posterior limbs generate most of the propulsive power in these animals (Snyder, 1952). Data were recalculated to a frame of reference moving with the belt, the X-axis oriented parallel to the running direction. The X-coordinates of the digitized points were then plotted against time. We thus obtained three curves for each sequence (Fig. 1): (1) The displacement of the pelvic marker through time. The slope of a least squares linear regression line through these points was taken as an estimate of running velocity (all $r^2 > 0.97$). (2) The displacement of the foot marker against time. This typically resulted in a repetitive series of horizontal plateaus alternated with steep slopes. Each slope corresponds to a forward movement of the foot, while the plateaus represent the phases in which the foot does not move (with respect to the belt) and therefore is in contact with the ground. (3) The displacement of the foot relative to the hip. This curve was obtained by subtracting the X-coordinate of the pelvic marker from that of the foot. The descending parts of this sinusoidally oscillating curve correspond to the propulsive phases. Gait characteristics (stride length and frequency, step length, duty factor) were estimated from these plots (using a Genius GT1212B digitizer).

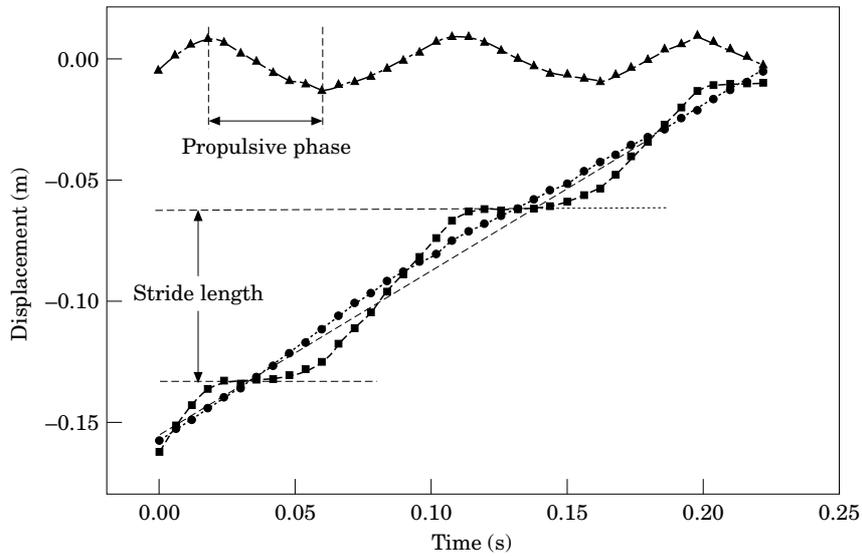


Figure 1. Graphs used to determine the gait characteristics. Symbols mark the displacement of the pelvis (●), the right hind foot (■) and the hind foot relative to the pelvis (▲) in the direction of motion. The displacements were obtained by digitizing markers on the respective body parts on high-speed video sequences. The slope of the linear regression of the pelvis displacement against time (---) is a measure of running speed. In this case, the animal was running at 0.67 m/s (12.75 SVL/s). Notice that step length is further adjusted (see text).

(1) *Stride length* is the distance travelled by the centre of mass of an animal in a complete cycle of limb movements (cf. Alexander, 1977a,b, 1982). The distance between two successive footprints of the same leg is a practical measure for it (McMahon, 1984; Bennett, 1992). For the present analysis stride length was defined as the vertical distance between two successive plateaus in the curve depicting forward displacement of the foot (see Fig. 1). Relative stride length is stride length over SVL.

(2) *Stride frequency* is the number of cycles per second. It was obtained from the ratio of running speed over stride length.

(3) *Step length* is the distance the body moves forward during the stance of a particular leg (Alexander, 1977a; McMahon, 1984). Usually, step length is estimated as the product of running speed and the time period that any part of the foot contacts the ground (i.e. contact time). Our experimental set-up (wide field of view, dorsal-view recordings) did not allow a direct estimation of this time period. As an alternative, we used the time needed for the backward displacement of the foot marker with respect to the hip. This was done by measuring the time increment from one local maximum to the next local minimum on the sinusoidal curves as shown in Figure 1. However, since the foot marker is located distally on the metatarsus (see above), parts of the toes can still be in contact with the ground as the proximal foot segments are already lifted again and move forward with respect to the hip (see e.g. Fieler & Jayne, 1995; Reilly & Delancey, 1997). To account for this, we added the length of the longest toe to the steplength as calculated above. This procedure may result in a (slight) overestimation of the actual steplength. We preferred to overestimate

