



## The effect of body armature on escape behaviour in cordylid lizards

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The possession of armour may affect escape behaviour in two ways. On one hand, by decreasing vulnerability to predators, armour may permit individuals to use habitats and behaviours that are too risky for unarmoured individuals. Alternatively, the possession of armour may have negative trade-offs on other traits involved in antipredator behaviour, such as sprint speed, thus constraining antipredator options relative to those available to unarmoured individuals. To examine these contrasting predictions, we examined species in the lizard family Cordylidae, which contains remarkable morphological diversity, ranging from completely unarmoured to heavily defended species. Moreover, phylogenetic analysis indicates that armour has been an evolutionarily labile trait. We found support for the second prediction. Degree of body armature was inversely correlated with distance run from a predator: heavily armoured species always entered refuges after short distances, whereas many unarmoured lizards continued to flee and could not be induced to enter a refuge. Possession of armour was also negatively related to use of vertical surfaces during escape behaviour. These results were unchanged when analysed in a phylogenetic context. Thus, we conclude that the morphological requirements for active flight and armoured defence are incompatible. Heavily armoured species are bulky, have short legs and run more slowly than less armoured species. Rather than constituting an alternative to behavioural antipredator tactics, we conclude that the possession of armour is part of an antipredator syndrome that includes habitat use and behaviour as well as morphology.

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Many different strategies exist for avoiding predation (reviewed in [Edmunds 1974](#)) and costs and benefits are associated with each ([Sih 1987](#); [Lima & Dill 1990](#); [Lima 1998](#)). One tactic that has evolved many times is the evolution of body armour, spines and other armature that decrease the ability of a predator to subdue and ingest a prey individual (examples include turtles, ankylosaurs, pangolins, porcupines, hedgehogs, armadillos, glyptodonts, sticklebacks, armoured catfish, millipedes, snails, crabs, woodlice and copepods; [Edmunds 1974](#)). Paradoxically, the possession of armour may have both a liberating and a constraining effect on antipredator behaviour. On the liberating side, protected individuals or species may be able to use habitats and engage in behaviours in the presence of predators that would be too risky for

unprotected individuals ([Greene 1988](#); [McLean & Godin 1989](#); [Lima & Dill 1990](#); [Abrahams 1995](#)). Conversely, armour also imposes costs. By its nature, armour is often heavy and inflexible and thus its possessors are generally not known for their speed or agility. As a result, reliance on flight may not be an effective method for armoured species to avoid predators. Consequently, the possession of armour may have both positive and negative effects on an animal's ability to avoid being preyed upon. Which effect predominates probably depends on the extent to which armour reduces vulnerability to predators relative to the degree to which it reduces an organism's ability to avoid predation by other means.

Few data are available to examine these ideas. The only two reports found are studies that have shown that armoured fish allow predators to approach more closely than do unarmoured species ([McLean & Godin 1989](#); [Abrahams 1995](#)); no study has directly compared the liberating and constraining effects of armour. The paucity of studies on the behavioural consequences of the evolution of morphological defensive structures is probably due, in part, to the fact that few heavily defended species

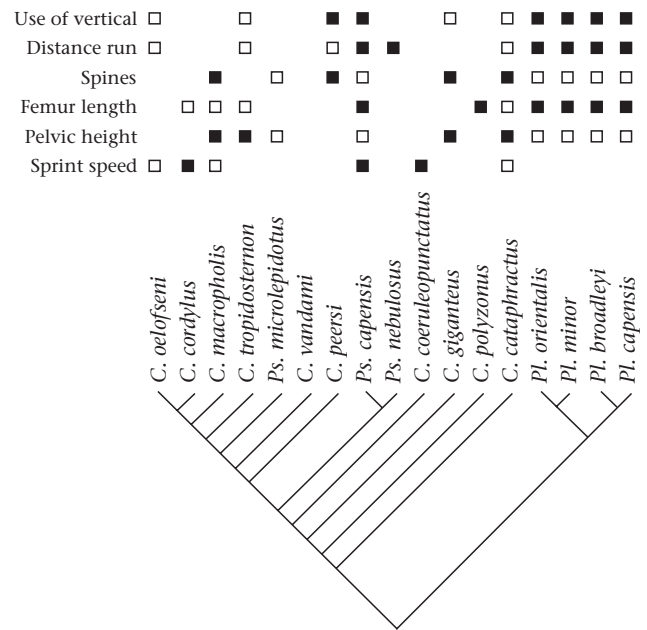
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have close relatives that are not so defended (Endler 1986). For example, the sister taxa of both turtles and pangolins are still controversial (e.g. Rieppel & Reisz 1999; Liu et al. 2001) and the closest relatives of other heavily defended taxa, such as hedgehogs, porcupines and armadillos, are species that are quite different in many aspects of their natural history. Consequently, comparative studies are difficult because comparisons must be drawn to distantly related taxa that differ in many other respects beside their lack of morphological defences, thus confounding interpretations. For this reason, what is needed is a study of a closely related set of species that vary in degree of morphological defence.

