Comparative studies that reveal close associations between a character and a common selective pressure (e.g., sexual dimorphism with polygamous mating systems [Campbell, 1972]; clutch size with foraging mode [Huey and Pianka, 1981]) can provide strong evidence for their adaptive value (Clutton-Brock and Harvey, 1979; Ridley, 1983). For morphological characters, the demonstration of the performance advantage to organisms possessing the trait in question strengthens conclusions of adaptive convergence suggested by form-environment correlations. Studies of differential performance among species varying in the expression of a character’s evolution (e.g., Alberch, 1981), but interspecific comparisons (e.g., Anderson and Karasov, 1981) are weaker than intraspecific ones because of possibly confounding differences in physiological or morphological features, especially if the species are not closely related. Intraspecific functional performance studies are difficult, as variation among conspecifics in the expression of a trait of purported adaptive significance is usually so slight that demonstrations of functional advantages are both difficult and rare (e.g., Herrera, 1978; Garland, 1984).

Comparative studies of morphological traits suggest three main characters that affect running in lizards: relative limb proportions (Snyder, 1954, 1962; Jaksić et al., 1980; Moermond, 1979), toe pads with lamellae (Russell, 1979; Williams and Peterson, 1982), and toe fringes (Mosauer, 1932; Luke, 1986). Experimental studies of the functional significance of these characters can be difficult. The first two are complex functional units, and, as with any such morphological system, manipulations (altering limb length or removing toe pads) to demonstrate their significance in increasing locomotor performance are problematic, as it is difficult to establish appropriate controls. Numerous intraspecific studies have quantified differential running performance in lizards (e.g., Ballinger et al., 1973; Bennett, 1980; Huey, 1982; Punzo, 1982; Hertz, 1983; Huey and Hertz, 1984), but none have studied characters presumed to have evolved specifically to aid locomotion (Laerm [1973] anecdotally reported reduced locomotor effectiveness in uncontrolled fringe removal experiments with water-running Basiliscus).

Laterally projecting toe fringes on sand-dwelling lizards have long been interpreted as an adaptation for running on sand (Stebbins, 1944; Norris, 1958) and are considered a classic case of convergent evolution (Mosauer, 1932; Bellairs, 1969). A comparative study shows that fringes have evolved at least 26 different times among five lizard families, being confined mainly to sand-dwelling species (Luke, 1986; they also occur in some lizards that run on water, e.g., Laerm, 1974), supporting an adaptive explanation for their evolution. In this study, I performed experimental removals of toe fringes of a sand-dwelling lizard, Uma scoparia, to assess whether they are indeed an adaptation that significantly increases locomotor performance on sand.

**MATERIALS AND METHODS**

The species used in this study is the Mojave fringe-toed lizard, Uma scoparia (Iguanidae). Twenty-six adults ($x$ snout-vent length $= 79$ mm; $x$ mass $= 18.5$ g) collected from Kelso Dunes, San Bernardino Co., California, were brought into the lab and maintained for two weeks before the start of the experiments under a controlled temperature and light regime (12D, 15°C/12L, 38°C) approximating field body temperatures (Stebbins, 1944). During this time, lizards were run daily on a racetrack (see below) to accustom them to the procedures. Body masses were monitored as a measure of physical condition. Because the lizards varied in response both to captivity (some lost mass) and to these preliminary runs (some refused to run), only 19 were used in the actual experiment. Locomotor performance was measured using a 2.4 m x 0.2 m race-track that had photocells spaced at 25 cm intervals (see Huey et al., 1981 for a complete description). These photocells transmitted a signal to a computer when the light beam was broken by a lizard running down the track. The computer had a built-in timer and computed the velocities and accelerations of the lizards over each 0.5 m segment of the racetrack.

