THE UNIVERSITY OF CHICAGO PRESS JOURNALS

Evolution of Escape Behavior Diversity

Author(s): Jos. J. Schall and Eric R. Pianka

Source: *The American Naturalist*, Apr., 1980, Vol. 115, No. 4 (Apr., 1980), pp. 551-566

Published by: The University of Chicago Press for The American Society of Naturalists

Stable URL: https://www.jstor.org/stable/2460484

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at https://about.jstor.org/terms

The American Society of Naturalists and *The University of Chicago Press* are collaborating with JSTOR to digitize, preserve and extend access to *The American Naturalist*

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms

EVOLUTION OF ESCAPE BEHAVIOR DIVERSITY

JOS. J. SCHALL AND ERIC R. PIANKA

Department of Zoology, University of California, Berkeley, California 94720;
Department of Zoology, University of Texas, Austin, Texas 78712

Submitted December 30, 1977; Accepted June 2, 1978

Natural selection favors predator efficiency in finding and capturing prey and, simultaneously, prey adeptness at avoiding or escaping predators. In the resulting antagonistic escalation, coevolution of predators and their prey has produced some exceedingly complex and, to many biologists, aesthetically pleasing, adaptations (but see Skutch [1972, pp. 231–232], who considers predation a "hideous blot on the fair face of nature."). One way prey can ameliorate effects of predation is by evolution of morphological or behavioral "aspect diversity" (Rand 1967), which lowers their predator's ability to form search images or predict prey escape behavior.

Cain and Sheppard (1954) suggested that balanced polymorphisms could be maintained by predators forming search images for the more common morph, but discounted this mechanism's importance in preserving color polymorphism in *Cepaea* snail populations (see also Jones et al. 1977). Using an analogy to game theory, R. A. Fisher (1958) explicitly stated the idea, concluding, "A . . . measure of uncertainty must be introduced into the reactions of 'natural enemies' in the state of nature, especially by discontinuous variations of the kind made possible by balanced polymorphisms affecting the appearance, or the behavior." Clarke (1962*a*, 1969) later proposed the term "apostatic selection" (= "reflexive selection" of Moment 1962*a*) for selection favoring rare phenotypes (hence, the apostates). Clarke (1969) argued that this sort of frequency-dependent selection is important in evolution of morphological diversity both within and among species.

Morphological diversity as an antipredator or antiherbivore tactic has been suggested for populations of snails (Clarke 1962*a*, 1962*b*, 1969; Owen 1963), brittle stars (Moment 1962*a*), moths (Sargent 1975, 1978), and frogs (Milstead et al. 1974), as well as among species in assemblages of conifers (Smith 1970), *Passiflora* vines (Gilbert 1975), katydids (Rand 1967), grasshoppers (Joern 1977, in prep.), and moths (Blest 1963; Rand 1967; Ricklefs and O'Rourke 1975; Sargent 1975). Paulson (1973) applied the argument to predators, proposing that extreme polymorphism in ventral pattern of hawks may make it difficult for their prey to form "hawk" search images (although hawk silhouette shape and flight behavior are probably more important to prey in identifying an approaching raptor). Other

Am. Nat. 1980. Vol. 115, pp. 551–566.
© 1980 by The University of Chicago. 0003-0147/80/1504-0008$01.30

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms

presently unexplained cases of polymorphism might well also be a result of apostatic selection.

Similarly, selection could favor diversity in escape behavior both within and among species (Fisher 1958; Humphries and Driver 1970; Sargent 1975). The resulting "protean" (Chance and Russell 1959) or unsystematic behavior would hinder a predator's ability to learn and predict the prey's escape actions.

The existence and utility of diversity as an escape tactic has not been widely accepted, primarily because it has yet to be demonstrated unequivocally. Most work on aspect diversity has been anecdotal; rigorous theory, testable hypotheses, and quantitative data generally are not presented (but see Clarke 1969; Emlen 1973; Paulson 1973; Ricklefs and O'Rourke 1975; Sargent 1975, 1978). Li (1962) and Moment (1962*b*) emphasized the need for caution in attributing a role in predator escape to cases of polymorphism unless alternative hypotheses can be discounted. Here we present an "escape-tactic diversity" hypothesis and attempt to test it against alternative hypotheses with data on escape behaviors of whiptail lizards (*Cnemidophorus*). To our knowledge, these results are the first quantitative data published on diversity of escape behavior.

