Ecology of Lizards in the Kalahari Desert, Africa

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Aspects of the ecology of lizards in the southern Kalahari semidesert of Africa were investigated from December 1975 through mid-March 1976 by Raymond B. Huey (principal investigator), together with Eric R. Pianka, and Carolyn M. Cavalier. This project followed up leads developed during a prior year-long study in 1969 and 1970 (e.g., Pianka, 1971, 1975; Huey and Pianka, 1974, 1977a, b, and c).

Summary of Fundamental Findings of this Research

Juvenile lizard mimics noxious beetle. Batesian mimicry is an important evolutionary phenomenon in which selection by predators favors individuals of a palatable or unprotected species (mimic) that deceptively resemble those of an unpalatable or protected species (model). While insects are frequently mimetic, very few vertebrates are involved in mimetic complexes. It is of interest that we discovered a Kalahari lizard that, while a juvenile, mimics a noxious insect (Huey and Pianka, 1977a). In fact, this is the first substantive example of a terrestrial vertebrate mimicking an invertebrate.

Juvenile lizards of the species *Eremias lugubris,* unlike adults of this species or juveniles of other *Eremias,* are jet-black with broken white body stripes and are thus conspicuous against red Kalahari sands (fig. 1). Instead of walking with lateral undulations typical of related lizards, juvenile *E. lugubris* walk stiffly and jerkily with arched backs, a unique locomotor style.

We discovered a reason for the conspicuous coloration and arch-walking. Apparently, these juvenile lizards are mimicking black-and-white, "oogpister" beetles (Carabidae: *Anthia* spp.) that can squirt a pungent fluid of formic acid and assorted other acids and aldehydes to discourage attackers.

Juvenile *Eremias lugubris* "metamorphose" to the adult coloration, pale red-tan, when they reach body lengths of 40 to 50 millimeters. At the same

size, they also begin walking with a normal-lizard style. The size of metamorphosis corresponds closely with the maximum size of oogpister beetles, suggesting that size as well as color and gait are involved in the mimicry.

We obtained indirect evidence that this mimicry might be effective in discouraging attacks by predators on juvenile *Eremias lugubris*. Using frequency of broken tails as an index of the relative intensity of predation, we found that of all related lizard species in the southern Kalahari, *E. lugubris* juveniles have the lowest frequency of broken tails. This indirect evidence is one of the few nonmanipulative, field examples supporting the hypothesis that natural selection promotes mimicry of species with stronger actual defenses.

Locomotor modifications in beetle-mimicking juvenile lizards. Live specimens of beetle-mimicking juvenile *Eremias lugubris* were brought back to the United States where Jane Peterson and Huey (in preparation) made films of their peculiar locomotion and that of normally moving lizards and of beetles. The preliminary analysis of these films demonstrates that beetle-walks and normal lizard-walks do share a few characteristics. Only beetle-walking lizards, however, repress lateral undulations, have strongly arched backs (140°), and have vertical flexion. Foreleg movement is also restrained producing a beetlelike attack angle and body pitch. Overall, these locomotor modifications result in an astoundingly insectlike walk.

Character displacement in a subterranean lizard. Character displacement is an evolutionary sequence in which selection favors divergence between individuals of two species because this reduces either competition for resources or gamete loss from hybridization. Prior work in the Kalahari (Huey et al., 1974; Huey and Pianka, 1974) had uncovered a possible case of "ecological" character displacement in a subterranean lizard, *Typhlosaurus lineatus*. In sympatry with the smaller *T. gariepensis* in the southern dune region of the Kalahari, *T. lineatus* are longer and also eat larger prey than in allopatry (adjacent flatland desert). These observations suggested morphological and behavioral character displacement had occurred that reduced dietary overlap and hence intensity of competition with *T. gariepensis*. However, because these allopatric samples were from flatland rather than from dune desert, the observed shift in morphology might alternatively reflect an evolutionary response to the physical environment of the dunes, not to competition with *T. gariepensis*.

