Trade-offs between sprinting and clinging ability in Kenyan chameleons

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Summary

1. We measured the force required to pull chameleons from perches of varying diameters and the sprint speed of chameleons on flat surfaces and on perches of varying diameters. The two species examined differ in their degree of terrestriality: *Chamaeleo jacksonii* is almost completely arboreal, whereas *C. dilepis* is semi-arboreal and is often observed on the ground.

2. We tested the following hypotheses: (a) each species has relatively greater sprinting and clinging abilities on surfaces corresponding to those it uses most frequently; or (b) a trade-off exists between maximizing clinging and sprinting abilities.

3. The results support the second hypothesis: *C. dilepis* runs faster than *C. jacksonii* on almost all diameters, but has poorer clinging ability on all diameters.

4. Differences in muscle architecture and composition may underlie this trade-off. Comparison with trade-offs in arboreal locomotor performance exhibited by less-specialized lizards indicates that the extreme adaptations of chameleons have allowed them to enter and diversify in a novel adaptive zone, but also may constrain the direction of subsequent adaptive change.

Key-words: Performance, sprint speed

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Introduction

Studies of locomotion are a fruitful avenue for investigation of the form and underlying mechanism of trade-offs in evolutionary adaptation (Huey & Hertz 1984; Huey *et al.* 1984; Webb 1984; Abu-Ghalyun *et al.* 1988; Garland 1988; Garland & Losos 1994). Locomotor capabilities (e.g. maximum sprint speed, endurance) have potential relevance to organismal fitness (Arnold 1983; Jayne & Bennett 1990) and are appropriate to test the evolutionary hypothesis that 'the jack-of-all-trades is master of none' — a trade-off between specialization for one task or niche and maintaining proficient capabilities in all contexts (Huey & Hertz 1984). For example, different species of fish can specialize for cruising and sprinting, rapid acceleration and turning, or manoeuvrability, but specialization for any of these capabilities apparently entails decreased abilities in the other two areas (Webb 1984). By contrast, Huey & Hertz (1984) found that individual lizards that ran relatively fast at one body temperature ran equally fast relative to other individuals at other temperatures. They suggested that either there were no trade-offs involved in maximizing sprint performance at a particular temperature, or

that if trade-offs exist, they involved exchanging increased speed at all temperatures with decreased performance in some other function.

In the context of performance capability, trade-offs could take two forms. First, trade-offs between contexts should occur only when the factors contributing to optimal performance are context dependent [e.g. long legs may enhance running speed in open habitats, but may be detrimental in cluttered areas (Jaksič & Núñez 1979)]. By contrast, trade-offs between performance abilities will occur either when some factor is positively related to one measure of performance, but negatively related to a second performance measure [e.g. wing aspect ratio of birds is directly related to speed and inversely related to agility (Norberg 1985)], or when the factors contributing to performance at the two tasks cannot be simultaneously optimized [e.g. energy can be invested either into growth or reproduction (Gadgil & Bossert 1970)].

Chameleons, renowned for their slow locomotion and their ability to grasp and move upon narrow objects, are useful for a study of trade-offs. Their locomotor attributes result from a unique suite of adaptations for arboreal locomotion on narrow surfaces, including a vertically compressed body, a pre-

hensile tail, enhanced arm and wrist mobility that allow a lizard to grasp an object regardless of its orientation, and zygodactylous hand and foot structure in which the toes are bound together into two pads (Gans 1967; Bellairs 1969; Peterson 1984). Despite their specialized morphology, some chameleons commonly move on the ground and all probably occasionally do so; a few species are almost exclusively terrestrial (Burrage 1973). We chose two species differing in their degree of terrestriality for a study of whether trade-offs in locomotor capabilities occur and, if so, what form they take. We considered two hypotheses:

1. Equivalent Specialization for Different Contexts: the performance capability of each species will be maximized in the environmental conditions it utilizes most frequently. For example, a more terrestrial species would be expected to run relatively faster on flat surfaces and relatively slower on narrow surfaces than would an exclusively arboreal species.