steplength rather than to underestimate it, because preliminary analyses suggested that one of the principal differences in gait between the two subspecies involved the presence/absence of a floating phase. Underestimating steplength would suggest floating phases where actually there are none. Thus, although data from other lacertid lizards suggest no significant difference in steplengths as determined from dorsal and from lateral views (Vanhooydonck, in prep.), steplengths in this paper should be considered as upper estimates. Relative steplength is steplength over SVL.

(4) *Contact time* (i.e. the period during which a leg is in stance; Alexander, 1977b, 1982) was recalculated according to the adjusted steplength. It is given by the adjusted steplength divided by the running speed. The *recovery time* is the duration of the entire cycle minus the contact time of the leg. The *duty factor* is calculated as the product of the (adjusted) contact time and the frequency (this is the fraction of a stride during which the foot is on the ground). In this way, duty factor is treated in a conservative way too : when it becomes smaller than 0.5 the step cycle includes a floating phase. In such cases, *floating distance* is given by the stride length minus twice the step length (cf. the trotting gait).

Scaling

From a biomechanical point of view, comparing gait data from different sized animals requires scaling to dynamically similar conditions. For terrestrial locomotion, dynamical similarity is obtained when Froude numbers are identical (Alexander, 1992a,b). [Froude number = $U^2/(g \times h)$, with U = running speed, g = gravitational acceleration, h = characteristic length related to locomotion]. The square roots of Froude numbers can be considered as dimensionless velocities (cf. Alexander, 1977a, b). However, from an ecological point of view, absolute (m/s) or relative velocities (SVL/s) seem more relevant. In our study, dimensionless velocities and relative velocities proved to be equivalent (linear regression, $r^2 > 0.99$). This is probably due to the relatively small size range of the animals used. We will therefore express (and regress) cycling frequency, relative stride length, relative steplength and duty factor against SVL/s. Contact and recovery times are regressed against frequency.

We tested for inter-subspecies differences in the relationships between the gait characteristics and relative velocity (or frequency in case of contact and recovery times) by calculating individual regression lines (both variables \log_{10} transformed) and comparing slopes and intercepts using *t*-tests.

RESULTS

Habitat quality: predator diversity

Predator diversity is much lower in the island than in the mainland study site (Table 1). Many birds, and all mammals and snakes that prey on *Podarcis hispanica* on the mainland of Spain are absent from Columbretes Islands.

Habitat quality: availability of hides

Lizards from both sites were on average closer to a potential refuge than the randomly selected points (Mann–Whitney-U-tests, both $P < 0.05$). Lizards seen at the

TABLE 1. Potential predators of *Podarcis hispanica* and their occurrence on the mainland of Spain (Castellón) and on Columbretes Islands (+ = present, - = absent, m = bird species that call at Columbretes Islands during their spring and/or autumn migration. References are to papers that have identified the animals as lizard predators