Just such an opportunity is provided by the lizard family Cordylidae. Cordylids (sensu stricto, following Lang 1991; Frost et al. 2001) include four genera that vary markedly in their armature. At one extreme, some species in the genus *Cordylus* are covered with spines on their heads, necks, legs, sides and tails. In addition, their skin is underlain with bony osteoderms. At the other extreme, all members of *Platysaurus* and some *Pseudocordylus* are completely lacking in spines and osteoderms (see photographs in Branch 1998; we do not consider the fourth cordylid genus, *Chamaesaura*, because its three species are nearly limbless and exhibit a natural history fundamentally different from other members of the family; Branch 1998). Examination of a phylogeny for the family reveals that armature has been an evolutionarily labile trait (Fig. 1): none of the four most heavily armoured species in our data set are sister taxa and these species occur in three distinct parts of the tree. Similarly, the least armoured species also occur in three clades.

Little is known about the antipredator behaviour of cordylids or even about which species prey on them (for a review of what is known about antipredator behaviour see Greene 1988; for a summary of natural history in general see Branch 1998, who reports that cordylid predators include snakes, small carnivores and raptors). All species use rock crevices or other refuges. Indeed, a number of the unarmoured species are extraordinarily flattened dorsoventrally (hence the name 'flat lizards' for platysaurs), which allows them to enter extremely narrow crevice openings. Whether and how spines and armour are used to deter predation is little known, but several uses for spines have been documented: *C. cataphractus* (the armadillo lizard) bites its tail immediately upon capture, presenting a predator with a doughnut-shaped item bristling with spines (Mouton et al. 1999), and *C. giganteus* (the sungazer) retreats headfirst into earthen burrows, where it jams its posterior pointing head spines into the roof of the burrow, which prevents the lizard from being pulled back out of the burrow. In addition, it lashes its heavily spined tail back and forth, an action that can draw blood on a human hand (Marais 1984). More generally, the spines and osteoderms of many *Cordylus* seem likely to prevent many small predators (e.g. some snakes) from subduing and ingesting them.

These observations suggest two hypotheses. (1) Being less vulnerable to predators, armoured species should use habitats that are more exposed to predators. Our specific prediction is that, although all species use



**Figure 1.** One of two phylogenies used in statistical analyses (from Frost et al. 2001). Genera are *Cordylus*, *Platysaurus* (*Pl.*) and *Pseudocordylus* (*Ps.*). Note that Frost et al. found *Cordylus* and *Pseudocordylus* to be mutually paraphyletic. *Cordylus vandami*, formerly a subspecies of *C. warreni*, was substituted for the latter species in the phylogeny. Dark squares indicate the species with the largest values for the three traits (all relative to body size, except sprint speed), whereas open squares indicate the species with the lowest values. Femur length was chosen to illustrate trends involving limb elements and pelvic height was chosen to represent degree of flattening. 'Spines' is the first axis of the principal component analysis on the seven spine measurements. Morphological data were not collected for *Ps. nebulosus* and behavioural data were not collected for *C. macropholis* and *C. coeruleopunctatus*. Sprint speed data were available for only six species. The other phylogeny only differs from the one pictured here in three respects: first, *C. vandami* is the sister taxon to the clade bounded in the figure by *C. oelofseni* and *C. giganteus*, rather than its position here as the sister to the clade bounded by *C. oelofseni* and *Ps. microlepidotus*; second, *C. polyzonus* and *C. cataphractus* form a clade that is the sister taxon to the clade bounded by *C. oelofseni* and *C. giganteus*, rather than being sequential outgroups to that clade; and, third, *C. coeruleopunctatus* is the sister taxon to the clade composed of *Ps. capensis* and *Ps. nebulosus*, rather than the entire clade bounded by *C. oelofseni* and *Ps. nebulosus*.

crevices, unarmoured species will be closer to theirs and thus will travel shorter distances to escape a predator. (2) If the evolution of armature is accompanied by functional limitations, unarmoured species may rely on flight more than armoured species.

## METHODS

Our approach is three-fold. First, to quantify the extent of armour of cordylid lizards, we measured the length of the spines that are found on many parts of the body of some cordylids. In addition, to examine correlates of antipredator behaviour, we also measured a variety of traits relevant to locomotion and the use of crevices, such as

limb length and body depth (Losos 1990; Bauwens et al. 1995; Bonine & Garland 1999; Vanhooydonck & Van Damme 2001). Second, we tested the hypothesis that degree of armature is related to locomotor ability by measuring the sprinting abilities of six species that differed greatly in extent of armature. Third, we examined how, among cordylid species, escape behaviour is related to armature and limb morphology.

