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LIZARD LOCOMOTION: HOW MORPHOLOGY MEETS ECOLOGY

by

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ABSTRACT

Biological evolution often leads, through natural selection, to an optimal fit between ‘design’ and ecology. However, the adaptation process may be impeded or slowed down by several constraints or trade-offs between conflicting functions. This is frequently observed by ecomorphological studies focusing on lower taxonomic levels: form-function relationships get blurred because subtle adaptive traits remain hidden or simply do not exist. Therefore, a rigorous analytic approach is required, (ideally) assessing the links between the four stages of the adaptive process simultaneously (*i.e.*, from genetic variation to variation in design, to variation in performance, to differential fitness), taking into consideration all potential factors hindering the normal progression of this process. Lizard locomotion is a good model for such an analysis. Locomotion is essential in many ecologically relevant functions (feeding, predator avoidance, etc.). It consists of several components (speed, acceleration, endurance, manoeuvrability, etc.) and modes (level running, climbing, etc.) with conflicting demands, leading to potential trade-offs. Moreover, several of its components proved to be heritable and obvious relations between habitat use and locomotor design are often absent (*e.g.*, in lacertid lizards). Two cases, focusing on the potential trade-off between climbing and level-running, are presented to illustrate the subtle interplay between variation in ecology, performance and design in lizard locomotion. (1) For two gekkotans (a climber and a ground dwelling species) the moments exerted by several important leg muscles appear to be tuned to their primary mode of locomotion. (2) In two sibling lacertid species, the inverse trade-off between climbing and running, put forward on the basis of observed substrate use, does not exist. Instead, a drastic difference in running performance, likely related to different running styles, emerged. The latter case illustrates the potential use of ‘integrated, dynamic design traits’ as an intermediate stage between variation in design and performance.

KEY WORDS: adaptation, locomotion, lizards.

INTRODUCTION

The great extent to which organisms are adapted to the tasks they have to fulfil in their specific environment has always been a subject of

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wonder and biological study. Pre-darwinian thinkers, from Aristotle to William Paley, considered this proof for the existence of a divine designer. Ironically, DARWIN (1859) turned the same match between form and function into one of the most powerful arguments for the existence of natural selection and its importance in biological evolution.

Over a wide taxonomical range, relationships between biological form and ecology are very often obvious and convincing. A classical example are the forelimbs of mammals, which evolved from a primitive state into wings in bats, spades in moles, running legs in antelopes, peddles in dugongs and so on, leaving no doubts about the adaptive nature of these evolutionary modifications.

Focusing onto lower taxonomic levels (*e.g.*, family level), however, the nice tight fit between the form and the ecological function frequently gets blurred or seems even not to exist. The degree to which morphological diversification tracks ecological radiation appears to be highly taxon-dependent. For instance, the morphological adaptation coupled to the trophic radiation of the cichlid fishes (COULTER, 1991) or Darwin finches (LACK, 1947; GRANT & GRANT, 1982; BOAG & GRANT, 1984; SCHLUTER & GRANT, 1984; SCHLUTER *et al.*, 1985) sharply contrasts with the high morphological resemblance of the sympatric *Pomatoschistus minutus* and *lozanoi*, sand gobies with different feeding niches (HAMERLYNCK, 1990; HAMERLYNCK & CATTRIJSSE, 1994; own observations) or with the absence of a correlation between morphology and diet in grassland birds (WIENS & ROTENBERRY, 1980). Similarly, while adaptation to habitat use has lead to clearly distinguishable ecomorphs in *Anolis* lizards on each of the major islands of the West Indies (COLLETTE, 1961; WILLIAMS, 1972; MOERMOND, 1979; LOSOS 1990a, b, c; 1992; LOSOS *et al.*, 1994; LOSOS, 1995; LOSOS *et al.*, 1998), the rather uniform appearance of lacertid lizards seems, at first glance, not to reflect the variable demands imposed by the diverse habitats these animals are living in (ARNOLD, 1989). The absence of a correlation between design and ecology may result from the adaptive traits being hidden or too subtle to be revealed by the applied analytic tools, or from actual constraints (environmental, historical, etc.) that slow down or prevent the proper progress of the adaptation process, thus disturbing the relation between form and function (GOULD & LEWONTIN, 1979; REEVE & SHERMAN, 1993; RIDLEY, 1993; WINSOR, 1993; DENNETT, 1995; SIH & GLEESON, 1995; FUTUYMA, 1998). If correlations between form and ecological niche do show up, proper testing of the adaptive nature of the traits remains a prerequisite. Emerging correlations can be non-adaptive for the function considered (for instance, when specialisation for climbing makes new food sources available, differentiation of the jaw apparatus may correlate with the locomotor mode without being causally linked), or can just be the result of the phylogenetic relationships between taxa (HARVEY & PAGEL, 1991; *e.g.*, the correlation between home range size and diet in Carnivora and ungulates in GARLAND *et al.*, 1993; the correlation between body shape and habitat use in lacertid lizards in VANHOOYDONCK & VAN DAMME, 1999).

Therefore, the study of ecomorphology asks for a rigorous analytic approach, taking into account all potential pitfalls and constraints, protecting against over-adaptationism or unfounded adaptive story-telling (GOULD & LEWONTIN, 1979; GOULD, 1996). The conceptual frame-work put forward by ARNOLD (1983) offers a firm basis for this.