Predator	Mainland	Island	References
MAMMALS			
<i>Atelerix algirus</i> (Vagrant Hedgehog)	+	-	Reeve, 1994
<i>Erinaceus europaeus</i> (Hedgehog)	+	-	Reeve, 1994
<i>Vulpes vulpes</i> (Red Fox)	+	-	Sequiera, 1980
<i>Mustela nivalis</i> (Weasel)	+	-	Erlinge, 1975
<i>Putorius putorius</i> (Polecat)	+	-	Walton, 1977
<i>Martes foina</i> (Beech Marten)	+	-	Heptner & Naumov, 1974
<i>Felis silvestris catus</i> (Domestic Cat)	+	-	Boag, 1973; Fitzgerald, 1988
BIRDS			
<i>Bubulcus ibis</i> (Cattle Egret)	+	-	Ruiz, 1985
<i>Ardea cinerea</i> (Grey Heron)	+	m	Castilla & Bauwens, 1996
<i>Ciconia ciconia</i> (White Stork)	-	m	Lázaro, 1984, Castilla & Bauwens, 1996
<i>Nycticorax nycticorax</i> (Night Heron)	+	m	Castilla & Bauwens, 1996
<i>Egretta garzetta</i> (Little Egret)	+	m	Castilla & Bauwens, 1996
<i>Milvus migrans</i> (Black Kite)	-	m	Castilla & Bauwens, 1996
<i>Milvus milvus</i> (Red Kite)	+	-	Blanco <i>et al.</i> , 1987
<i>Buteo buteo</i> (B buzzard)	+	-	Bustamante, 1985
<i>Accipiter gentilis</i> (Goshawk)	+	m	Castilla & Bauwens, 1996
<i>Accipiter nisus</i> (Sparrowhawk)	+	m	Castilla & Bauwens, 1996
<i>Circus aeruginosus</i> (Marsh Harrier)	+	m	Castilla & Bauwens, 1996
<i>Circus pygargus</i> (Montagu's Harrier)	-	m	Castilla & Bauwens, 1996
<i>Falco eleonorae</i> (Eleonora's Falcon)	-	+	Castilla & Bauwens, 1996
<i>Falco naumanni</i> (Lesser Kestrel)	-	-	Cramp, 1980, Franco & Andrada, 1976
<i>Falco peregrinus</i> (Peregrine)	+	+	Castilla & Bauwens, 1996
<i>Falco tinnunculus</i> (Kestrel)	+	-	Valverde, 1967; Otero <i>et al.</i> , 1978
<i>Pernis apivorus</i> (Honey Buzzard)	-	m	Castilla & Bauwens, 1996
<i>Otus scops</i> (Scops Owl)	+	m	Castilla & Bauwens, 1996
<i>Tyto alba</i> (Barn Owl)	+	-	Herrera, 1973; Camacho, 1975
<i>Bubo bubo</i> (Eagle Owl)	-	-	Cramp, 1985
<i>Athene noctua</i> (Little Owl)	+	-	Máñez, 1983
<i>Strix aluco</i> (Tawny Owl)	+	-	Villarán & Medina, 1983
<i>Lanius excubitor</i> (Great Grey Shrike)	+	-	Valverde, 1967
<i>Lanius senator</i> (Woodchat Shrike)	+	m	Castilla & Bauwens, 1996
<i>Pica pica</i> (Magpie)	+	-	Domínguez <i>et al.</i> , 1980
<i>Corvus corax</i> (Raven)	+	-	Cramp, 1985
<i>Corvus corone</i> (Carrion Crow)	+	-	Cramp, 1985
<i>Coracias garrulus</i> (Roller)	+	-	Cramp, 1985
<i>Garrulus glandarius</i> (Jay)	+	-	Cramp, 1985
<i>Monticola saxatilis</i> (Rock Thrush)	+	m	Castilla & Bauwens, 1996
<i>Larus cachinnans</i> (Yellow-legged Gull)	+	+	Castilla & Bauwens, 1996
<i>Larus audouinii</i> (Audouin's Gull)	+	+	Castilla & Bauwens, 1991
SNAKES			
<i>Malpolon monspessulanus</i> (Montpellier Snake)	+	-	Arnold, Burton & Ovenden, 1978; Gruber, 1989
<i>Coluber hippocrepis</i> (Horseshoe Whip Snake)	+	-	Arnold, Burton & Ovenden, 1978; Gruber 1989
<i>Elaphe scalaris</i> (Ladder Snake)	+	-	Gruber, 1989
<i>Coronella girondica</i> (Southern Smooth Snake)	+	-	Arnold, Burton & Ovenden, 1978; Gruber, 1989
<i>Vipera latasti</i> (Blunt-nosed Viper)	+	-	Arnold, Burton & Ovenden, 1978; Gruber, 1989

TABLE 2. Mean (\pm SD) SVL and limb dimensions of the two subspecies of *Podarcis hispanica*. *P*-values result from two-way-ANOVAs on the original data, testing for differences in dimensions between subspecies and between sexes, with SVL entered as a covariate. The *P*-values refer to the significance of the interpopulation difference. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