Individuals were run first on a rubber surface, then on smoothed surface sand collected from their habitat. Because the sand dune habitats where Uma live are composed of both level and sloping areas, two sand runs were performed, the first with the track horizontal, the other with the track at a 30° slope. After these runs, the toe fringes were cut off and the lizards were again run on rubber, smoothed level sand, and smoothed sloped sand. Fringe removal seemed to induce little, if any, trauma and bleeding, and an attempt to glue the fringes folded shut was unsuccessful due to their semirigid nature (they do not fold). Because fringes were not expected to influence running performance on rubber, running the lizards on rubber before and after removing the fringes served as a control to determine whether physical trauma from the removal procedure might cause a poorer performance. The six trials (rubber, then level sand, then sloped sand [both before and after fringes were removed]) were run on alternate days, with two extra rest days between the pre- and post-
removal runs. Four runs per individual were conducted on a given test day, with an hour rest period between each run. From these runs, the maximum velocity and acceleration attained were used to represent performance.

**Hypothesis**

Biomechanical considerations (C. A. Luke, pers. comm.) indicate that fringes function to reduce foot slippage in sand (by increasing the frictional force and reducing pressure) only during acceleration; at maximum running speeds (when acceleration is zero), slippage, and hence the advantage of fringes, should be minimal. The lizards in this study do not attain their maximum running speed (24 km/hr; Norris, 1951) because of the short length of the racetrack. Therefore, I expected to find faster sprint speeds for fringed (versus unfringed) *Uma* in addition to the expected higher accelerations afforded by the presence of fringes. Because of the fluid-like mechanical properties of sand, its tendency to shift increases with slope (Taylor, 1948). Therefore, I expected lower accelerations and velocities on uphill slopes than on level sand particularly for lizards without toe fringes, because of this effect. It was for this reason that the sloped versus level comparisons were made.

The data were not normally distributed. Therefore, one-tailed Wilcoxon paired-sample tests were used to determine whether the speeds and accelerations of individuals differed with and without fringes. The hypothesis was that locomotor performance on sand should be greater for lizards with fringes than without them, and that a greater difference should be found on sloped sand than on level sand. (The study was restricted to an intraspecific performance comparison only, as genera closely related to fringe-toed lizards [e.g., *Callisaurus*] differ from them in limb proportions and probably physiology as well. As discussed earlier, such uncontrollable differences complicate interspecific performance comparisons.)

**Results and Discussion**

There were no significant differences in either maximum running velocity or acceleration on rubber before and after removal of fringes, demonstrating that the removal procedure itself did not influence performance. However, locomotor performance of lizards on sand was significantly decreased after fringes had been removed (Table 1). Reduction in velocity on sand was near 15% for level and 9% for sloped surfaces. Acceleration was reduced 22% on sloped surfaces. As predicted, the removal of fringes affected acceleration on sloped sand more than on level sand.

These results quantitatively demonstrate the locomotor advantage of toe fringes in a sand-dwelling lizard and provide evidence for an advantage on uphill sloping surfaces. When avoiding potential predators, *Uma* normally rely on short bursts of speed to reach areas of concealment, and their habitats are typically composed of sloping sand dune faces. Thus, the greatest measured advantage of the fringes (initial acceleration on slopes) very likely has ecological significance (e.g., escape from predators, prey capture).

In order to claim a character is an adaptation sensu Williams or Darwin (Gould and Vrba, 1982), one must first reject nonadaptive explanations, as the character
may be present as an engineering artifact or as a retained feature that had some other advantage in a remote ancestor. The possibility of allometric artifact is rejected, because fringe presence or absence in the sce-loporine radiation to which Uma belongs (Etheridge and de Queiroz, 1986) is independent of size and age. Toe fringes are a derived character of Uma within sce-loporines (Etheridge and de Queiroz, 1986), and hence their presence in Uma cannot be a result of the reten-tion of a primitive character. This leaves adaptive hy-potheses as the probable explanation. Toe fringes ap-pear to have evolved in association with the occupation of a sandy environment. Although fringes have been widely believed to aid in running, Stebbins (1944) also of a sandy environment. Although fringes have been widely believed to aid in running, Stebbins (1944) also suggested that they may aid shimmy-burial, a behavior used for submersion into granular substrates. However, the ecological importance of this behavior seems un-likely to be as great as that of running performance. Shimmy-burial is inferred to be primitive in sce-loporines because of its widespread occurrence (Hall, 1973). If fringes evolved primarily as an adaptation associated with shimmy-burial, then the presence of fringes should be a widespread, primitive character in the group as a whole. Since it is not, it is unlikely that fringes are an exaptation for running, co-opted from another function (shimmy-burial) for which they were adapted originally (Gould and Vrba, 1982). The correlation of fringes with a particular environment and the repeated evolution of the structures among lizards (Luke, 1986) argues strongly for an adaptive explanation involving loco-motion in sandy environments. My results demon-strate the clear biological role toe fringes play in run-ning performance. Toe fringes in U. scoparia may be a system in which one may fruitfully pursue a labora-tory/field study of morphological adaptation (Arn-old, 1983).