ESCAPE TACTIC DIVERSITY HYPOTHESIS

Many predators form appropriate search images for common prey (Tinbergen 1960; Mueller 1977); diversity of prey morphology, foraging site, or hiding location should obstruct this process of search image formation. (Selection of foraging or hiding locations can be an antipredator behavior. However, we here restrict usage of the term "escape behavior" to mean behaviors used in evading the immediate attack of a predator.) Likewise, diverse escape behaviors should reduce predator efficiency in predicting escape behavior of detected prey. Such diverse tactics reduce the apparent abundance of each prey morph. Predator classes are unlikely to specialize on different rare prey (MacArthur and Pianka 1966).

Morphological diversity is primarily a function of interindividual differences (color change is one common exception) and interferes with the search phase of predator foraging. Behavioral diversity could result from differences among individuals (polyethism of Chance 1959), and/or within-individual plasticity in escape behavior. Diverse prey escape behaviors hinder the pursuit phase of foraging predators.

Because morphologically or behaviorally diverse escape tactics interfere with predator learning, prey populations faced with higher per capita predation pressure should evolve more diverse escape tactics than less heavily predated conspecific populations, assuming (somewhat unrealistically) that average learning abilities of predator assemblages are uniform. Also, an assemblage of prey species with similar densities in the same habitat (or in different habitats that are utilized in a fine-grained fashion by wide-ranging predators) should diverge in escape tactics. Hence there may be a limiting similarity among escape tactics of species in an assemblage, analogous to the limiting similarity considered in resource partitioning theory (MacArthur and Levins 1967). In fact, escape space has been viewed as a resource that could limit the number of coexisting species in an

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms

assemblage (Blest 1963; Ricklefs and O'Rourke 1975; Joern 1977, in prep.). Last, assuming equal potential predation pressures, a population in an assemblage of species with a diversity of escape tactics, or high community-wide escape diversity, would experience lower realized predation pressure and have a lower populational escape diversity than a solitary population. That is, given a particular level of potential predation, overall escape diversity of a prey community should be approximately constant, whether the community is composed of one or several species.

These statements assume that when realized predation pressure is low, selection will favor simple escape tactics within populations. That is, at low predation levels selective forces other than those leading to diversity would be relatively more important in shaping escapes. For example, escape behaviors might converge on a few efficient low-cost tactics. Similarly, under low predation pressures the need for intraspecific recognition might constrain the level of morphological diversity.

METHODS

We have observed escape tactics of many lizard species in the deserts of North America and other regions. To reduce expected behavioral differences among species resulting from differing phylogenies or major ecological differences, we restrict discussion here to escape behaviors of whiptail lizards (*Cnemidophorus*). These abundant, diurnal, rapidly moving, widely foraging insectivores are easily located by visually orienting predators, including humans and other vertebrates. They are eaten by numerous species of birds, mammals, and snakes, as well as by some lizards (Burt 1931; Pianka 1970; personal observation).

Populations of *Cnemidophorus tigris* occurring in the absence of other sympatric whiptail species were studied at 12 sites scattered over the flatland desert in western North America from about 29° to 42° N lat. Locations and other data on most of these sites are given by Pianka (1967, 1970). In southwestern Texas seven whiptail species are broadly sympatric, and as many as four, in various combinations, are often syntopic (Schall 1976). Five common widespread species of whiptails were observed at approximately 50 sites. Three are bisexual (*C. tigris, C. gularis*, and *C. inornatus*) and two are parthenogenetic (*C. exsanguis* and *C. tesselatus*). Various aspects of the ecology of this assemblage are described by Schall (1976, 1977, 1978) and Scudday and Dixon (1973).