2. Between Performance Tasks: the evolution of chameleons involved a trade-off of decreased sprinting ability for increased grasping ability. More terrestrial chameleons may be expected to have reversed this by gaining increased sprint abilities at the cost of decreased grasping abilities.

Materials and methods

We studied two species of Kenyan chameleons. *Chamaeleo dilepis* Leach occupies scrubby and forested habitats at low and mid-elevations in east Africa (Hebrard & Madsen 1984). We commonly observed *C. dilepis* on the ground, particularly crossing roads (for example, eight lizards were seen during a 2-h period on the road from Kibwezi to Kitui, Kenya). *Chamaeleo jacksonii* Boulenger is a mid-to-high elevation species common in the garden shrubbery in some areas of Nairobi. It was almost invariably observed on thin twigs (1–4 mm in diameter) and was never observed on the ground, even though we spent considerably more time in areas inhabited by this species than in areas occupied by *C. dilepis*.

Animals were captured and transported within 1 day to a laboratory at the University of Nairobi. Animals to be used immediately in experiments were kept in cloth collecting bags; others were housed in terraria, supplied with food (locally collected insects) and misted with water. The following measurements were made on all animals: mass, snout–vent length (svl), and hind-limb length, which was measured by holding the limb outstretched and perpendicular to the body and measuring the distance from the body wall to the base of the foot pad (the toes of all chameleon feet are fused into two opposable pads comprised of three and two toes, respectively; we considered where the two pads met to be the base of the foot pad).

Length of the longer pad (measured from base to furthest claw) on both the fore- and hindfoot and forelimb length were measured on a subset of the specimens.

We measured two aspects of performance, sprint speed and clinging force, and investigated how performance varied as a function of the diameter of the support on which the lizards ran or to which they clung. Sprint speed was measured by first placing lizards in cloth bags under heat lamps and adjusting their position to produce a body temperature of $30.0 \pm 2.0\,°C$ [approximately the field and preferred body temperatures in these species (A. F. Bennett, unpublished observations)]. Chameleons were then placed on a dowel suspended approximately 1 m above the ground and induced to run with taps or light pinches to the tail. Time taken to cover a pre-marked 50 cm distance was measured with a stop-watch. As soon as the lizard covered 50 cm, it was returned to the starting position and induced to run a second time. A third similar trial was conducted if the lizard stumbled or failed to run the entire 50 cm in either of the first two trials. The fastest time was used in subsequent analyses. The lizard's temperature was then taken with a quick-reading cloacal thermometer. Trials in which the chameleon's temperature had dropped below 27.5 were discarded and were repeated after the lizard had rested and rewarmed for >30 min. The dowel sizes and the order in which they were used were (in mm): 10, 1.5, 20, 3, 6, 10. Dowels were made of brass (1.5 and 3 mm), copper (6 mm), and wood (10, 20 mm). All were roughened with sandpaper before the experiments. The chameleons appeared to have more trouble on the copper dowel than on the others, even after it was roughened a second time. An additional trial on a flat, 21 cm wide piece of astroturf placed between two cardboard walls was conducted after all the dowel trials. Animals were allowed a minimum of 45 min rest between trials. Performance of some animals decreased during the experiment. Lizards with a score in the first trial 30% greater than in the last trial (both on 10-mm dowels) were excluded. Fourteen *C. jacksonii* and eight *C. dilepis* met these criteria. Only adults were used because both sprinting and clinging ability increase ontogenetically in *C. jacksonii* (J. B. Losos, B. M. Walton & A. F. Bennett *et al.*, unpublished data) and no juvenile *C. dilepis* were available. Both sexes were used, but gravid females were excluded.