	<i>P. h. atrata</i> ($n = 53$)	<i>P. h. hispanica</i> ($n = 34$)	<i>P</i>
snout-vent length (mm)	58.21 \pm 6.91	45.18 \pm 4.95	***
femur length (mm)	7.98 \pm 1.17	6.62 \pm 1.13	-
tibia length (mm)	8.46 \pm 1.23	7.29 \pm 0.98	-
hindfoot length (mm)	2.99 \pm 0.57	2.72 \pm 0.44	*
toe length (mm)	9.26 \pm 1.10	7.69 \pm 0.87	*
humerus length (mm)	5.86 \pm 0.88	4.69 \pm 0.61	-
ulna length (mm)	5.76 \pm 0.87	4.84 \pm 0.55	-
frontfoot length (mm)	2.00 \pm 0.48	1.75 \pm 0.33	-
toe length (mm)	5.48 \pm 0.84	4.58 \pm 0.67	-

Castellón mainland site were on average at a greater distance from the nearest hide than lizards on Columbrete Grande (means \pm SD: mainland: 21.59 \pm 29.49 cm; island: 1.90 cm \pm 6.80 cm; Mann-Whitney-U-test, $z = 4.47$, $P < 0.001$). Random points within the lizards' habitat were also on average further away from potential refuges in the mainland site than in the island site (mainland: 43.33 \pm 61.09 cm; island: 33.13 \pm 59.54; Mann-Whitney-U-test, $z = 1.92$, $P = 0.05$), indicating that the habitat on Columbretes in general offers more hiding opportunities.

Morphometrics

Adult island lizards (SVL $x = 58.21 \pm 6.91$ mm, $n = 53$) are considerably larger than adult mainland lizards ($x = 45.18 \pm 4.95$ mm, $n = 34$, ANOVA: $F = 89.99$, $df = 1$ and 83, $P < 0.001$). We found no differences in SVL between sexes ($F = 2.03$, $df = 1$ and 83, $P = 0.2$) and the sex-by-subspecies interaction effect on SVL was not significant either ($F = 0.25$, $df = 1$ and 83, $P = 0.6$). Body mass scaled approximately as SVL^3 in both subspecies [combined regression: $\log_{10}(\text{mass}) = -4.83 \pm 0.06 + 3.11 \pm 0.11 \log_{10}(SVL)$ with mass in g and SVL in mm].

With the exception of ulna length in the mainland population ($P = 0.02$), all limb dimensions scaled isometrically with SVL in both subspecies (all $P > 0.06$).

We performed a multiple analysis of variance on the total set of morphological features to investigate subspecies, sex and subspecies-by-sex effects on general morphology. SVL was introduced into the analysis as a covariate. Variances were homogeneous across cells (Box M-test, $P > 0.10$) and there were no significant interactions of the covariate with the between-groups factors (Rao R-test, $P > 0.05$). The analysis revealed a significant multivariate subspecies-by-sex interaction effect (Pillai's statistic = 0.33, $F = 2.01$, $df = 16$ and 64, $P = 0.03$). Subsequent univariate *F*-tests on the separate traits showed a significant interaction effect on mass ($P < 0.0001$). Lizards from both sexes were more massive on the island, but the difference was more pronounced in males. As for the limb dimensions (Table 2), only the length of the hind foot and of its fourth toe differed between subspecies. Mainland lizards had larger hindfeet (ANOVA, $F = 6.1$, $df = 1$ and 82, $P = 0.01$) and toes ($F = 5.77$, $df = 1$ and 80, $P = 0.02$) than island lizards of comparable SVL. Hindfoot length did

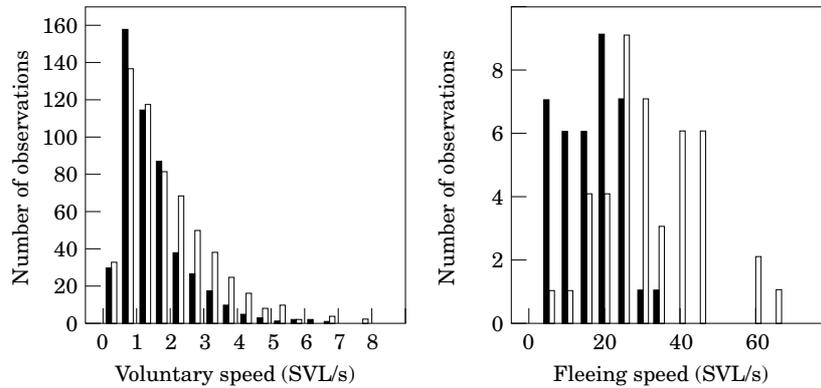


Figure 2. Frequency of relative moving velocities of *P. h. hispanica* (□) and *P. h. atrata* (■) during voluntary locomotion in a terrarium (left) and when fleeing (right).