### Morphological Measurements

We examined 129 preserved adult specimens of 24 species in the genera *Cordylus*, *Pseudocordylus* (*Ps.*) and *Platysaurus* (*Pl.*). Twelve morphological measurements were taken: snout–vent length (SVL), tail length, head height, head width, pelvis width and seven spine measurements. SVL and tail length measurements were made with a metric ruler by pressing the specimen flat against a dissecting tray. If the specimen's body was stiff and could not be straightened sufficiently to produce an accurate measurement, tail and SVL measurements were made in no more than three segments and summed. Lizards with broken tails were not included in the analyses involving tail length. Measurements of head height, head width and pelvis width were made with metric calipers. Head height was measured at the deepest place on the head. Head width was measured at the widest part of the head. Some specimens have spines at this point on their head, just anterior to the tympanum. Due to its placement, this spine was included in the measurement of head width.

Spine length was measured at seven points on each specimen: tail, hindleg, side of the trunk, neck and three head spines: the longest spine directly anterior to the tympanum, the longest spine on the posterior margin of the head, and the longest spine on the side of the head posterior to the tympanum. All measurements were of spines on the right side of the specimens. In each case, the longest spine was identified through multiple measurements; only the longest spine measurement was recorded. Large spines were measured with needle-nosed calipers. Smaller spines were measured under a binocular dissecting microscope using either needle-nosed calipers or an ocular micrometer. Tail, hindleg, trunk and neck spines were measured as the distance along the posterior edge of the spine from the tip to the point where the hardened scale meets soft tissue at the base of the spine. Because many specimens have no spines or raised scales on their head, for head spines we measured the length of the keel on the appropriate head scale, or, on those specimens without a pronounced keel, the width of the longest anterior–posterior axis of each scale. All morphological measurements were made twice and averaged.

Following these measurements, specimens were radiographed. Because the forelimb often was contorted, the right foreleg was removed from each specimen and laid flat on the x-ray plate. MorphoSys (Meacham & Duncan 1990) was used to measure skeletal elements from radiographs. Five limb measurements were taken: humerus, ulna, femur, tibia and the proximal phalanx of the third metatarsal. All long bones were measured from the most

proximal point to the most distal point on the right side of the specimens when possible. If the bones were not flat or were broken, the measurement was taken from the left side. Two aspects of the skull were measured: maximum width, from the most lateral point on one side to the most lateral on the other, most often occurring near the orbit, and jaw width from the points at which the quadrates articulate with the skull. If either of the limbs or the head did not lie flat on the radiograph plate, measurements were not taken on that variable. All measurements were taken twice and averaged.

### Sprint Speed Measurement

As a preliminary approach to study whether sprint speed is related to degree of body armature, we measured sprint speed on adult males and females of six species of cordylid varying in armature: *C. cataphractus*, *C. coeruleopunctatus*, *C. cordylus*, *C. macropholis*, *C. oelofseni* and *Ps. capensis*. Lizards were captured by noosing them with a 3-m fishing pole in the Western Cape under Cape Nature Conservation Board Permit No. 284/2001 and kept singly or in pairs in glass terraria (400 × 600 × 300 mm) with a 40-W spotlight as heat source. Water and food (mealworms and crickets) were provided ad libitum. Sprint speed trials were conducted following standard protocols (Miles & Smith 1987; Losos et al., in press) in climate-controlled rooms set at 30 °C except for *Ps. capensis*, which was tested outside in bright sunlight at air temperatures in the shade of 32 °C (most cordylid species examined in the field are active at body temperatures of 30–32 °C; P. Le Fras N. Mouton, unpublished data). Tests were conducted on a racetrack (3 m long, 15 cm wide), which had infrared sensors spaced every 20 cm. Sensors were linked to a computer that calculated speed over every 20-cm section. The track was flat with high walls on each side and a rough surface (the back of a carpet) for traction; the far end was covered with a cardboard box to give the impression of a crevice towards which the lizards would run for cover. Each lizard was tested at least three times with at least a 20-min rest between trials and the maximal speed over a 20-cm section was used as the estimate of an individual's maximal sprinting capabilities. Individuals judged to not be using their maximal capabilities (as evident by irregular motions, running into the side of the track and gait) were excluded from analysis. All sprint speeds were determined within 1 month of capture, except for *Ps. capensis*, which was not cooperative during initial testing, but performed well when retested 7 months after capture. All lizards were released at their capture sites following testing.

### Behavioural Observations

We collected escape behaviour data on 243 adult lizards of 15 species (range per species 3–50), 14 of which were included in the morphological data set. Study sites were distributed throughout South Africa. Most, but not all, species occupy rocky habitats, although the size of the rocky material and the extent of vegetative cover varied

among sites and species. More detailed descriptions of species' habitats can be found in Branch (1998).

To observe escape behaviour, study areas were surveyed with binoculars to locate lizards. Then, to simulate the approach of a potential predator, the observer advanced directly towards the lizard at a constant pace of approximately 0.5 m/s. The distance lizards moved until they entered a refuge was recorded. If a lizard did not enter a refuge, the observer continued to move in its direction until it had moved at least 5 m, which sometimes occurred in one movement, and other times in several, from its starting position. Escape distance was the distance moved; all lizards moving more than 5 m were given a score of 5 m. Analyses were conducted using all of the data and using only those individuals that entered refuges (88% of all individuals, 100% of the individuals in 10 species, <50% in only one species, *P. orientalis*). Species mean values for the two data sets were highly correlated ( $r=0.995$ ) and statistical analyses were virtually identical, so we only report results using the entire data set.