We devised a new method to quantify the grasping capabilities of lizards. Clinging force was measured by suspending a horizontal bar from a 500-g Pesola scale. A chameleon was grasped dorsally and allowed to grab onto the bar with one hindfoot. The chameleon was then slowly moved downward, pulling the bar down with it. The maximum clinging ability of a lizard was the force (in g) registered on the Pesola scale when the lizard could no longer hold onto the bar. Trials in which the lizard voluntarily
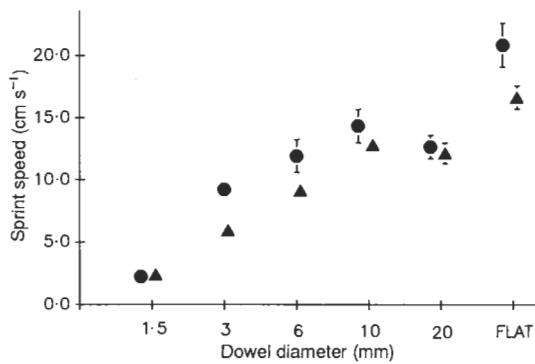
Fig. 1. Mean sprint speed (± 1 SE) on each surface. Error bars smaller than the symbols are not visible: *Chamaeleo dilepis* (●); *C. jacksonii* (▲).

released the bar (i.e. not measurements of maximum capabilities) could be determined by careful observations. Such trials were excluded. After one hindfoot had been used, the chameleon was immediately re-tested using the other foot. Scores were usually quite similar between feet ($r = 0.81$); the maximum score was used in subsequent analyses. Dowels were wrapped in masking tape, which allowed a good grip, and were presented at intervals of ≥45 min in the following order (diameters in mm): 8·5, 5, 11, 3, 2, 7. For one set of 19 lizards, trials were conducted over a 2-day period. All trials were conducted with animals at room temperature (21–27 °C); clinging force is not dependent on temperature within the temperature span used in this study (A. F. Bennett & B. M. Walton unpublished data). Sample sizes were 15 for *C. jacksonii* and 13 for *C. dilepis*. As with sprint measurements, sample sizes were smaller for the smallest dowel because some individuals voluntarily let go of the dowel in all trials with either foot.

Results

MORPHOLOGY

Chamaeleo dilepis (mass ± 1SE = 20·1 ± 2·2 g; SVL = 111·2 ± 4·3 mm) and *C. jacksonii* (mass = 22·4 ± 1·8 g; SVL = 106·9 ± 2·4 mm) were statistically indistinguishable in mass ($t = 1.28$, $P > 0.20$; values ln-transformed in all comparisons) and SVL ($t = 0.68$, $P > 0.45$), but there was a suggestion that *C. dilepis* was more slender (greater SVL relative to mass) than *C. jacksonii* (analysis of covariance, difference in slopes, $F_{1,54} = 3.89$, $P < 0.055$). *Chamaeleo dilepis* and *C. jacksonii* did not differ in relative limb length (ANCOVA, with mass as covariate; forelimb: difference in slopes, $F_{1,21} = 3.27$, $P > 0.05$, difference in intercepts, $F_{1,22} = 2.40$, $P > 0.10$; hindlimb: difference in slopes, $F_{1,54} = 0.26$, $P > 0.60$, difference in intercepts, $F_{1,55} = 1.10$, $P > 0.25$). Both the forefeet (difference

in intercepts, $F_{1,20} = 9.78$, $P < 0.01$) and hindfeet (difference in intercepts, $F_{1,21} = 9.75$, $P < 0.01$) of *C. jacksonii* were longer than those of *C. dilepis*.

SPRINT PERFORMANCE

Among adult chameleons, sprint speed and body mass were generally not significantly related (regression of speed on mass for each dowel size for each species; only one of 12 regressions significant at $P < 0.05$). In both species, sprint speed generally decreased with decreasing surface diameter, with speeds on flat surfaces greater than on any of the dowels (Fig. 1). On the flat and all dowels except the smallest and the 20-mm dowel, *C. dilepis* ran significantly faster than *C. jacksonii* (flat, $t = 3.10$, 17 df, $P < 0.01$; 3-mm dowel, $t = 4.87$, 27 df, $P < 0.001$; 6-mm dowel, $t = 2.28$, 24 df, $P < 0.05$; 10 mm: $t = 2.38$, 27 df, $P ≤ 0.025$). In both species, speed decreased steadily with decreasing dowel size from 20 to 3 mm and declined sharply on the 1·5-mm dowel (to 10·6–14·5% of speed on the 20-mm dowel). Many lizards were not able to maintain an upright posture while moving on the 1·5-mm dowel, and ended up moving while suspended upside down, hanging like a sloth.