To determine whether observed morphological shifts might relate to the dune environment or to competition, we collected and compared new series of *Typhlosaurus lineatus* from the northern dune area (*T. gariepensis* is restricted to the southern dunes) and from the northern flatland desert. These new data (Pianka, Huey, and Lawlor, 1979) show insignificant differences in body lengths of both adult males and adult females between these two habitats and

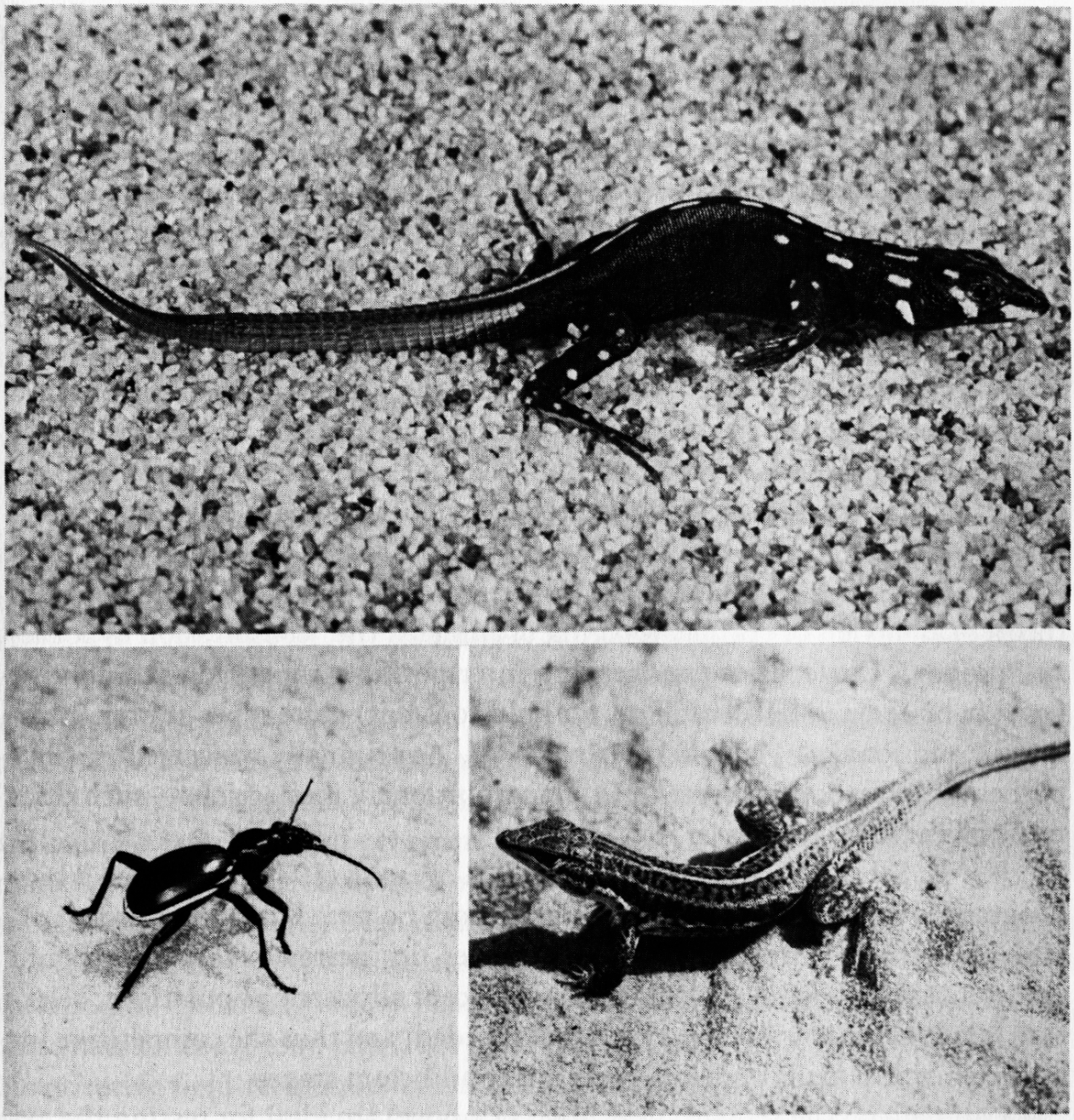

FIG. 1. Lateral view of arch-walking juvenile *Eremias lugubris* (above), an oogpister beetle *Anthia* (left), and an adult *E. lugubris* (right).

are thus consistent with the hypothesis that the shift to large size by *T. lineatus* in the southern sandridge desert is a response to competition with *T. gariepensis,* not to the physical nature of the sandridges. Our new data thus strengthen our case of morphological character displacement.

Ecological interactions and species distributions in Kalahari skinks. Ecologists are frequently concerned with the determinants of distributions of species. In prior research we had discovered that geographic ranges of two semiarboreal species of skinks *(Mabuya)* overlap only narrowly in the southern Kalahari, whereas ranges of two ground-dwelling skinks overlap broadly both with each

other and with the arboreal species. The semiarboreal pair were nearly identical ecologically, in striking contrast to all other pairwise comparisons, suggesting that interspecific competition for resources might be too strong for the semiarboreal species to coexist over large areas.