THE CONCEPT APPLIED TO LOCOMOTION

A central element in Arnold's conceptual frame (fig. 1) is the measurement of performance: the degree to which individual organisms can fulfil ecologically important functions, that is, functions with a clear potential relevance to the survival and/or reproduction of the organism. For many animals, locomotion is ecologically important as they need to move in order to escape from predators, to find food or mates, to defend territories, etc. (HUEY & STEVENSON, 1979; ARNOLD, 1983; HERTZ *et al.*, 1988; GARLAND *et al.*, 1990; JAYNE & BENNETT, 1990a; LOSOS 1990a, b; GARLAND, 1994; GARLAND & LOSOS, 1994). Although rarely tested explicitly (but see for instance JAYNE & BENNETT, 1990a; GARLAND & LOSOS, 1994), it seems logical that locomotory performance affects the fitness of individuals.

Performance is the endpoint of the so-called 'performance gradient' and at the same time the start of the 'fitness gradient' (cf. ARNOLD, 1983; see fig. 1). The study of the performance gradient investigates the causes of individual differences in performance. This requires three types of analyses.

— The first focuses on performance and addresses an important type of evolutionary constraint: the existence of trade-offs between functions (LEWONTIN, 1978; ROSE, 1982; LOSOS *et al.*, 1989; STEARNS, 1992; RIDLEY, 1993) or between different components of one single function. Locomotion includes several components which may be important for survival (and reproductive success; see further). Maximal attainable speed, acceleration capability, endurance and manoeuvrability or different locomotor modes (for instance climbing *versus* level-running) are examples of this. Evolutionary optimisation of performance of one component may have a negative effect on the performance in an other, because two functions might involve radically different requirements with respect to design

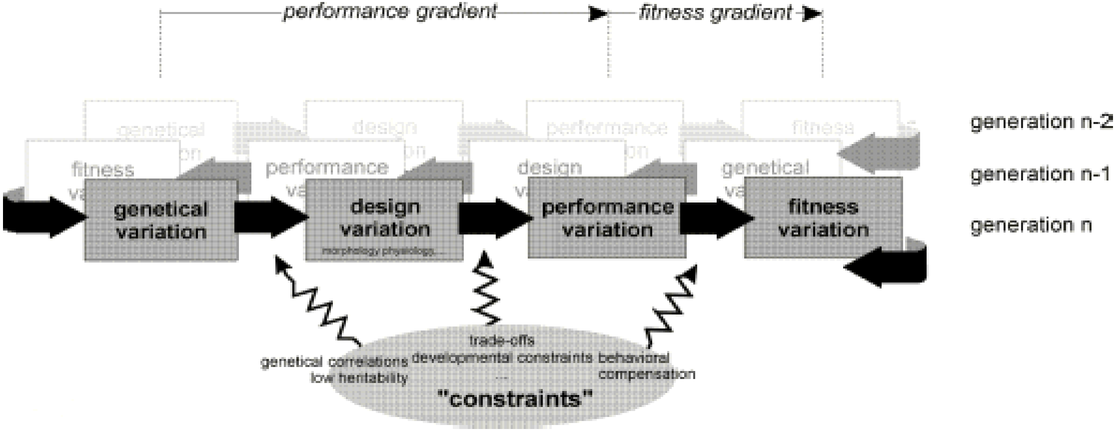

Fig. 1. Scheme representing the adaptation process (based on ARNOLD, 1983).

traits such as muscle type, skeletal proportions, etc. High speeds and accelerations, for instance, can be expected to be important for both prey capture and predator evasion (*e.g.*, HUEY & STEVENSON, 1979; BENNETT, 1980; ARNOLD, 1983; BENNETT & HUEY, 1990; HUEY *et al.*, 1990; JAYNE & BENNETT, 1990a; GARLAND & LOSOS, 1994), but are thought to conflict with endurance capacity (explosive force development for speed *versus* sustained force development for endurance; BENNETT, 1978; BENNETT *et al.*, 1984; HUEY *et al.*, 1984; ESBJÖRNSSON *et al.*, 1993; SORCI *et al.*, 1995) or manoeuvrability (practical in particular environments like dense vegetation, rocky terrain). Thus, locomotion seems an ideal function for the study of the importance of trade-offs in evolution (HUEY & HERTZ, 1984; ABU-GHALYUN *et al.*, 1988; LOSOS *et al.*, 1993), the more because many of its components can relatively easily be quantified in the lab and that individual performance generally proves to be quite repeatable, even over longer time periods (HUEY & DUNHAM, 1987; BENNETT & HUEY, 1990; HUEY *et al.*, 1990; JAYNE & BENNETT, 1990b).

— The second line of research analyses the relation between design (*i.e.*, assembled morphological, physiological, biochemical and other aspects of form) and performance. Older ecomorphological studies are typically limited to a correlative approach, looking for statistical relationships between any of a large number of design traits and performance (cf. Arnold, 1983). This approach is not only time-consuming but also potentially misleading, because performance is a complex result of many biochemical, physiological and morphological factors and it is well possible that the search for relationships centres on the wrong design features. Indeed, an increasing number of investigations has shown that the relation between form and function can be surprisingly subtle (GARLAND, 1994; MILES, 1994; VAN DAMME *et al.*, 1998). One way to tackle this problem is to study the mechanistic basis of individual variation in performance, by inserting this analysis as an extra step between 'design' and 'performance' in Arnold's scheme. In the case of locomotion, spatio-temporal gait characteristics (stride lengths and frequencies, step lengths, duty factors, etc.) can provide this extra step (see for instance VAN DAMME *et al.*, 1998; this paper). We argue that these characteristics are the outcome of the complex interaction of all design traits of the entire locomotor apparatus (neurological, physiological, structural, physical traits). Put this way, spatio-temporal gait characteristics can be considered as integrated, dynamic design traits of organisms as such, possibly directly related to their ecology and performance (see fig. 2). Research on lizards, for instance, has shown that superficially identical individuals with markedly different performances show equally marked differences in their kinematic patterns (VAN DAMME *et al.*, 1997; 1998; see also this paper).