Each lizard also was scored for whether it moved laterally or upward on a surface that was inclined at an angle of 45° or greater. For each species, the proportion of lizards that moved on such surfaces (combining individuals that moved laterally and those that moved upward) was tabulated and arcsine square-root transformed for statistical analysis. All observations were taken on sunny days on which lizards were active between 0900 and 1630 hours. Data were collected during October–November 1997, September–November 1998 and December 2000.

### Statistical Analyses

Natural log-transformed mean species values were used in all analyses. All morphological variables increased interspecifically with increasing body size. To remove the effects of differences in body size, each variable was regressed against snout–vent length and residuals were retained. To reduce the dimensionality of the data, principal components analyses (PCAs) were conducted using correlation matrices. In these analyses, all axes were retained in which at least one variable was significantly correlated to that axis.

If a phylogenetic effect exists (i.e. if closely related species are more phenotypically similar than would be expected by chance), comparative studies that do not account for phylogenetic relationships may produce elevated levels of type I error (Felsenstein 1985). Consequently, we used the independent contrasts method to examine whether probability values from correlation analyses suffered from this problem. A recent study of the phylogeny of the Cordylidae (Frost et al. 2001) included all species in this study except the four species of *Platysaurus* (other species of *Platysaurus* were included) and *C. vandami* (however, *C. vandami* formerly was considered a subspecies of *C. warreni*, which was included in the study). Frost et al. (2001, Figures 1–2) proposed two phylogenetic hypotheses (see Fig. 1); we conducted independent contrasts analyses on both (which we

**Table 1.** Principal components analysis on non-size-adjusted data

| Variable*            | PC axis |        |
|----------------------|---------|--------|
|                      | 1       | 2      |
| Snout–vent length    | 0.929   | –0.349 |
| Tail                 | 0.560   | –0.771 |
| Humerus              | 0.828   | –0.527 |
| Ulna                 | 0.826   | –0.531 |
| Femur                | 0.759   | –0.626 |
| Tibia                | 0.730   | –0.650 |
| Metatarsal           | 0.664   | –0.730 |
| Jaw width            | 0.971   | –0.085 |
| Skull width          | 0.960   | –0.118 |
| Head height          | 0.929   | 0.124  |
| Head width           | 0.978   | 0.013  |
| Pelvic height        | 0.928   | 0.261  |
| Tail spine           | 0.713   | 0.667  |
| Leg spine            | 0.750   | 0.608  |
| Trunk spine          | 0.517   | 0.740  |
| Neck spine           | 0.570   | 0.733  |
| Ear spine            | 0.782   | 0.563  |
| Posterior head spine | 0.773   | 0.515  |
| Lateral head spine   | 0.829   | 0.385  |
| Eigenvalue           | 12.2    | 5.4    |
| % Variance           | 64.3    | 28.2   |

\*All variables are species means, ln-transformed.

henceforth refer to as Phylogeny A and Phylogeny B). In both cases, relationships among the four *Platysaurus* were resolved with the clade of *Pl. broadleyi* and *Pl. capensis* being the sister taxon to the clade of *Pl. minor* and *Pl. orientalis* (I. Scott, S. Keogh & M. Whiting, personal communication). Because branch length information was not provided in Frost et al. (2001), all branch lengths were set to equal lengths, thus assuming a special model of character evolution. Diagnostic methods were used to check that all contrasts were appropriately standardized (Garland et al. 1993); no cases of inadequate standardization were detected. The effect of size was removed in contrast analyses by calculating residuals of contrasts of a morphological variable against contrasts in SVL.

## RESULTS

### Morphology

In the PCA on non-size-adjusted data, all variables loaded strongly and positively on the first axis (Table 1). The second axis reflected an inverse relationship between limb and tail lengths versus spine lengths. The PCA on size-adjusted data revealed an inverse relationship between head dimensions, girdle height and spine lengths, on one hand, versus limb lengths on the other (Table 2; Fig. 1). Spine lengths were all highly intercorrelated. In a PCA on only spine lengths using non-size-adjusted data, the first axis accounted for 87.2% of the variation and all measurements loaded strongly and positively; a similar result was found for size-adjusted spine lengths (Table 3).