At each site we observed behavior of lizards upon our approach. Occasional observations of lizards chased by nonhuman predators confirm that whiptails evade human and nonhuman predators in similar ways. We recorded escape behavior of 1,722 *C. tigris* at single species sites and 1,023 escape attempts by five whiptail species in the southwestern Texas assemblage.

Lizard escape behaviors were grouped into categories. These escape classes are subjectively delimited, and other observers watching the same animals might well formulate somewhat different categories. We have spent a total of approximately 6,000h in the field observing lizards under natural conditions, about half of this time in areas where *Cnemidophorus* were present. Categories used here reflect biolog-

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms

ical reality; no matter how classes are described verbally, lizards grouped into one category behaved differently than those grouped in another. We are confident that this study could be replicated by other workers using their own escape behavior classes and that trends observed would parallel ours.

In southwestern Texas escape categories were: (1) lizard ran quickly from shrub to shrub without stopping; (2) ran from one open area to another; (3) ran into base of a shrub and remained there even when the observer approached; (4) did not move; (5) fled down a burrow; (6) ran to the edge of shrub, did not enter the shrub, remained there immobile until approached; (7) ran into base of a shrub, calmed down and walked out of shrub within a few seconds; (8) ran in a long straight line often through open vegetation or grass (similar in some cases to category 2 except run was longer); (9) ran in a zig-zag path in open areas (similar to category 1 except lizard did not enter base of vegetation); (10) ran into base of vegetation, remained wary and within a few seconds ran out again; (11) ran from shrub base into open; (12) ran into vegetation and was not observed again (overlaps with category 5).

Observed escape behavior diversity could well be biased by varying environmental heterogeneity among geographically scattered single-species sites (several checks on the effectiveness of these classes in eliminating such bias are examined below). We thus use only nine very broad escape classes for these areas: (1) lizard ran into sunny side of large, dense vegetation; (2) ran into shady area of large dense vegetation; (3) similar to category 1 except into a small, open shrub; (4) similar to category 2 except into a small shrub; (5) down burrow; (6) ran into other shady areas; (7) ran into open sun; (8) ran into sunny area between shrubs; (9) did not move. At single-species sites numbers of runs made by fleeing animals were recorded, offering an estimate of relative wariness.

Escape behavior could vary with time of day, ambient thermal conditions, and body temperature. Analysis of interpopulational or interspecific differences should not be biased by these factors because we observed and recorded escapes during the entire whiptail activity period and sampled each site several times during each season.

Diversity of escape behavior (D) was quantified using Simpson's (1949) index: $D = 1/\sum_{i=1}^{n} p_i^2$, where p_i is the proportion of the ith escape behavior.

The escape tactic diversity hypothesis predicts that species in the whiptail assemblage should diverge in escape behavior. Therefore significant differences should be observed in frequency of various escape classes. Such differences would demonstrate that species have not converged on a single or the few most efficient tactics. However, escape behavior divergence need not be a result of coevolution among species but could have arisen from independent evolutionary histories. Are differences among whiptail species greater than would be expected if due merely to independent evolution? To attempt to test this, escape diversity of the observed assemblage was compared with artificial assemblages with randomized escape behaviors. These random assemblages were generated in four ways.

The first two maintained each species' observed escape diversity by simply randomly rearranging observed frequencies. In one routine (R3) all were rear-

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms

ranged, and in the second (R4) only nonzero elements were. In the other two routines all escape classes were assigned new percentages. These were generated by randomly drawing from the uniform random distribution and dividing the values by their column sum (values for each species thus summed to 100%). Again, in one (R1) all elements were replaced and in the other (R2) only the nonzero elements were. Mean overlap in escape tactics among 10 possible pairs for the observed assemblage was compared with that for 100 artificial assemblages using each of the four randomization routines. Overlap in escape behavior (O) is estimated by a symmetric measure (Pianka 1973; May 1975):

$$O = \frac{\sum_{i=1}^{n} p_{ij} p_{ik}}{\left(\sum_{i=1}^{n} p_{ij}^2 \sum_{i=1}^{n} p_{ik}^2 \right)^{\frac{1}{2}}},$$

where p_{ij} and p_{ik} are the proportions of the ith escape tactic used by the jth and kth species (this same index was also used to calculate overlap in microhabitat for fig. 5).