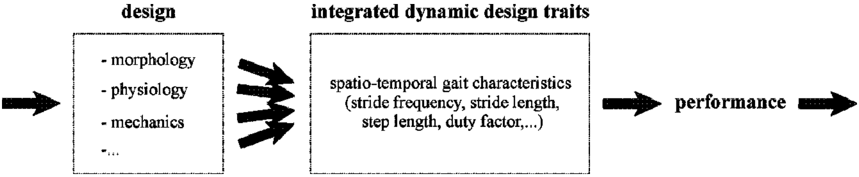

Fig. 2. Integrated dynamic design traits as an extra step between design and performance (see text).

— The third line of research in the performance gradient investigates (by means of quantitative genetics) whether variation in design and performance has the genetic basis needed for evolution. In the few species where this has been studied, locomotory performance proved to be heritable (at least to some degree: VAN BERKUM & TSUJI, 1987; GARLAND, 1988; TSUJI *et al.*, 1989; JAYNE & BENNETT, 1990b; SORCI *et al.*, 1995), an appreciated feature in racehorse, greyhound or pigeon breeding programs. From this, locomotion appears again to be an ideal model function to study the process of adaptation. Additionally, testing for genetic correlations adds to the understanding of the presence or absence of trade-offs between locomotor components (BENNETT & HUEY, 1990), whereas the search for genotype-environment interactions can reveal the effect of environmental constraints (*e.g.*, when different genotypes perform optimally at different temperatures).

Performance is not only an element of the performance gradient but also an element in the fitness-gradient (fig. 1). In other words: does variation in performance translate into a differential fitness (*i.e.* combined survival and reproductive success)? Due to the practical problems involved in testing this, performance itself is often advanced as a direct measure for fitness. However, this approach neglects phenomena such as behavioural compensation and links between behaviour, design and performance. 'Slow' individuals of *Thamnophis* snakes with the right colour pattern and anti-predator behaviour, for instance, survive better than 'fast' individuals with the wrong combination of colour and behaviour (BRODIE, 1989). Treating speed as a direct measure for fitness obviously leads to a misconception in this case. Also, trade-offs between functions (*e.g.*, between speed and manoeuvrability) or between the fitness components themselves (*e.g.*, better survival at the cost of lower reproduction) can bring about better performance which does not translate into higher fitness. A complete study of the adaptation process should therefore directly assess the effect of performance variation on fitness. For this purpose, individual organisms with known performance should be followed under natural conditions for a long period. In practice, however, such tests are often very hard to perform. Yet, as an approximation, the link between variation in performance and fitness can be assessed indirectly by evaluating the individual's efficiency for ecological functions with an obvious effect on fitness. For locomotor capacity (speed, manoeuvrability, etc.), for instance, it can be tested, whether the faster individuals have higher chances to escape from predators or to take prey items.

Ideally, ecomorphological studies should consider all the links mentioned in figure 1, before decisive conclusions about adaptation can be formulated. Therefore, input is needed from widely different fields of biology (quantitative genetics, morphology, biomechanics, ecology, ethology, etc.), asking for intensive integration of various classic biological specialisations. Taking further into account that any of these links can be hampered by constraints of different nature (environmental constraints, historical constraints, genetic correlations, genotype-environment correlations, behavioural compensations, etc.), the genuine ecomorphological research objectives may appear utopic, indeed. This is, however, no argument to avoid further research efforts in the field of ecomorphology. One must strive to implement Arnold's concept (ARNOLD, 1983; figure 1) as completely as possible in a single research program, but we believe that also partial analyses, when properly conceived in the context of the global framework, definitely add to the gradual resolution of the ecomorphological question posed.

LIZARD LOCOMOTION

Species of one lizard family often occur in a wide variety of habitats with radically different demands for locomotion. We mentioned already the example of the lacertids, found in many biotopes (ranging from tundra over high altitude mountains, Mediterranean scrubs and tropical forest to desserts; ARNOLD, 1989) and microhabitats within these biotopes. Such ecological diversification obviously asks for different locomotor skills, making trade-offs between locomotor components and adaptations in design likely to occur. Nevertheless, form-function relationships are apparently not reflected in the gross-morphology of the species (ARNOLD, 1989; VANHOOYDONCK & VAN DAMME, 1999).

Is in such cases the process of adaptation constrained, conserving the design of a generalist, irrespective the diversity of the habitat? Or are the adaptations hidden, beyond the scope or the resolution of the analysis (see also VANHOOYDONCK & VAN DAMME, 1999)? From this point of view, lizard locomotion offers a useful model to address (in the context of Arnold's framework) the subtlety of the interplay between variation in ecology, performance and design.