not differ between sexes ($F=3.79$, $df = 1$ and 82 , $P=0.06$), but males had proportionally longer toes in both subspecies ($F=9.12$, $df = 1$ and 80 , $P<0.001$). Thus, a mainland specimen has feet (hindfoot + toe length) that are 1.086 times that of an island specimen of similar SVL. Measurements of metatarsalia length on X-ray photographs of a subsample of lizards confirmed the differences in hindfoot length between subspecies (two-way ANOVA with SVL entered as a covariate, $F=6.89$; $df=1$ and 20 ; $P=0.016$).

None of the other characters showed differences between subspecies or sexes when the effect of body size was removed (all $P>0.1$).

Behavioural observations

In unrestrained conditions, lizards from both subspecies moved mostly at velocities between 0.1 and 0.3 m/s. A nested ANOVA on \log_{10} -transformed voluntary speeds showed individual variation within ($F=3.29$, $df=8$ and 1067 , $P=0.001$) but no difference between subspecies ($F=0.66$, $df=1$ and 8 , $P=0.44$). When speeds were expressed relative to SVL, mainland lizards moved at higher speeds than island lizards (2.25 ± 3.61 SVL/s versus 1.50 ± 1.01 SVL/s; $F=5.96$, $df = 1$ and 8 , $P=0.04$, Fig. 2). In the test terrarium, fleeing mainland lizards used higher absolute burst speeds than island lizards ($F=24.74$, $df = 1$ and 14 , $P<0.001$).

Gait analysis

Lizards from both subspecies enhanced their speed by increasing stride frequency and stride length (Table 3), but they did not do so in the same way. Stride frequency was similar in lizards from both subspecies at lower relative speeds, but increased more rapidly with increasing relative speed in the island lizards than in the mainland

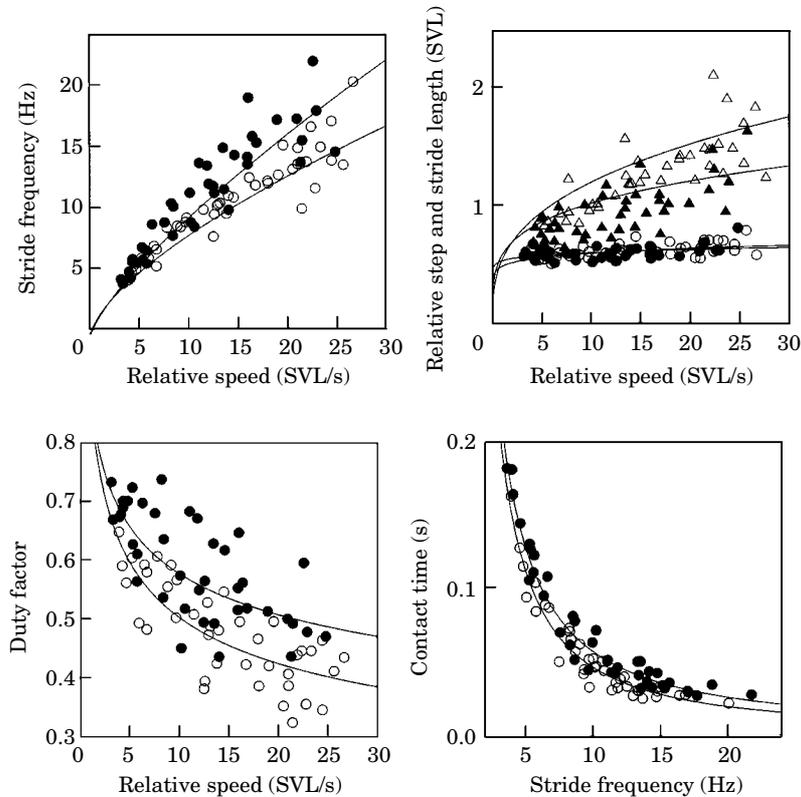


Figure 3. Relationships between gait characteristics. Filled symbols: *P. h. atrata*; open symbols: *P. h. hispanica*. The curves represent the regression equations given in Table 3.