**Table 2.** Principal components analysis on size-adjusted data

| Variables*           | PC axis |        |        |
|----------------------|---------|--------|--------|
|                      | 1       | 2      | 3      |
| Tail                 | -0.861  | -0.056 | 0.195  |
| Humerus              | -0.769  | 0.573  | 0.152  |
| Ulna                 | -0.767  | 0.525  | 0.135  |
| Femur                | -0.859  | 0.386  | 0.298  |
| Tibia                | -0.873  | 0.396  | 0.198  |
| Metatarsal           | -0.917  | -0.014 | 0.198  |
| Jaw width            | 0.849   | -0.190 | 0.444  |
| Skull width          | 0.807   | -0.339 | 0.426  |
| Head height          | 0.888   | -0.212 | 0.064  |
| Head width           | 0.906   | 0.016  | 0.311  |
| Pelvic height        | 0.917   | 0.108  | -0.057 |
| Tail spine           | 0.969   | 0.113  | 0.026  |
| Leg spine            | 0.914   | 0.274  | 0.008  |
| Trunk spine          | 0.795   | 0.497  | -0.249 |
| Neck spine           | 0.830   | 0.470  | -0.143 |
| Ear spine            | 0.942   | 0.134  | 0.125  |
| Posterior head spine | 0.849   | 0.302  | 0.139  |
| Lateral head spine   | 0.743   | 0.594  | 0.055  |
| Eigenvalue           | 13.3    | 2.1    | 0.8    |
| % Variance           | 74.1    | 11.9   | 4.7    |

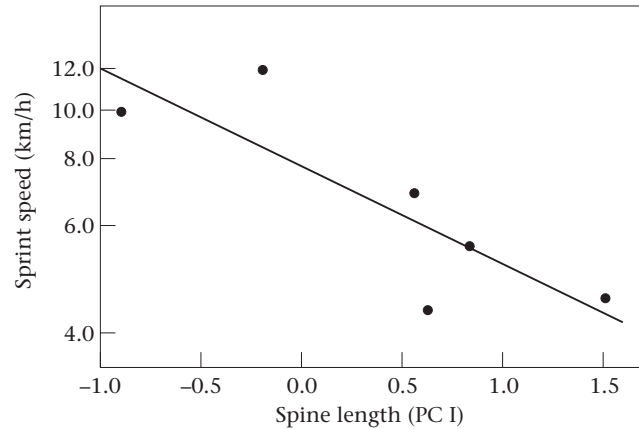
\*Values are residuals from regressions on snout-vent length, using species means, ln-transformed.

**Table 3.** Principal component analyses on spine measurements

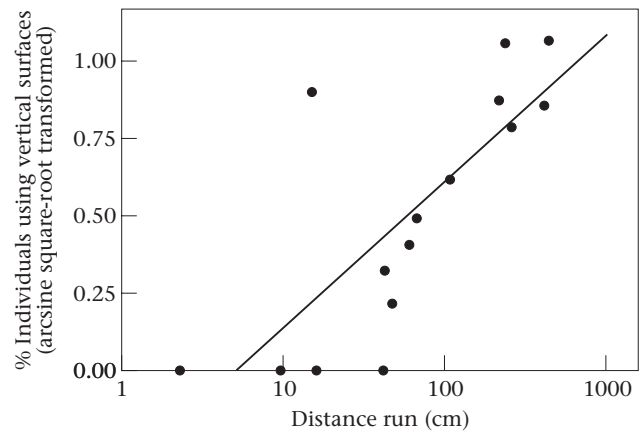
|                    | Axis 1                 |                    |
|--------------------|------------------------|--------------------|
|                    | Non-size-adjusted data | Size-adjusted data |
| Tail spine         | 0.958                  | 0.947              |
| Leg spine          | 0.969                  | 0.962              |
| Trunk spine        | 0.902                  | 0.926              |
| Neck spine         | 0.931                  | 0.946              |
| Ear spine          | 0.948                  | 0.934              |
| Posterior head     | 0.920                  | 0.898              |
| Lateral head spine | 0.905                  | 0.902              |
| Eigenvalue         | 6.1                    | 6.1                |
| % Variance         | 87.2                   | 86.7               |

**Sprint Speed**

Sprint speed was not related to overall body size (Pearson correlation:  $r_4 = -0.04$ ,  $N=6$ , NS), but was related to size-adjusted spine length (as represented by the first PC axis in the analysis on size-adjusted spine lengths;  $r_4 = -0.84$ , one-tailed  $P < 0.025$ ; Fig. 2). This relationship was significant with Phylogeny A ( $r_4 = -0.83$ ,  $P < 0.025$ ), but not Phylogeny B ( $r_4 = -0.40$ ,  $P < 0.25$ ). In Phylogeny B, the two fastest and least armoured species, *Ps. capensis* and *C. coeruleopunctatus*, are sister taxa, suggesting that the concordant evolution of speed and decreased armour occurred only once, whereas in Phylogeny A, *C. coeruleopunctatus* is the sister taxon to a clade containing *Ps. capensis* and several of the more heavily armoured species, which implies multiple evolutionary events in which speed and armour evolved concordantly.



**Figure 2.** Sprint speed versus spine length (as represented by the first principal component axis in the analysis using size-adjusted spine lengths).



**Figure 3.** Distance run versus use of vertical surfaces. Distance run is shown on a log scale with regression lines for illustrative purposes, but correlation analyses were conducted on natural log-transformed data.