The next two examples deal with the potential trade-off between climbing and level-running. Based on theoretical considerations about the different effect of gravity, several morphological differences between species generally running on flat and species living on inclined or vertical surfaces can be expected (see VAN DAMME *et al.*, 1997; 1998; ZAAF *et al.*, 1999) and it has been suggested that specialisation in one direction may conflict with performance in the other (KRAMER, 1951; PETERSON, 1984; CARTMILL, 1985; LOSOS *et al.*, 1993; MILES, 1994).

Climbing and level-running in two gekkotans

Gecko gekko (the tokay) is well known for its climbing ability on vertical structures. For this purpose, its feet are equipped with robust claws and under each toe a series of adhesive lamellae is present (HILDEBRAND, 1988; CARTMILL, 1985). Moreover, these animals are dorso-ventrally flattened and climb with the limbs in a wide sprawling posture. This brings the centre of mass close to the substrate which is beneficial when climbing on vertical surfaces. *Eublepharis macularius* (the leopard gekko), on the other hand, is a ground dwelling gekkotan with a less flattened body that lives in the desert. During running, the body is clearly lifted from the surface to reduce friction. Despite the fact they do not possess adhesive pads like the tokay and have only small claws, specimens of this species are nevertheless able to climb vertical walls, as we learned from their escapes from the terrarium in the laboratory. However, their climbing performance in terms of speed is very poor: animals able to run at speeds up to 1.1 m/s realised climbing speeds of merely 0.1 m/s (snouth-vent length of the animals about 13 cm; own data). *Gecko gekko* specimens of the same size, however, performed about as well on the flat as they did on their preferred vertical substrate: climbing speeds up to 1.2 m/s and running speeds up to 1 m/s were measured (own data).

It thus seems that a trade-off between climbing ability and running is present in the leopard gekko, but not in the tokay. Yet, it is hard to induce level-running in *Gecko gekko*. Most often specimens simply refuse to run, starting defensive threatening or, if the opportunity exists, they use the side walls of the enclosure to escape. So, is it conceivable that, although tokays are able to run on the flat, the muscular configuration is not really tuned to do so, resulting in a high, but uncomfortable performance (*e.g.*, high stresses, local fatigue, energetically expensive; compare, for instance, to race walking in humans Alexander, 1992a, b)?

Based on straightforward mechanical considerations, one can speculate on specialisations of the limb musculature of either a vertical climber or a level runner. The former should possess more forcefully built limb retractors crossing shoulder and hip because these muscles must provide propulsive forces not only to surmount inertia, but also to counteract gravity. Moreover, since vertical climbing requires tension by the front legs to avoid tumbling backwards when the hind legs push for propulsion (see for instance CARTMILL, 1985; ALEXANDER, 1992a), strong elbow flexors can be expected in *Gecko gekko*. Level runners, on the other hand should possess better developed elbow and knee extensors, as (in addition to their role in propulsion) these muscles have to sustain the body weight throughout locomotion to keep the body elevated from the substrate. In addition, in level-running, propulsion is also powered by ankle and wrist extension (see for instance FIELER & JAYNE, 1998; own observations). This probably does not occur in the tokay, because hyperextension has first to lift the phalanges from the substrate to detach the adhesive pads (GENNARO, 1969; RUSSELL, 1975). This difference should be reflected in the extensors of the ankle and wrist joints, too.

Dissection of the appendicular musculature of both gekkotans revealed no striking differences (except from some smaller muscles related to the presence of the adhesive pads in the tokay). Presence, origin and insertion sites and general shape of the limb muscles are highly similar for both species (ZAAF *et al.*, 1999). However, when several quantitative, functional features (*i.e.* angles of pinnation, physiological cross-sections, moment arms) are combined to estimate the moments exerted by the leg muscles about the involved joints in a standardized parasagittal leg configuration, the subtle adaptation of the locomotor morphology to the substrate use (apart from the obvious adhesive pads in the tokay, for instance) can be fully appreciated (ZAAF *et al.*, 1999). About the shoulder, the moment exerted by the main retractor (latissimus dorsi) is about 50% to 100% higher in the climbing species (ZAAF *et al.*, 1999). The same holds true for the main hip retractors (caudofemoralis longus and brevis, flexor tibialis externus; ZAAF *et al.*, 1999). Concerning the elbow and knee extensors, the opposite picture emerges: the triceps (elbow) and the ambiens and femorotibialis (knee) of the leopard gekko show moments exceeding those of the tokay by 50% to 100% (ZAAF *et al.*, 1999). Of the seven elbow flexors, two in *Gecko gekko* are more powerful in terms of exerted moments (*i.e.*, 200% to 400% for the brachialis bundles; ZAAF *et al.*, 1999), whereas the moments of others are comparable for both species. As predicted, the moments of the major ankle (gastrocnemius, flexor tarsi, flexor digitorum longus) and wrist (flexor carpi ulnaris, flexor carpi radialis and flexor digitorum longus) of the level-runner are two- to three-fold those of the specialist climber (ZAAF *et al.*, 1999).

Locomotor styles in two sibling Spanish wall lizard species[1]

The rather small specimens of the lacertid species *Podarcis hispanica* (snout-vent length = 45.2 mm ± 5.0 SD, n = 34) live on the Spanish mainland (presently sampled from the region of Castellón). They are fast and alert and are very often observed on vertical structures like walls, rocks and stony slopes (VAN DAMME *et al.*, 1997; 1998). The species *Podarcis atrata* only occurs on the Columbretes islands, a small archipelago about 50 km out of the coast from Castellón. These island specimens are on the average somewhat bigger than specimens of the mainland population (snout-vent length = 58.2 mm ± 6.9 SD, n = 53), they are sluggish and are practically always observed on nearly horizontal substrates (VAN DAMME *et al.*, 1997; 1998).