TAIL-BREAK FREQUENCIES AND PREDATION PRESSURE

Whiptails, like many lizards, readily lose their tails when physically attacked. Breaks are facilitated by elaborate anatomical adaptations to insure sharp fracturing but little blood loss (Smith 1946). When cornered by a human "predator," whiptails sometimes position their posterior toward the observer and raise and undulate the tail as if tempting an attack. Tail loss is costly for lizards, as growth rate is reduced during tail regeneration (Zweifel and Lowe 1966), and in *Cnemidophorus* subsequent locomotion is affected (Urban 1965). Lizard tail-loss strategies are intimately related to other aspects of their biology (Vitt et al. 1977).

We use tail-break frequencies as a measure of relative predation rates, a technique first used by Rand (1954) that has become fairly standard in lizard ecology studies. However, T. W. Schoener (in prep.) designed a simple model which suggests that frequency of broken tails may have little to do with predation intensity. For example, such frequencies would be useful only if the proportion of attacked lizards that escaped, minus a tail, was constant among sites. Otherwise tail-break frequencies would be more a measure of predator efficiency than predation levels. In organisms as disparate as arboreal lizards, butterflies, and fish, injury frequencies have been correlated with predator efficiency rather than predation pressure (T. W. Schoener, in prep.; J. Endler, personal communication). For counterexamples, see Pough and Brower (1977) and Shaffer (1978). Confusing the issue even more, tail loss undoubtedly reduces a lizard's fitness; lizards should thus evolve techniques to reduce predator efficiency in making any physical contact.

A cohort of lizards should accumulate broken tails over time. Frequency of broken tails increases with body size, and presumably with age, in many lizard

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms

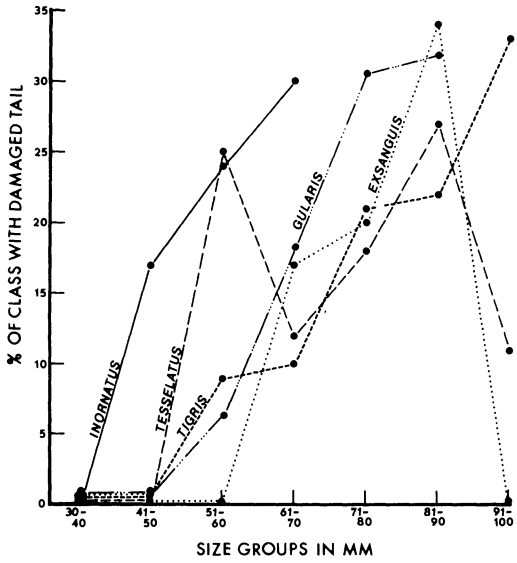

FIG. 1.—Tail-break frequencies for size classes of five *Cnemidophorus* species in southwestern Texas. *Cnemidophorus inornatus* gets no larger than 70 mm. The low percentage of broken tails for the largest size class of *C. tesselatus* and *C. exsanguis* is probably an artifact of small sample size.

species (see, for example, Parker 1972; Parker and Pianka 1973), including the five west Texas *Cnemidophorus* (fig. 1). Populations in which individual lizards live longer should have a higher tail-break frequency than other, shorter-lived, populations. Frequency of recently broken tails presumably would correct for this bias, but such lizards are encountered too infrequently to get meaningful data. We have no data on relative survival of various populations of whiptails.

Lizard tails are sometimes lost through intraspecific agonistic interactions (Vitt et al. 1974). In some populations male whiptails have much higher frequencies of broken tails than females, suggesting loss through male-male fights (Schall 1975). However, males and females of bisexual Texas species do not differ significantly in break frequencies (table 1; χ^2 tests, $P > .25$). Likewise, no intersexual differences were detectable among *C. tigris* populations at single-species sites (Pianka 1970).