CLINGING PERFORMANCE

Within each species, clinging ability increased with body size at each dowel size ($r^2 > 0.56$, P ≤ 0.005 in all cases; Fig. 2), except no relationship was apparent for *C. dilepis* on the smallest (2 mm) dowel ($P > 0.35$). *Chamaeleo jacksonii* has greater clinging ability than *C. dilepis* on all dowel sizes (analysis of covariance, difference in slopes always non-significant, difference in intercepts always $P < 0.001$), except on the smallest dowel (difference in slopes, $F_{1,13} = 1.22$, $P > 0.25$; difference in intercepts, $F_{1,14} = P > 0.20$).

To examine whether the species differ on which dowel they cling best, scores for each individual were
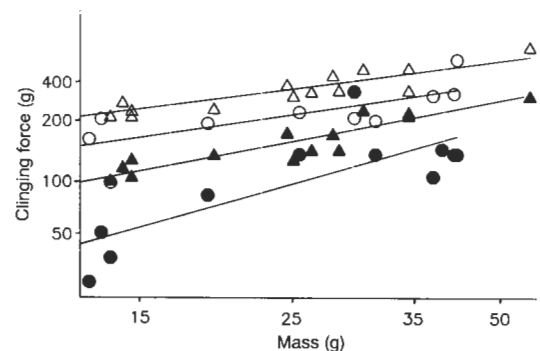

Fig. 2. Clinging ability *vs* body mass on two representative dowel sizes: the 3- (○, △) and 11-mm (●, ▲) dowels. *Chamaeleo jacksonii* (△, ▲); *C. dilepis* (○, ●).
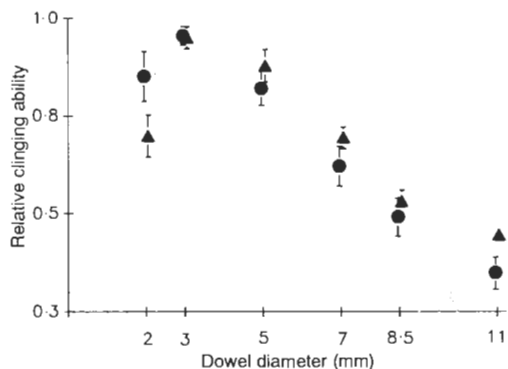
Fig. 3. Mean relative clinging ability (i.e. for each lizard, clinging ability on a given dowel size divided by maximum ability for that lizard on any dowel). Symbols as in Fig. 1.

divided by that individual's highest score, which had the effect of scaling all scores between 0 and 1. Both species had modal distributions with the relatively highest scores on the 3-mm dowel (Fig. 3). Relative clinging ability differed significantly between the two species only on the 11-mm dowel ($t = 2.33$, 16.1 df, $P < 0.035$). Standardization of scores did not entirely remove effects attributable to differences in size. For both species on both the 7- and 11-mm dowels, larger individuals had relatively greater clinging ability than smaller ones ($r^2 = 0.281 - 0.321$, $0.031 > P > 0.015$); on all other dowels, size and relative clinging ability were not related.

Discussion

The remarkable adaptations of chameleons for utilizing thin arboreal surfaces (Gans 1967; Bellairs 1969; Peterson 1984) allow them to move effectively on surfaces on which even arboreal specialists from other lizard families have difficulty (e.g. Losos & Sinervo 1989). Relatively large chameleons could move with ease (if somewhat slowly) on structures as small as 3 mm in diameter. Nonetheless, several species of *Chamaeleo* have become secondarily terrestrial (Crumly & Rieppel, personal communication): at the extreme, *C. namaquensis* is primarily-to-entirely terrestrial in the sand-dunes of the Namib Desert (Fitzsimons 1943; Burrage 1973; Wager 1983). *Chamaeleo dilepis* is probably less terrestrial than *C. namaquensis* (though so little is known about the natural history of chameleons that definitive statements are impossible to make), but it appears to walk on the ground considerably more frequently than do most other *Chamaeleo*, including *C. jacksonii*.