Despite the high resemblance in appearance, the quantified difference in substrate use between both populations raised the question whether they show an inverse trade-off in performance between climbing and level-running. To test this, 15 specimens of each population ran several times on a racetrack equipped with photocells at 25 cm intervals, either placed in a horizontal position (substrate = cork) or at an incline of 65° (substrate = schists). The highest speed measured over two successive measuring intervals was treated as the individual maximal sprinting (climbing) performance. As expected, the mainland species were the better climbers (0.62 m/s ± 0.23 SD, n = 14 *versus* 0.13 m/s ± 0.19 SD, n = 11 for the island specimens; see VAN DAMME *et al.*, 1997). Surprisingly, however, the smaller mainland specimens (see above) were also by far the better sprinters (2.03 m/s ± 0.40, n = 14 *versus* 1.09 m/s ± 0.42 SD, n = 15; see VAN DAMME *et al.*, 1997). In other words, the trade-off expected on the basis of the observed differences in substrate use seems not confirmed. This could not be explained by motivational differences between the two test populations. Whereas frequency distributions of voluntary locomotor speeds of the test specimens were identical for the mainland and island population (obtained from video recordings of animals during undisturbed behaviour in large terraria), the frequency distribution obtained from fleeing mainland specimens (evoked escape responses) significantly shifts to higher speeds compared to those of the island group (VAN DAMME *et al.*, 1998).

Can differences in design explain the substantial difference in running performance? It is not just a matter of size, because the smaller species is

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[1] Only recently, Castilla *et al.* (1998) revised, based on molecular data, the taxonomical status of these species. Formerly, they were considered subspecies (*i.e. Podarcis hispanica hispanica* and *Podarcis hispanica atrata*).

also the fastest. Further, the overall appearance of the two species is very alike. In a first effort to find design differences, morphological measures of the front and hind limb segments (lengths) were taken for a number of specimens (island: n = 53; mainland: n = 34). No significant differences could be found between the species, except for the length of the hind foot: for individuals of similar snout-vent length, the combined length of tarsus and longest toe of the mainland specimen amounts to 1.09 times the length of the foot of the island specimen. Expressed in terms of total leg length, this is a difference of merely 5% (VAN DAMME *et al.*, 1998).

Although it is obvious that animals with longer legs might be able to run faster (as they can take larger steps), it is very doubtful that this small (but significant) difference in leg length suffices to explain the nearly two-fold difference in running speed (see above). However, many other design traits (muscle physiology, metabolic rates, etc.) can be in play. Therefore, spatio-temporal gait characteristics were determined over a range of speeds for 8 specimens of each test population, since these variables can be considered as integrated, dynamic design traits (see above). These measurements revealed interesting differences (VAN DAMME *et al.*, 1998): to increase their running speeds, lizards of both populations take larger strides at higher frequencies, but the specimens from the mainland primarily increased the stride length (including a floating phase), keeping the frequency relatively low, whereas the island specimens employed the inverse strategy (shorter strides at higher frequencies). The step lengths did not differ between the species and were pretty constant over the five-fold range of speeds. For a given frequency, duty factors were identical, too. In other words, since *Podarcis hispanica* and *Podarcis atrata* do use different running styles, these species seem to vary in some (integrated dynamic) design traits. However, the causal link between these specific design features and the large divergence in performance must still be established (cf. the theoretical framework, see fig. 1, 2).

Imagine that a slow island specimen would be able to switch its ‘high-frequent/short stride’ running style into the ‘long stride/low-frequent’ strategy observed on the mainland. Since the frequency of the cycling legs can be expected to be bounded by an upper limit (dictated by the force-velocity relationships of the leg muscles) it seems plausible that this specimen is able to run faster: at the speed coinciding with maximal performance in the normal mode, its legs would cycle (in the newly adopted mode) at a frequency which is 22% below that used in the natural running style (VAN DAMME *et al.*, 1998). As a consequence of the adopted ‘long stride/low-frequent’ style, however, muscles will have to contract more forcefully, since larger strides (including a floating phase) likely require larger forces, and since higher muscle forces imply lower shortening velocities (*cf.* force-velocity relationship), the maximally attainable cycling frequency can be expected to be negatively affected. Unfortunately, ground reaction force recordings are not available to date. Therefore, it is impossible to estimate to what extent the maximal frequency would be reduced by adopting the new running style. But, awaiting the results of further research (see further), it seems plausible that the '22% frequency-margin' mentioned above might allow an increased performance.

The above scenario assumes identical musculature (architecture, fibre types) in the island and the mainland species. The differences in running style could merely be a consequence of the presence of more forceful muscles in the mainland specimens (*i.e.* a component of the integrated design trait). On the other hand, it is challenging to speculate on minimal design changes that might have the potency to induce drastic changes in performance. So, building further on the assumption that island specimens can run faster by adopting the mainland running style, it is necessary to exploit how this altered style can be achieved. Most likely, the neuromotoric drive to the leg muscles would have to be modified in order to act in the new 'long stride/low-frequency mode'. We want to speculate, however, on an alternative explanation. In reality, mainland specimens show a small (but statistically significant) difference in foot length (see above; VAN DAMME *et al.*, 1998). These segments are important during final propulsion in a stride (REILLY & DELANCEY, 1997; FIELER & JAYNE, 1998). Could just this small length change automatically lead to the observed differences in running style? At the moment, this possibility cannot be excluded. Keeping joint torques identical, changed lever-arms must result in altered movement patterns and in configurational changes which can affect in turn the spatio-temporal features of the applied gait. Yet, it is equally well possible that differences in foot length are just a non-causal coincidence of the differences in performance (and running style). Forward dynamic modelling (deductive approach) or assessment of the relation between subtle morphometric variation and individual performance and running style for a large number of specimens belonging to one single population (inductive approach) can be used to test this.