**Escape Behaviour**

Use of vertical surfaces was related positively to distance moved ( $r_{13} = 0.77$ ,  $N=15$ ,  $P < 0.001$ ; Fig. 3). Body size (as represented by log SVL) was not correlated with either of these behavioural variables ( $-0.33 < r_{12} < -0.04$ , NS;  $N=14$  in all comparisons involving morphology and behaviour). However, each of the five size-adjusted limb measurements was positively correlated with distance run ( $r_{12} > 0.76$ ,  $P < 0.002$ ; Fig. 4a) and use of vertical surfaces ( $r_{12} > 0.72$ ,  $P < 0.005$ ; Fig. 5a). Conversely, size-adjusted head height and width, body height and spine length (axis I of the PCA analysis on spine measurements) were all negatively correlated with distance run ( $r_{12} < -0.75$ ,  $P < 0.0025$ ; Fig. 4b, c) and use of vertical surfaces ( $r_{12} < -0.64$ ,  $P < 0.02$ ; Fig. 5b, c).

In almost all morphological and behavioural analyses, nonphylogenetic and phylogenetic (independent contrasts) analyses produced qualitatively identical results. The only exceptions were a few cases in which non-phylogenetic analyses were significant, whereas contrasts analyses produced slightly nonsignificant results (ulna

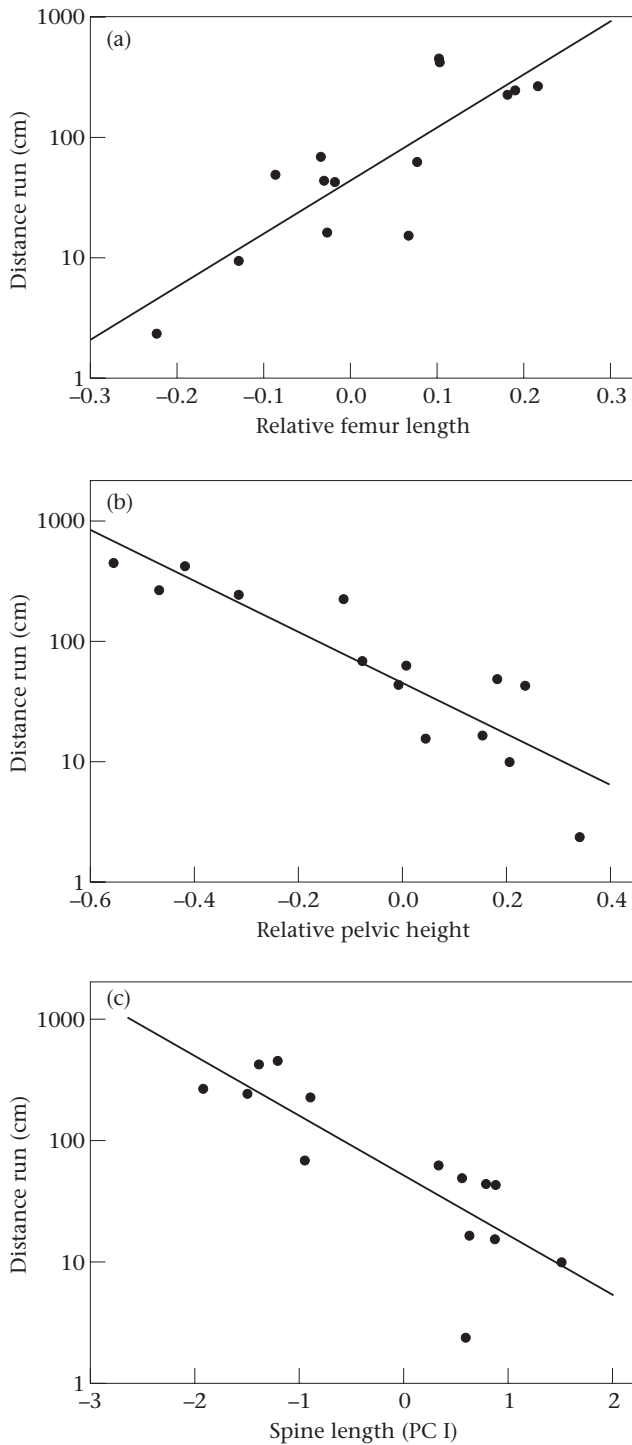


Figure 4. Morphological variables versus distance run.

length versus use of vertical surfaces, Phylogeny A,  $P < 0.06$ ; Phylogeny B,  $P < 0.10$ ; humerus length versus use of vertical surfaces: Phylogeny B,  $P < 0.06$ ; head height and width versus use of vertical surfaces: both phylogenies,  $P < 0.15$  in all four cases). Given the evolutionary lability of behavioural and morphological traits, all of which exhibit substantial levels of convergent evolution (Fig. 1), the congruence between phylogenetic and