TABLE 3. Regression equations describing the relationship between kinematical parameters of lizards running on the moving belt. Regression parameters are for pooling data of all individuals per subspecies. The *t*-test compares subspecies means of individual regression lines. * $P < 0.05$; ** $P < 0.01$

y	log(y) = a + b*log(x)	<i>P. h. atrata</i>		<i>P. h. hispanica</i>		slopes	
		a	b	a	b	<i>t</i>	<i>P</i>
stride frequency (Hz)	relative speed (SVL)	0.23	0.76	0.26	0.66	3.0	**
step length (SVL)	relative speed (SVL)	-0.27	0.05	-0.31	0.09	-1.2	—
stride length (SVL)	relative speed (SVL)	-0.23	0.24	-0.25	0.34	-3.0	**
duty factor (s)	relative speed (SVL)	-0.05	-0.19	-0.05	-0.25	2.3	*
contact time (s)	frequency (Hz)	-0.07	-1.17	-0.05	-1.28	-0.5	—
recovery time (s)	frequency (Hz)	-0.65	-0.75	-0.56	-0.72	-0.5	—

lizards (Fig. 3, *t*-test on the slopes of individual regressions of frequency on relative speed: $t = 3$, $df = 14$, $P = 0.01$). The reverse pattern was observed for relative stride length, which increased more rapidly with relative speed in the mainland population compared to the island population (Fig. 3, *t*-test on slopes: $t = 3$, $df = 14$, $P = 0.01$). Relative step length was similar for both subspecies and increased scarcely (but significantly) throughout the observed range of sprinting speeds (Table 3, Fig. 3).

Therefore, lizards increase their stride lengths mainly by reducing the double stance phase (the phase during which both hindlegs are in contact with the substrate). This is confirmed by the negative relationship between duty factor and relative speed (Fig. 3). At relative velocities above 10 SVL/s, the mainland lizards further increase their stride lengths by including a floating phase, during which neither hindfoot is in contact with the substrate. Such floating phase was rarely observed in the island lizards. This is corroborated by the fact that at velocities above 10 SVL/s, duty factors often drop below 0.5 in the mainland population, but seldom in the island population (Fig. 3). Contact time and recovery time decreased with increasing frequency (Fig. 3), and the decline was similar in both subspecies (contact time : t -test on slopes: $t=2.03$, $df=14$, $P=0.062$; recovery time : t -test on slopes: $t=-0.52$, $df=14$, $P=0.611$).

DISCUSSION

Although speed is generally assumed to increase with body size (review in Garland & Losos, 1994), we found no differences in voluntary speed between the smaller mainland lizards, *P. h. hispanica*, and the larger island lizards, *P. h. atrata*. On average, individuals from the mainland flee at higher speeds than specimens from the island. These observations confirm our earlier findings: when lizards are prompted to sprint at full power on a race track, mainland specimens run at absolute speeds that double those of island specimens, in spite of their smaller body size (Van Damme *et al.*, 1997).

In addition to this variation in locomotor behaviour and performance, subspecies also differed in their strategy for modulating velocity. High speed video recordings revealed that both subspecies raised their speed by increasing cycle frequency and stride length, but also that the rate of increase of these two parameters varied between subspecies. Whereas modulating speed is more frequency-mediated in the island subspecies, the mainland subspecies increases its speed primarily by taking larger strides. These findings raise following questions: (1) are the differences in the gait characteristics related to the differences in performance? (2) which design parameters cause the observed variation in the gait characteristics? and (3) which ecological conditions may possibly have lead to the observed interpopulational differences?

Modulation strategy and performance

An animal's strategy for modulating speed may affect its locomotor behaviour in two ways. Firstly, physiological or mechanical restrictions to step frequency, step length or floating distance may limit maximal attainable velocity directly. Secondly, the energetic cost of locomotion at a given speed may also depend on the strategy used for modulating velocity, and animals may refrain from running at speeds that are too costly. In the next paragraphs, we will use the term 'frequency modulator' to indicate an animal that increases its speed mainly by increasing its cycling frequency (as in the case of the island subspecies *P. h. atrata*); by a 'stride modulator' we mean an animal with a stride-based speed modulation (such as in the mainland population of *P. h. hispanica*).