Irrespective the proximate (mechanistic) cause(s) of the performance difference between the two species, ultimate (ecological) explanations should be offered as well. As mentioned above, the importance of locomotor performance in lizards must be framed primarily in a context of feeding and predation avoidance. Differences in diet might be present (MELLADO *et al.*, 1975; ESCARRE & VERICAD, 1981; PÉREZ-MELLADO, 1983; CASTILLA *et al.*, 1987), but decisive conclusions cannot be drawn (VAN DAMME *et al.*, 1998). Predation pressure, however, does differ between the two habitats. On the island there are many, nearby hides and predators are rare. On the mainland, hides are scarce and distant and several predators species are present (mammals, birds, snakes; see VAN DAMME *et al.*, 1998). So, it seems conceivable that, on the mainland, the slow (short-footed) specimens are more vulnerable to predation, thus being eliminated from the population.

These examples nicely illustrate that, even in the absence of conspicuous form-function relations, morphology finally meets ecology. Analyses grafted on ARNOLD's (1983) concept, not only revealed subtle adaptive traits, but also generated new, challenging hypotheses, being the subject for future research programs.

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REFERENCES

ABU-GHALYUN, Y., L. GREENWALD, T.E. HETHERINGTON & A.S. GAUNT, 1988. The physiological basis of slow locomotion in chamaeleons. J. Exp. Zool. **245**: 225-231.

ALEXANDER, R. MCN., 1992a. *Exploring biomechanics. Animals in motion*. Scientific American Library, New York.

ALEXANDER, R. MCN., 1992b. *The human machine*. Natural History Museum Publications, London.

ARNOLD, E.N., 1989. Towards a phylogeny and biogeography of the Lacertidae: relationships within an Old-World family of lizards derived from morphology. Bull. Brit. Mus. Nat. Hist. (Zool.) **55**: 209-257.

ARNOLD, S.J., 1983. Morphology, performance and fitness. Am. Zool. **23**: 347-361.

BENNETT, A.F., 1978. The thermal dependence of activity in lizards. Am. Zool. **18**: 653-653.

BENNETT, A.F., 1980. The thermal dependence of lizard behaviour. Anim. Behav. **28**: 752-762.

BENNETT, A.F. & R.B. HUEY, 1990. Studying the evolution of physiological performance. In: D.J. Futuyma & J. Antonovics (Eds): *Oxford survey in evolutionary biology, Vol. 7*: 251-284. Oxford University Press, Oxford.

BENNETT, A.F., R.B. HUEY & H. JOHN-ALDER, 1984. Physiological correlates of natural activity and locomotor capacity in two species of lacertid lizards. J. Comp. Physiol. B **154**: 113-118.

BOAG, P.T. & P.R. GRANT, 1984. The classical case of character release: Darwin's finches (*Geospiza*) on Isla Daphne Major, Galapagos. Biol. J. Linn. Soc. **22**: 243-287.

BRODIE, E.D., 1989. Genetic correlation between morphology and antipredator behaviour in natural populations of the garter snake *Thamnophis ordinoides*. Nature **342**: 542-543.

CARTMILL, M., 1985. Climbing. In: M. Hildebrand, D.M. Bramble, K.F. Liem & D.B. Wake (Eds): *Functional vertebrate morphology*: 73-88. Harvard University Press, Cambridge.

CASTILLA, A.M., J. JIMENEZ & I. LACOMBA, 1987. Los reptiles de Columbretes. In: L.A. Alonso Matilla, J.L. Carretero & A.M. Garcia Carrascosa (Eds): *Islas Columbretes. Contribucíon al estudio de su medio natural*: 181-194. Generalitat Valenciana, Valencia.

CASTILLA, A.M., V. FERNÁNDEZ-PEDROSA, J.D. HARRIS, A. GONZÁLEZ, A. LATORRE & A. MOYA, 1998. Mitochondrial DNA divergence suggests that *Podarcis hispanica atrata* (Squamata: Lacertidae) from the Columbretes islands merits specific distinction. Copeia **1998**: 1037-1040.

COLLETTE, B.B., 1961. Correlations between ecology and morphology in anoline lizards from Havana, Cuba and southern California. Bull. Museum Comp. Zool. **125**: 137-162.

COULTER, G.W., 1991. *Lake Tanganyika and its life*. Oxford University Press, London.

DARWIN, C., 1859. *On the origin of species by means of natural selection of the preservation of favored races in the struggle for life*. Murray, London.

DENNETT, D.C., 1995. *Darwin's dangerous idea*. Simon & Schuster, New York.

ESBJÖRNSSON, M., C. SYLVÉN, I. HOLM & E. JANSSON, 1993. Fast twitch fibres may predict anaerobic performance in both females and males. Int. J. Sports Med. **14**: 257-263.