TRADE-OFFS WITHIN A GIVEN PERFORMANCE ABILITY IN DIFFERENT CONTEXTS

Despite the difference in habitat between *C. dilepis* and *C. jacksonii*, relative sprinting and clinging abilities on different-sized dowels are the same

species: sprinting ability is greatest on flat surfaces and declines steadily as surface diameter decreases, whereas clinging ability is greatest on 3-mm dowels. Why have the performance capabilites of these species not diverged to reflect differences in habitat use? One possibility is that selection may not favour such divergence despite differences in habitat use. *Chamaeleo jacksonii* may move on the ground at least occasionally and thus need to maintain sprint capabilities to avoid predators [e.g. late in the day in experimental trials, *C. jacksonii* occasionally left the isolated bushes into which they had been placed (A. F. Bennett, unpublished data)]. Similarly, *C. dilepis*, although more terrestrial than *C. jacksonii*, still uses arboreal structures extensively (Hebrard & Madsen 1984; J. B. Losos, B. M. Walton & A. F. Bennett, unpublished observation) and thus must maintain the ability to grasp narrow supports. Conversely, there probably is no particular premium on high-speed arboreal locomotion because rapid movements are not involved for either prey capture or predator avoidance in the trees. Arboreal chameleons catch prey either via ambush or through slow stalking (Burrage 1973); predator avoidance usually involves crypsis, slow escape, or dropping from the branch (Brain 1961; Burrage 1973).

Alternatively, chameleons may not be able to evolve to maximize performance on a particular surface diameter. Instead, decreased sprinting capability may be an inescapable biomechanical consequence of movement on narrow surfaces (Peterson 1984; Cartmill 1985). Indeed, lizards generally show decreased sprinting abilities on narrow surfaces (Abu-Ghalyun *et al.* 1988; Losos & Sinervo 1989; Sinervo & Losos 1991). By contrast, optimal dowel size for clinging should be a function of toe-pad size (Cartmill 1985). Nonetheless, our data indicate that interspecific differences in toe-pad length do not lead to differences in the dowel diameter at which clinging ability is maximal. Regardless of the underlying causes, for both sprinting and clinging, the data do not indicate the existence of trade-offs between performance capabilities in different habitat contexts.

TRADE-OFFS BETWEEN PERFORMANCE ABILITIES

By contrast, the data do suggest the possibility that a trade-off exists between maximizing sprinting and clinging abilities. *Chamaeleo dilepis* sprints faster than *C. jacksonii* on most surfaces (Fig. 1), but has weaker clinging abilities on all dowel sizes (Fig. 2). The importance of enhanced sprinting abilities for *C. dilepis* is clear: a chameleon moving on the ground is extremely vulnerable to predation (further, the green-to-yellow *C. dilepis* was extremely conspicuous against the red soil of southern Kenya); in addition, prolonged exposure to sun in open habitats may lead to rapid and excessive heat gain (Walton & Bennett 1993). Why *C. jacksonii* might need greater clinging

ability is unclear, though male chameleons are known to engage in vigorous combat (Gans 1967; Parcher 1974) — more study of both species is necessary to determine if they differ behaviourally.

One possible explanation for the trade-off is that increased sprint speed comes with a necessary cost of decreased clinging ability. However, the morphological basis for a linkage in performance abilities is not obvious. The longer toe-pads of *C. jacksonii* may be related to increased clinging ability (Cartmill 1985; see above), but it is not clear why they should affect sprint speed. In comparisons among lizards, sprint speed generally correlates with body size and relative limb length (Losos 1990; Garland & Losos 1994), but the two species studied herein differ in neither.