Research efforts on our recent trip were designed to map carefully the region of overlap. However, this work uncovered a pattern that suggested a reinterpretation of species distributional boundaries was necessary: because the zone of overlap seemingly corresponds with a zone of subtle habitat change (rainfall and tree species), we now suspect that the narrow zone of sympatry actually reflects different adaptations of these species to aspects of the physical environment that are geographically discontinuous in the Kalahari. Intense competition for resources, inferred from the near niche identity, may help restrict the zone of sympatry, but is probably not its primary cause (Huey and Pianka, 1977b).

A biogeographic extension of the "compression hypotheses." Developed from theoretical models of optimal foraging of animals, the "compression hypothesis" proposes that species experiencing interspecific competition should visit fewer habitat types but should eat (or hold constant) more types of prey (MacArthur and Pianka, 1966; Schoener, 1974). As originally conceived this hypothesis applies only to short-term, nonevolutionary interactions—such cases must be very rare in nature.

T. W. Schoener, R. B. Huey, and E. R. Pianka (1978) developed a biogeographic extension of the hypothesis that can be tested using data from species in narrow sympatry. Because species in narrow sympatry should experience considerable gene flow from adjacent allopatric populations, selection for divergence in sympatry will be impeded; and thus the competitive interaction will remain in its original, nonequilibrium stages.

Our data on the semiarboreal *Mabuya* (above) are ideal for testing the extension. In narrow sympatry these skinks visited fewer habitats (3 of 4 comparisons) but ate more prey types (4 of 4 comparisons) as predicted by the compression hypothesis. Thus, some seemingly paradoxical ecological patterns can be neatly accounted for by the compression hypothesis (Schoener, Huey, Pianka, 1978).

Foraging patterns of Kalahari lacertid lizards. The seven species of lacertid lizards in the southern Kalahari are readily separated into "widely-foraging" or "sit-and-wait" predators. We gathered extensive data quantifying rates of movement and of position changes for all species (Pianka, Huey, and Lawlor, 1979). By comparing foraging style and actual diets of these lizards, we determined whether and how foraging gait relates to diet. One conspicuous trend is that widely foraging lacertids tend to eat far more termites than do sit-and-

wait lizards—this may result from the greater likelihood that only a widely foraging lacertid should frequently encounter patchily distributed and relatively sedentary clumps of food.

It is of interest that we have discovered that the foraging gait of a lizard also seems to influence the type of predators on those lizards. For example, horned adders (sit-and-wait snakes that prey on lizards) eat primarily widely foraging lizards. Our analysis (Huey and Pianka, 1981) emphasizes that theoretical models of optimal foraging must incorporate considerations of the consequences of foraging style on risk of predation as well as on dietary gains.

Miscellaneous Projects

Y. J. Kim, G. C. Gorman, and R. B. Huey (1978) examined genetic differences between *Typhlosaurus lineatus* and *T. gariepensis* using starch-gel electrophoresis. In common with other subterranean lizards that have been examined, both species of *Typhlosaurus* have extremely low levels of genetic heterozygosity. Despite similarity in external morphology, these lizards differ strikingly in shared alleles; indeed, electrophoretic evidence suggests that the two species last shared a common ancestor 25 million years ago.

M. Wake (Department of Zoology, University of California, Berkeley) is analyzing a large series of pregnant *Typhlosaurus* in a general survey of fetal-maternal anatomical relations of reptiles and amphibians. No skink of this subfamily has previously been examined.

On our first trip to the Kalahari, we gathered extensive data on seasonal variation in thermoregulatory behavior of diurnal lizards. We supplemented these data on the second trip (Huey and Pianka, 1977c). We also developed a quantitative field technique for measuring the thermoregulatory orientation of lizards to the sun: an agamid lizard oriented perpendicular to the sun at low ambient temperatures (thereby increasing rate of heat gain), but flipped to a "parallel" orientation at high ambient temperatures (slowing rate of heat gain). The behavioral response was either perpendicular or parallel but not graded as prior workers have assumed.

We also gathered additional data on comparative ecology, resource utilization, thermal biology, and niche segregation among the gekkonid lizards (Pianka and Huey, 1978). Kalahari geckos do not necessarily converge ecologically with Australian geckos (Pianka and Pianka, 1976). The frequency of interspecific pairs with high overlap in ecologies is greater among intercontinental comparisons than it is among intracontinental ones, suggesting a competition-induced limit to the similarity of potentially competing species.

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