ESCARRE, J. & R. VERICAD, 1981. *Fauna alicante. I. Saurios y ofidios*. Alicante.

FIELER, C.L. & B.C. JAYNE, 1998. Effects of speed on the hindlimb kinematics of the lizard *Dipsosaurus dorsalis*. J. exp. Biol. **201**: 609-622.

FUTUYMA, D.J., 1998. *Evolutionary biology*. Sinauer Associates, Sunderland.

GARLAND, T. JR., 1988. Genetic basis of activity metabolism. I. Inheritance of speed, stamina, and antipredator displays in the garter snake *Thamnophis sirtalis*. Evolution **42**: 335-350.

GARLAND, T. JR., 1994. Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. In: L.J. Vitt & E.R. Pianka (Eds): *Lizard Ecology. Historical and experimental perspectives*: 237-259. Princeton University Press, Princeton.

GARLAND, T. JR., A.W. DICKERMAN, C.M. JANIS & J.A. JONES, 1993. Phylogenetic analysis of covariance by computer simulation. Syst. Biol. **42**: 265-292.

GARLAND, T. JR., E. HANKINS & R.B. HUEY, 1990. Locomotor capacity and social dominance in male lizards. Funct. Ecol. **4**: 243-250.

GARLAND, T. JR. & J.B. LOSOS, 1994. Ecological morphology of locomotor performance in squamate reptiles. In: P.C. Wainwright & S.M. Reilly (Eds): *Ecological morphology. Integrative organismal biology*: 240-302. The University of Chicago Press, Chicago.

GENNARO, J.G. JR., 1969. The gecko grip. Nat. Hist. **78**: 36-43.

GOULD, S.J., 1996. The tallest tale. Is the textbook version of giraffe evolution a bit of a stretch? Nat. Hist. **5**: 18-57.

GOULD, S.J. & R.C. LEWONTIN, 1979. The sprandels of San Marco and the panglossian paradigm: a critique of the adaptationist programme. Proc. R. Soc. London B **205**: 581-598.

GRANT, B.R. & P.R. GRANT, 1982. Niche shifts and competition in Darwin's finches: *Geospiza conirostris* and congeners. Evolution **36**: 637-657.

HAMERLYNCK, O., 1990. The identification of *Pomatoschistus minutus* (Pallas) and *Pomatischistus lozanoi* (de Buen) (Pisces, Gobiidae). J. Fish Biol. **37**: 723-728.

HAMERLYNCK, O. & A. CATTRIJSSE, 1994. The food of *Pomatoschistus minutus* (Pisces, Gobiidae) in Belgian coastal waters, and a comparison with the food of its potential competitor *P. lozanoi*. J. Fish Biol. **44**: 753-771.

HARVEY, P.H. & M.D. PAGEL, 1991. *The comparative method in evolutionary biology*. Oxford University Press, New York.

HERTZ, P.E., R.B. HUEY & T. JR. GARLAND, 1988. Time budgets, thermoregulation, and maximal locomotor performance: are reptiles olympians or boy scouts? Am. Zool. **28**: 927-940.

HILDEBRAND, M., 1988. Form and function in vertebrate feeding and locomotion. Am. Zool. **28**: 727-738.

HUEY, R.B., A.F. BENNETT, H. JOHN-ALDER & K.A. NAGY, 1984. Locomotor capacity and foraging behaviour of Kalahari lacertid lizards. Anim. Behav. **32**: 41-50.

HUEY, R.B. & A.E. DUNHAM, 1987. Repeatability of locomotor performance in natural populations of the lizard *Sceloporus merriami*. Evolution **41**: 1116-1120.

HUEY, R.B., A.E. DUNHAM, K.L. OVERALL & R.A. NEWMAN, 1990. Variation in locomotor performance in demographically known populations of the lizard *Sceloporus merriami*. Physiol. Zool. **63**: 845-872.

HUEY R.B. & P.E. HERTZ, 1984. Is a jack-of-all-temperatures a master of none? Evolution **38**: 441-444.

HUEY, R.B. & R.D. STEVENSON, 1979. Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. Am. Zool. **19**: 357-366.

JAYNE, B.C. & A.F. BENNETT, 1990a. Selection on locomotor performance capacity in a natural population of garter snakes. Evolution **44**: 1204-1229.

JAYNE, B.C. & A.F. BENNETT, 1990b. Scaling of speed and endurance in garter snakes: a comparison of cross-sectional and longitudinal allometries. J. Zool. (London) **220**: 257-277.

KRAMER, G., 1951. Body proportions of mainland and island lizards. Evolution **5**: 193-206.

LACK, D., 1947. *Darwin's finches*. Cambridge University Press, Cambridge.

LEWONTIN, R.C., 1978. Adaptation. Scient. Am. **239**: 156-169.

LOSOS, J.B., 1990a. Concordant evolution of locomotor behaviour, display rate and morphology in *Anolis* lizards. Anim. Behav. **39**: 879-890.

LOSOS, J.B., 1990b. Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. Ecol. Monogr. **60**: 369-388.

LOSOS, J.B., 1990c. The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. Evolution **44**: 1189-1203.

LOSOS, J.B., 1992. The evolution of convergent structure in Caribbean *Anolis* communities. Syst. Biol. **41**: 403-420.

LOSOS, J.B., 1995. Community evolution in Greater Antillean *Anolis* lizards: phylogenetic patterns and experimental tests. Phil. Trans. R. Soc. Lond. B. **349**: 69-75.