Modulation strategy and maximal running speed

The performance of musculo-skeletal systems—in terms of speed, force or acceleration—is constrained by a complex, dynamic interaction of the mechanical relationships that rule the functioning of muscles and tendons (e.g. length-tension and force-velocity relationships, contraction conditions, see Van Leeuwen, 1992; Komi, 1992; Enoka, 1994). The force-velocity relationship for the maximally activated leg muscles (at the according strain range and for a given load) will determine the upper cycling frequency of the leg. The frequency modulator is likely to reach that maximal frequency at a lower speed than the stride modulator. One may argue that a stride modulator requires larger push-off forces to generate the floating distances that are typical for its gait, and therefore will have a lower maximally attainable frequency. However, the size of the difference in cycling frequency at the maximal speeds reached on the running belt (nearly 20%, see Fig. 3) strongly suggests that the alternative running styles contribute to the marked difference in maximal running performance between both subspecies. This conforms to findings for human sprinting where subjects with inferior performance reach maximal step cycle frequency at much lower running speeds (Mero, Komi & Grego, 1992; Enoka, 1994).

Modulation strategy and energy consumption

What are the consequences of running style for the energetic costs of locomotion? In the absence of direct measurements of metabolic energy consumption, it is hard to predict the magnitude of the differences in energy consumption that can be expected. However, theoretical considerations and literature data may at least indicate the direction of such differences. Since gait characteristics of both populations are highly similar at low speeds, we do not expect to find large differences in the energetic costs of locomotion when lizards are moving at voluntary speed. At elevated speeds, we expect the stride length-modulated running style of the mainland lizards to be energetically more favourable than the frequency-modulated style of their island conspecifics. We develop our arguments in the next paragraphs.

If we neglect the energy required to overcome air resistance, energy for locomotion is spent in accelerating and decelerating the centre of mass (external work) and in moving body parts with respect to the centre of mass during the locomotor cycles (internal work: leg movements, undulations of the body). At a given *frequency*, the internal work—and therefore the energy fluctuations involved—must be similar in island and mainland specimens, because body shape, contact times and steplengths are similar (see Fig. 3 and below). Thus, at a given *running speed*, the energetic costs linked to this internal work component are probably higher for the frequency modulator.

On the other hand, the external work is expected to be higher for the stride modulating mainland specimens, especially at high speeds when their long strides require large push-off forces. Thus, the magnitude and direction of potential differences in the economics of both running styles will depend on the relative energy requirements imposed by the internal and external work components. In a recent paper, Farley and Ko (1997) found the external work component for a skink with a size and overall habitus comparable to our experimental animals to be 1.5 J/kg/m. In the same species, overall metabolic costs of locomotion were 52 J/kg/m (recalculated from Farley & Emshwiller, 1996). Assuming a 20% efficiency for

converting metabolic energy to mechanical work (McMahon, 1984), only about 15% of the metabolic costs of locomotion appears to go to external work. The remaining 85% is spent in leg movements with respect to the centre of mass, and in body undulations. Since this internal work is relatively less expensive in the mainland specimens, we expect these lizards to run more economically than their island conspecifics. It would be interesting to verify this hypothesis by direct measurement of the energetic costs of locomotion.

Modulation strategy and design

Which design parameters may cause the observed interpopulation variation in frequency and stride length? The most obvious answer is probably that the neuro-motoric drives regulating locomotion differ between subspecies. The neuro-motoric drive (in balance with the external load) determines the precise manner in which each leg segment (upper leg, lower leg, foot segments) moves throughout the cycle (e.g. the pattern of angular displacement of the upper leg with respect to the mid-sagittal axis during retraction starting from a certain angle X and ending with a final angle Y). These movement patterns are largely constrained by contact time (a measure for the velocity of the movements carried out) and steplength in relation to leg dimensions (confining the position of the leg segments to certain geometric configurations). At a given frequency, steplength and contact time are highly similar for specimens with equal dimensions belonging to both populations (Fig. 3D). This suggests that the precise patterns in which the leg segments move through a locomotor cycle are very similar at any cycling frequency for the two populations. This argues against differences in neuro-motoric design.

Could the differences in gait characteristics result from differences in limb morphology between the subspecies? Our morphometric analysis revealed but small deviations in metatarsal and toe length (Table 2). Although it may sound counter-intuitive, it is not impossible that the 10% elongation of the foot segments of mainland specimens may contribute significantly to the change in gait characteristics and performance. It has been shown elsewhere that subtle morphological changes may have important consequences for performance (Moreno & Carrascal, 1993; Miles, 1994). We are currently investigating this possibility by applying the technique of forward dynamic modelling.