Despite these and other such problems, tail-break frequencies of these *Cnemidophorus* populations probably index predation levels crudely. Number of potential predators observed at single-species sites increases from north to south (fig. 2, *top*). Percentage of tails broken also increases toward lower latitudes (fig. 2, *bottom*) and percentage broken is correlated with number of predators ($r_s = .49$, $P < .05$). Also, patterns described below are difficult to interpret if tail breaks simply reflect predator efficiency or lizard life expectancy.

For several reasons, then, we emphasize percentage of tails damaged rather than numbers of predators as an appropriate and operational measure of predation pressure. (1) Quantifying percentage of tails broken or regenerated is easier and

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms

TABLE 1

TAIL-DAMAGE FREQUENCIES FOR FIVE SOUTHWEST TEXAS *Cnemidophorus* SPECIES

Species	% Damaged	*N*	% ♀♀ damaged	*N*	% ♂♂ damaged	*N*
C. tigris	15	305	14	108	15	197
C. tesselatus ...	21	167	...	...	...	...
C. gularis	23	159	22	74	25	85
C. exsanguis ...	20	208	...	...	...	...
C. inornatus ...	24	335	21	151	25	184

NOTE.—*Cnemidophorus tesselatus* and *C. exsanguis* are all-female species.

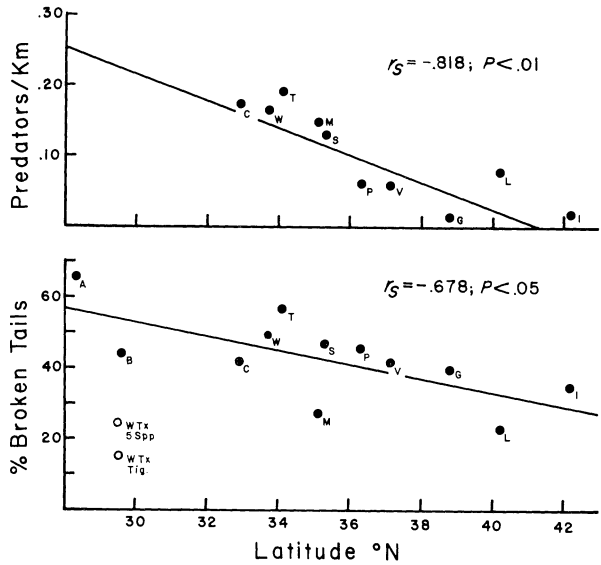

FIG. 2.—Number of potential whiptail predators seen per km walked by an observer (*top*) and percent tails damaged (*bottom*) plotted against latitude for various sites scattered over the North American desert where *Cnemidophorus tigris* is the only whiptail species. Also plotted (bottom) are percent broken tails for southwestern Texas *C. tigris* and for overall whiptail assemblages of five species (open circles).

probably more precise than counting predators. (2) Data on tail-break frequencies are available for more sites than are data on predator abundances. (3) Different species of predators must vary in their efficiency at catching lizards and in the number they attack and eat per unit time. (4) Predator abundance measures present predation pressure whereas tail break frequencies measure past predation rates which presumably have influenced present lizard behavior.

ESCAPE DIVERSITY AT SITES WITH ONE WHIPTAIL SPECIES

Escape behavior diversity of *Cnemidophorus tigris* is loosely but significantly correlated with frequency of broken tails (fig. 3). Site L is an outlier at which

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms

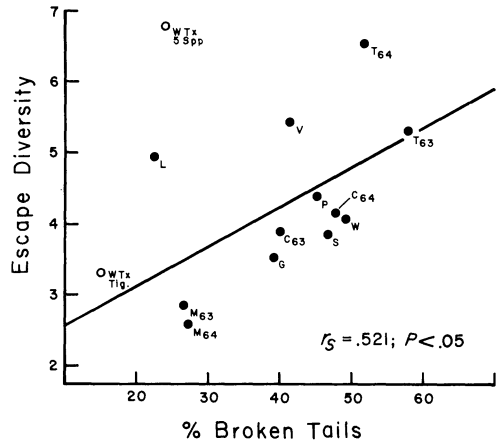

FIG. 3.—Escape behavior diversity plotted against percent of tails damaged for populations of *Cnemidophorus tigris* at various sites. Also plotted are southwestern Texas *C. tigris* and entire Texas whiptail assemblage of five species (open circles). Because different escape behavior classes were used for single-species sites and Texas, southwest Texas escape diversities were standardized by no. of classes for comparison with single-species sites.