LOSOS, J.B., D.J. IRSCHICK & T. SCHOENER, 1994. Adaptation and constraint in the evolution of specialization of Bahamian *Anolis* lizards. Evolution **48**: 1786-1798.

LOSOS, J.B., T. R. JACKMAN, A. LARSON, K. DE QUEIROZ & L. RODRIGUEZ-SCHETTINO, 1998. Contingency and determinism in replicated adaptive radiations of island lizards. Science **279**: 2115-2118.

LOSOS, J.B., T.J. PAPENFUSS & J.R. MACEY, 1989. Correlates of sprinting, jumping and parachuting performance in the butterfly lizard, *Leiolepis belliani*. J. Zool. (Lond.) **217**: 559-568.

LOSOS, J.B., B.M. WALTON & A.F. BENNETT, 1993. Trade-offs between sprinting and clinging ability in Kenyan chameleons. Funct. Ecol. **7**: 281-286.

MELLADO, J., F. AMORES, F. PARREÑO & F. HIRALDO, 1975. The structure of a mediterranean lizard community. Doñana, Acta Vertebrata **2**: 145-160.

MILES, D.B., 1994. Covariation between morphology and locomotory performance in Scleropine lizards. In: L.J. Vitt & E.R. Pianka (Eds): *Lizard ecology. Historical and experimental perspectives*: 207-235. Princeton University Press, Princeton.

MOERMOND, T.R., 1979. Habitat constraints on the behavior, morphology and community structure of *Anolis* lizards. Ecology **60**: 152-164.

PEREZ-MELLADO, V., 1983. Alimentación de dos especies simpatridas de saurios en el Sistema Central. Studia Oecologica **4**: 89-114.

PETERSON, J.A., 1984. The locomotion of *Chamaeleo* (Reptilia: Sauria) with particular reference to the forelimb. J. Zool. **202**: 1-42.

REEVE, H.K. & P.W. SHERMAN, 1993. Adaptations and the goals of evolutionary research. Q. Rev. Biol. **68**: 1-32.

REILLY, S.M. & M.J. DELANCEY, 1997. Sprawling locomotion in the lizard *Sceloporus clarkii*: quantitative kinematics of a walking trot. J. exp. Biol. **200**: 753-765.

RIDLEY, M., 1993. *Evolution*. Blackwell Scientific Publications, Cambridge.

ROSE, M.R., 1982. Antagonistic pleiotropy, dominance, and genetic variation. Heredity **48**: 63-78.

RUSSELL, A.P., 1975. A contribution to the functional analysis of the foot of the tockay, *Gekko gecko* (Reptilia: Gekkonidae). J. Zool. (Lond.) **176**: 437-476.

SCHLUTER, D. & P.R. GRANT, 1984. Determinants of morphological patterns in communities of Darwin's finches. Am. Nat. **123**: 175-196.

SCHLUTER, D., T.D. PRICE & P.R. GRANT, 1985. Ecological character displacement in Darwin's finches. Science **227**: 1056-1059.

SIH, A. & S.K. GLEESON, 1995. A limits-oriented approach to evolutionary ecology. Trends Ecol. Evol. **10**: 378-382.

SORCI, G., J.G. SWALLOW, T. JR. GARLAND & J. CLOBERT, 1995. Quantitative genetics of locomotor speed and endurance in the lizard *Lacerta vivipara*. Physiol. Zool. **68**: 698-720.

STEARNS, S.C., 1992. *The evolution of life histories*. Oxford University Press, Oxford.

TSUJI, J.S., R.B. HUEY, F.H. VAN BERKUM, T. JR. GARLAND & R.G. SHAW, 1989. Locomotor performance of hatchling fence lizards (*Sceloporus occidentalis*): quantitative genetics and morphometric correlates. Evol. Ecol. **3**: 240-252.

VAN BERKUM, F.H. & J.S. TSUJI, 1987. Inter-familiar differences in sprint speed of hatchling *Sceloporus occidentalis* (Reptilia: Iguanidae). J. Zool. (Lond.) **212**: 511-519.

VAN DAMME, R., P. AERTS & B. VANHOOYDONCK, 1997. No trade-off between sprinting and climbing in two populations of the lizard *Podarcis hispanica* (Reptilia: Lacertidae). Biol. J. Linn. Soc. **60**: 493-503.

VAN DAMME, R., P. AERTS & B. VANHOOYDONCK, 1998. Variation in morphology, gait characteristics and speed of locomotion in two populations of lizards. Biol. J. Linn. Soc. **63**: 409-427.

VANHOOYDONCK, B. & R. VAN DAMME, 1999. Evolutionary relationships between body shape and habitat use in lacertid lizards. Evol. Ecol. Res. **1**: 785-805.

WIENS, J.A. & J.T. ROTENBERRY, 1980. Patterns of morphology and ecology in grassland and shrubsteppe bird populations. Ecol. Monogr. **50**: 287-308.

WILLIAMS, E.E., 1972. The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. Evol. Biol. **6**: 47-89.

WINSOR, D.A., 1993. Constructing scientific knowledge in Gould and Lewontin's 'The spandrels of San Marco'. In: J. Selzer (Ed.): *Understanding scientific prose*. University of Wisconsin Press, Madison.

ZAAF, A., A. HERREL, P. AERTS & F. DE VREE, 1999. Morphology and morphometrics of the appendicular musculature in geckoes with different locomotor habit. Zoomorphology **119**: 9-22.