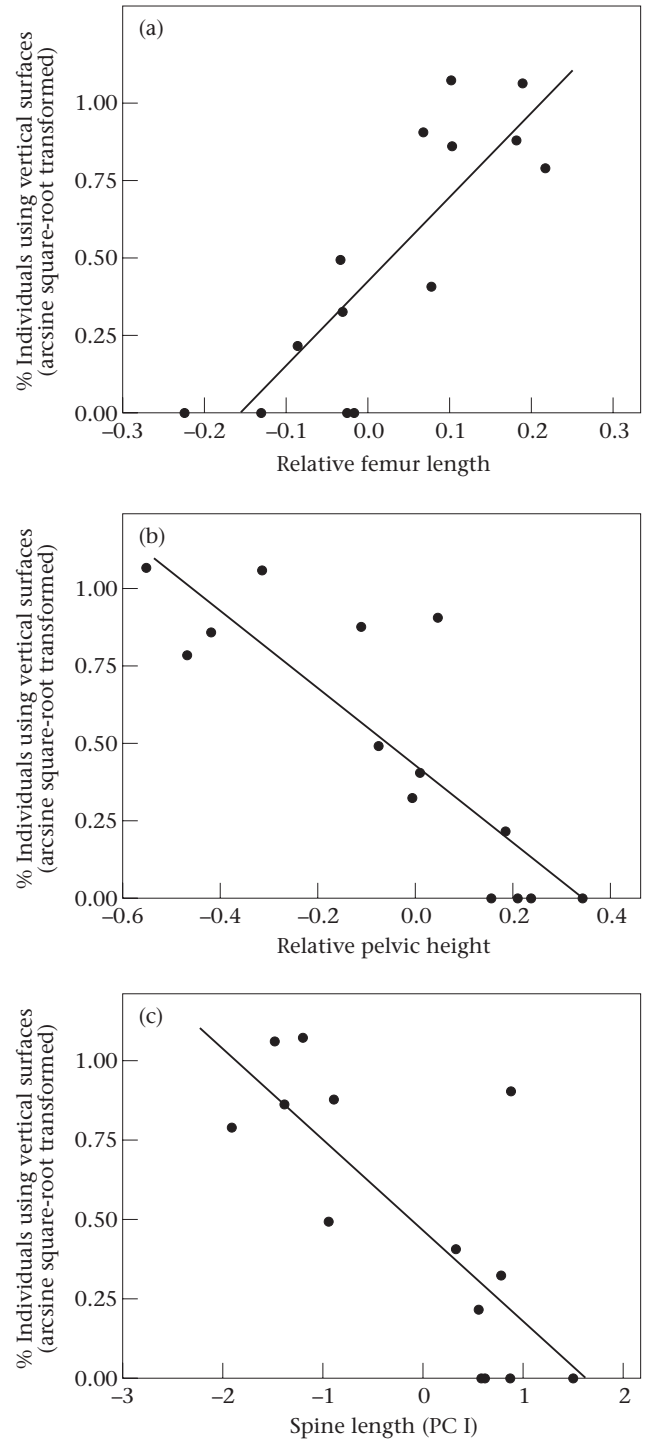


Figure 5. Morphological variables versus percentage of individuals using vertical surfaces.

nonphylogenetic results is not surprising (Ricklefs & Starck 1996; Price 1997; Losos 1999).

## DISCUSSION

In experimental studies, armoured sticklebacks use more dangerous habitats and flee less readily in the presence of predators than do unprotected fish (McLean & Godin

1989; Abrahams 1995). Armour has both positive and negative consequences for sticklebacks: it negatively affects speed and manoeuvrability (Bergstrom 2002; M. V. Abrahams, personal communication), but makes fish more difficult to subdue and ingest by predators (Reist 1980; Reimchen 1994). Hence, the behaviour of armoured fish may result either from their reduced vulnerability or their reduced escape abilities: failure to flee may represent either indifference to the presence of predators or reliance on crypsis, rather than flight (McLean & Godin 1989).

In a similar vein, armoured cordylids also have spines that should make them less vulnerable to at least some of their predators. Other lizards (e.g. *Moloch*, *Phrynosoma*) have evolved similar structures that are effective against predators (Pianka & Pianka 1970; Pianka & Parker 1975; Sherbrooke 1981). Thus, a reasonable prediction would be that species with substantial body armature such as *C. giganteus* and *C. cataphractus* would venture farther from protected areas and remain in the open longer than related unarmoured species.

However, like sticklebacks, the morphology of armoured cordylids comes with a cost that could affect other antipredator options. Armoured cordylid species are not only bulky and short-limbed, but also apparently quite slow. The existence of alternative phylogenetic topologies introduces uncertainty into our understanding of the relationship between extent of armour and sprint speed; none the less, we expect that data for additional species is likely to confirm the negative relationship that already is strongly supported both in nonphylogenetic analysis and in an analysis using one of two phylogenetic hypotheses (Frost et al. 2001). We have two reasons for this expectation: first, *Platysaurus* species, which were not included in the sprint studies, represent an independent lineage of lightly armoured and very fast (Rose 1962; M. Whiting, personal communication) cordylids; consequently the addition of data for *Platysaurus* species is likely to produce significant results even using Phylogeny B. Second, comparison to other armoured lizards suggests that a negative relationship exists between armour and sprint speed; both *Phrynosoma* and *Moloch* are bulky, short-legged and heavily armoured lizards and both are extremely slow sprinters (Irschick & Jayne 1999; J. B. Losos, personal observation).