We will now explore potential evolutionary causes.

Evolutionary causes

Like most lacertids, *P. hispanica* is a diurnal heliothermic lizard that alternates periods of basking with foraging bouts, during which it actively searches its surroundings for invertebrate prey. The animals are thought to rely on short bursts to capture prey and to escape predation. It therefore seems likely that food availability, predator abundance and types of prey and predator present could play a prominent part in the evolution of locomotor performance in this lizard. Effects of prey composition and predation risk on lizard movement patterns have been documented in other lacertids (Huey & Pianka, 1981). Unfortunately, conclusive information on these

ecological parameters is scanty for the subspecies under study and our hypotheses must therefore remain tentative.

Podarcis hispanica is considered a 'food generalist' that will eat whatever invertebrate prey is available. While the diet of this species has been studied quite extensively on the Spanish mainland (Mellado *et al.* 1975; Escarre & Vericad, 1981; Pérez-Mellado, 1983), the only data available for the island subspecies *P. hispanica atrata* come from a preliminary analysis report by Castilla, Jimenez and Lacomba (1987). Qualitative comparisons of both data sets suggest important differences between the mainland and the island population. However, in the absence of data on food availability and foraging tactics, it remains unclear whether this dietary shift relates to differences in locomotor performance of the lizards.

Predation risk probably differs considerably between island and mainland. Table 1 clearly shows that the Columbretes Islands accommodate a much lower predator diversity than does the mainland. The only potential residential predators on Columbretes Islands are gulls and falcons. Although gulls may take lizards occasionally, these birds mainly forage at sea and certainly do not specialize on *P. h. atrata*. The impact of migrating birds that visit the islands on their way over the Mediterranean Sea is probably small (Castilla, pers. comm.). At present, no mammals or snakes reside on Columbretes Grande. A large population of snakes (probably the saurophagous viper *Vipera latastei*) did inhabit the island, but was eradicated at the end of the 19th century. Current predation pressure is likely to be much higher on the mainland, where numerous mammals, birds and snakes can predate on *P. h. hispanica*. Some of these animals, such as smooth snakes, corvids and shrikes are known to take lizards frequently. Feral cats and human children, trying to catch lizards for fun, may be an additional threat to the mainland population.

With many aerial predators around, the amount of vegetation cover may be an important determinant of predation risk. Our habitat analyses suggest that on both mainland and island, lizards prefer to stay within close distance from potential refuges. However, lizards from the mainland population tend to have less cover from vegetation within their entire home range. This could add to the susceptibility of these lizards to predation, as they have to cross more open terrain on their way from one site to the other within their living area.

These reflections suggest a higher predation pressure on the mainland, and it is tempting to relate this to the divergence in locomotor behaviour and performance capacity (Crowley, 1985 a,b; Snell *et al.*, 1988). Because of the abundant presence of predators and the reduced availability of cover, natural selection may have favoured individuals of *P. hispanica* that were able to cross relatively large distances at high speeds. Moreover, as locomotor costs constitute a substantial component of the daily energy budget of certain species of lizards (White & Anderson, 1994), selection may have economized locomotion at high speeds in this subspecies. The absence of these forces on Columbretes Island may have precluded adaptations for high speed of the locomotor system, perhaps also because they were in conflict with other interests.

Implicit to these assertions is the assumption that the lizards' locomotor capacities are ecologically relevant, either on a day-to-day base, or during rare, but significant events. For *P. hispanica*, as for most other animals, this assumption remains to be tested.

ACKNOWLEDGEMENTS

We thank the director of the Natural Park Illes Columbretes and the Conselleria d'Agricultura I Pesca, Generalitat Valenciana for permission to work on the island and for logistic support. We are especially grateful to Dr Juan Jiménez, Director of the Natural Park, and to Dr Aurora M. Castilla for their generous support. We thank Valentín, Carlos and Javier, park rangers, for their aid and companionship. Dirk Bauwens commented on a previous version of this manuscript. We are very thankful to Prof. R. McN. Alexander (Leeds University) for discussions and for his valuable comments on the manuscript. RVD is a senior research assistant and PA a research associate of the Belgian National Science Fund (NFWO). BV is supported by an IWT grant (no. 951359).

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