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Examples of distinct morphological classes within the males of a species include numerous insects (scarabaeid beetles, fig wasps, and others [Eberhard, 1979; Hamilton, 1979]), birds (ruffs [Hogan-Warburg, 1966]), fish (bluegill sunfish [Gross and Charnov, 1980] and Pacific salmon [Gross, 1985]); and mammals (red deer [Darling, 1937]). Such polymorphisms in the elaboration of horns, antlers, exaggerated mandibles, and fighting ability are related to mating competition and may evolve through disruptive selection acting on the trade-off between the mating advantage of sexually selected traits versus the survivorship cost of bearing them (Gadgil, 1972).

Polymorphisms also occur in females but usually only in populations in which males are also polymorphic, e.g., the light and dark morphs of the peppered moth (Kettlewell, 1958), the lesser snow goose (Cooke and Findley, 1982), and the arctic skua (O’Donald and Davis, 1959) and also wing-length polymorphisms in homopteran leafhoppers (Denno, 1979), and water striders (Vepsailainen, 1978); and the mimetic complexes observed in Heliconius (Turner, 1965). Such shared polymorphisms are usually related to predator avoidance or to life-history organization.

Because the potential for increasing reproductive success through enhanced mating effort is much less for females than for males in most mating systems, dichotomization of female mating types into distinct morphs is comparatively less likely to arise. An exceptional example in which females alone are polymorphic involves the mimetic complexes in Papilio butterflies (Clarke and Sheppard, 1963). Other examples of female polymorphism are the two color morphs in damselflies of the genus Ischnura (Robertson, 1985) and in the mayfly Dolania americana (Peters and Peters, 1977). The damselfly females show a cryptic morph and a brighter one that may function as a male mimic (Robertson, 1985). The mayfly females have either light or dark abdomens, but because they are active only in the pre-dawn (Peters and Peters, 1977), it is difficult to ascribe a mating or predator avoidance function to the color patterns.

Here we report a striking case of female dimorphism in a male monomorphic species. In the treehopper Microcentrus perditus (Insecta: Homoptera: Membracidae [Deitz, 1975]) females may possess either greatly enlarged, or very small, pronotal "horns," while males possess only small horns. We describe these morphologies and examine possible causes of both the dimorphism and its sex-limited expression.

In insects of this small genus are solitary, sedentary, and highly cryptic. They are widespread in eastern North America (Kopp and Yonke, 1973), feeding on the sap of oak (Van Duzee, 1917; Kopp and Yonke, 1973; pers. observ.) and possibly hickory (Quisenberry et al., 1978). Adults feed and mate on exposed twigs, and after ovipositing in such twigs, females may guard the eggs until they hatch (Loye, unpubl.). Observations reported here are from central Oklahoma in 1983 and 1985.

As in other membracids, the pronotum of this species is enlarged dorsally and covers portions of the head and abdomen as well as the thorax. Rising forward from the thorax, the pronotum expands into a pair of projections that are either laterally bent and sharp (males) or more upright and rounded (females). Females may be classified as either "long-horned" or "short-horned," whereas males fall into a single distinct class (Fig. 1). The lack of overlap between the