Thus, like other armoured lizards (Pianka & Pianka 1970; Pianka & Parker 1975; Sherbrooke 1981), we might predict that armoured cordylids would not rely on flight as a primary means of escaping predators. Consequently, in direct opposition to the reasoning of our first prediction, we might predict that armoured cordylids would use an alternative antipredator tactic. Given that all cordylid species generally use refuges to escape predators, our specific prediction is that armoured species would be found closer to refuges and remain in the open less than unarmoured species.

Our results strongly support this second prediction. Rather than being positively correlated, degree of armature was negatively correlated with distance run from a predator (Fig. 4c). Individuals of the most heavily armoured species almost always were found very near

rocky crevices, which they immediately entered when approached; all individuals of the eight spiniest species ran into crevices when approached. By contrast, the least armoured species were more variable; although capable of entering even extraordinarily narrow crevices (which they use at night; Branch 1998), individuals of some unarmoured individuals would only use such retreats after being persistently approached and some individuals could not be induced to enter a refuge at all.

Consequently, we suggest that a trade-off exists, not between morphological and behavioural antipredator strategies, but between different behavioural approaches to evade predators. One approach is exemplified by slow-moving armoured species, which stay near refuges to which they quickly retreat and in which they use their armour and spines to prevent predators from subsequently extracting them. The alternative approach is characterized by fast, unarmoured species that rely on rapid and agile locomotion across all available surfaces (a similar dichotomy is also apparent in their foraging behaviour; Cooper et al. 1997).

These two antipredator approaches have incompatible morphological requirements. Rapid escape on flat surfaces requires long limbs, and on vertical surfaces it requires a flattened body and long, laterally oriented limbs (Vanhooydonck & Van Damme 2001; see also Arnold 1998), traits that are exhibited by unarmoured cordylids and by a wide variety of other lizards that use vertical rock surfaces (e.g. *Petrosaurus*). Heavy body armature makes rapid locomotion difficult, not only due to the added mass and inflexibility, but also because legs tend to be short and covered with spines, rather than being long and gracile.

Consequently, we conclude that armour is part of an antipredator syndrome that includes habitat use and behaviour as well as morphology. The reason that armour does not have a liberating effect for cordylids is that it reduces, but does not eliminate, the threat of predation. Given the relatively small size of cordylid lizards (the largest species is *C. giganteus* with a total length of 40 cm; Branch 1988) relative to the size of the predators with which they naturally coexist (e.g. large raptors, medium and large carnivores), not even the most heavily armoured species is likely to be immune from predation. As a result, we would expect all species, both armoured and unarmoured, to use behavioural antipredator tactics (cf. Sweitzer & Berger 1992, on porcupines) and the appropriate question is how different behavioural tactics are related to functional capabilities and morphology.

One alternative explanation for the inverse correlation between degree of armour and distance run from a predator is that both variables, rather than being directly related, are consequences of habitat use. As a result of habitat differences, some species may be more vulnerable to predators than are other species; in other words, in environments with high predation risk, a syndrome of antipredator responses might exist that includes both heavy body armature and escape into nearby retreats, whereas in low-predation environments, neither may be necessary. Unfortunately, little is known about the natural predators and rates of predation on cordylids

(what little is known is summarized in: Greene 1988; Branch 1998). Arguing against this hypothesis is the observation that at several of our study sites, sympatric species differing in degree of armature could often be found in relatively close proximity, and thus may have shared predators, yet these species differed greatly in their escape behaviour, with the less armoured species always running considerably farther. In addition, the fact that sympatric armoured species are similar in escape behaviour argues against escape behaviour diversity (Schall & Pianka 1980) as another alternative explanation for interspecific differences in antipredator behaviour.

More generally, this study suggests two recommendations for future research on the behavioural consequences of the evolution of body armature. First, comparative studies will provide the most insight when they focus on clades of closely related species that vary in the extent of armature. Many heavily armoured groups do not have close relatives that are less well protected. Hence, comparisons are confounded by the many other differences that occur among distantly related taxa (e.g. hedgehogs versus other insectivores, armadillos versus other edentates). By contrast, our analysis avoided such problems by focusing on closely related species that share many similarities in natural history and that occur in the same geographical region, which allowed us to identify behavioural and morphological factors that may have played a role in behavioural evolution. Other groups for which this approach might profitably be taken include a variety of spiny lizards (e.g. tropidurids, *Sceloporus*, and some skink clades, although none of these is as well armoured as are some cordylids), catfish, sticklebacks (McLean & Godin 1989 compared populations of sticklebacks varying in armature) and a variety of invertebrates. Species that display phenotypic plasticity in the development of armature, often induced by the presence of predators (e.g. Spitze 1992; Trussell 1996), would also be extremely interesting to study. Finally, this comparative framework could also be extended to taxa defended by means other than armature, such as noxious taste, toxicity, or electric discharge.

Second, this work highlights the critical importance of natural history knowledge (Greene 1986). On one hand, the insights we have been able to derive were only possible as a result of what is known about the biology of these species. Conversely, many questions yet remain, and they can only be addressed by more detailed studies of cordylid behaviour and ecology.

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