In at least some respects, however, the design requirements for clinging and sprinting may be antagonistic. Several important differences in the limb musculature of the two species (P. Wainwright & A. F. Bennett, unpublished data) could be responsible for the negative relationship between sprinting and clinging ability. The proximally inserted flexors of *C. dilepis* can produce more rapid movement (Hildebrand 1985), but also provide less mechanical advantage for sustained clinging. By contrast, the more distally inserted flexors of *C. jacksonii* can apply more torque to resist falling or being pulled or pushed from a perch. The high proportion of tonic fibres in *C. jacksonii* (G. Mutungi, personal communication) implies that their limb flexors should contract more slowly and only in response to tetanic stimuli, and should generate greater maximal force than can the flexors of *C. dilepis* (see Abu-Ghalyun *et al.* 1988). Further, tonic fibres are thought to be important primarily during stationary postural support. Consequently, a large proportion of tonic fibres would be advantageous for clinging, but probably would not be functional, or even activated, during rapid movement. One possible consequence is that stretching the non-active and extensive population of tonic fibres in *C. jacksonii* acts as a resistance that must be overcome by activated twitch fibres. This fact, coupled with the possibility of a relatively smaller population of twitch fibres, may mean that the active twitch fibres are functioning at higher work loads, and consequently slower shortening velocities, in comparison to *C. dilepis*. Similar mechanisms were suggested by Abu-Ghalyun *et al.* (1988) to explain differences between *Chamaeleo* and *Agama*.

TRADE-OFFS AND THE EVOLUTION OF
ARBOREALITY IN LIZARDS

Comparison to two similar studies may provide an interesting perspective on the evolution of arboreality in lizards. At the level of differentiation among populations within *Sceloporus occidentalis*, morphological differences exist [more arboreal populations have longer legs and are more slender (Sinervo & Losos

1991; B. Sinervo, personal communication)], but are relatively minor. In terms of sprint performance, a direct trade-off exists: terrestrial populations run faster on broader surfaces, but are more severely affected by decreasing diameter and consequently run more slowly than arboreal populations on thinner surfaces. Among four species of *Anolis*, the morphological differences are more marked: *A. valencienni* commonly uses twigs and is slender, with enhanced girdle mobility, allowing greater arm rotation and manoeuvrability (Peterson 1974; Losos & Sinervo 1989). Among these species, the trade-offs are between two performance capabilities, sprint speed and 'surefootedness', but the trade-offs are still habitat dependent: on narrow surfaces, *A. valencienni* has considerably less difficulty moving than longer-legged species, but on broad surfaces these latter species, which use wider surfaces in nature, can run considerably faster than *A. valencienni* (Losos & Sinervo 1989). Among chameleons, all species of which show a suite of extreme adaptations for utilizing narrow surfaces, the trade-offs are between different aspects of performance and are only slightly habitat dependent. *Chamaeleo dilepis* runs faster on all but the narrowest surfaces, but has poorer clinging ability on all diameter surfaces.

This pattern supports the hypothesis that the evolution of extreme specialization may serve to constrain the direction of subsequent adaptation (Riedl 1978; Donoghue 1989). Whereas *Sceloporus* can fine tune its sprint-speed abilities to adapt to the particular habitat it uses, the specializations of chameleons as a group have bought enhanced ability to grasp and move upon extremely narrow surfaces at the cost of diminished locomotor speed on all surfaces. Consequently, evolutionary avenues available to chameleons are limited: they may be able to adapt to particular circumstances either by evolving increased clinging or sprinting abilities, but not both. Further, not only is the evolution of enhanced performance at one task accompanied by decreased abilities at another task, but these trade-offs are consistent in all contexts. Thus, unlike the trade-offs in *Sceloporus* and *Anolis*, chameleons cannot avoid the costs of decreased performance by using only those habitats in which performance is negatively affected. Ironically, the adaptations that have allowed chameleons to occupy a novel adaptive zone and diversify may also serve to constrain the direction of subsequent evolutionary change.

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