lizards had a high escape diversity but low frequency of broken tails (omitting site L improves the correlation; $r_s = .75, P < .01$). Site L was adjacent to a rock ledge where prairie falcons (*Falco mexicanus*) roost and raise their young and have presumably done so for many years. Hawks probably capture whole lizards more frequently than smaller birds or snakes, so tail-break frequency at site L may underestimate true predator pressure. Escape-behavior diversity was also positively correlated, although not significantly, with predators/km, estimated predator biomass/km, and estimated predator biomass weighting birds tenfold over snakes (r's $\approx .40$).

Escape behavior diversity at single-species sites was not significantly correlated with plant volume diversity, a measure of environmental heterogeneity ($r = .13, P > .05$; foliage data from Pianka 1967) nor with percent of ground covered with vegetation ($r = -.52, P > .05$). Indeed, escape diversity is actually negatively correlated with plant species diversity ($r = -.71, .01 < P < .05, N = 9$). Also, site L mentioned above was one of the most northern and vegetationally simple areas, yet escape behavior diversity there was quite high. Hence escape behavior classes do not appear to be biased by varying environmental heterogeneity among sites.

Measured escape diversity was very similar at a site among a season's visits, although there were differences between years at at least one site (Site T, fig. 3). At site M a population crash occurred between 1963 and 1964 (Pianka 1970). Escape diversity changed very little between years but animals were more wary in 1964. In 1963 24% of sighted animals did not run upon an observer's approach, whereas in 1964 all animals fled (χ^2 test, $P < .005$).

Lizards were generally, but not always, more wary on areas with high tail-break frequencies. Mean number of runs, an estimate of wariness, increased from north

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms

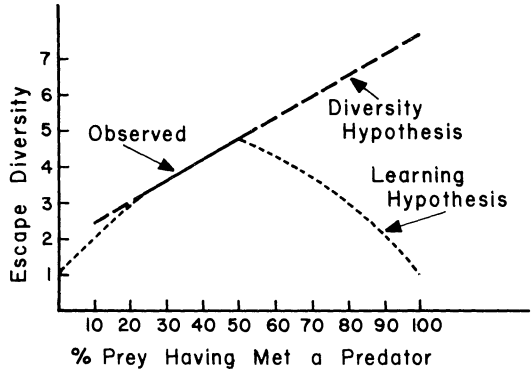

FIG. 4.—Diversity and learning hypotheses contrasted. Diversity hypothesis predicts escape diversity should rise monotonically with predator pressure; one possible form is plotted as a dashed line. Learning hypothesis predicts diversity should first rise with increasing predator pressure and then fall at still higher predation rates; one possible shape of this curve is also plotted (short dashes); observed data (regression from fig. 3) = solid line; placement assumes all lizards which were attacked by a predator were either killed or lost their tails.

to south ($\bar{X}$ runs vs. latitude, $r = -.79$) as did diversity in number of runs (SD of runs vs. latitude, $r = -.65$). However, the latter trend is simply a result of increasing mean number of runs (coefficient of variation of runs is not correlated with latitude, $r = .06$). As might be expected, humans have difficulty catching a wary animal; percentage of sighted animals collected by shooting is negatively correlated with mean number of runs ($r = -.56$, $P < .05$). We emphasize that *C. tigris* were not only more wary when faced with higher predation levels, but also escaped in a greater diversity of ways. In fact, at some sites where lizards had high escape diversities and high tail-break frequencies, mean number of runs was low. Mean number of runs and escape diversity are not correlated ($r = .12$).

Obviously escape behavior is not a perfect antipredator tactic. If it were, tail-break frequency would remain fairly constant with varying predation pressure, which it does not. Nevertheless, escape behavior diversity varies among sites and is positively related with several estimates of predation pressure. We conclude that varying potential predation levels have influenced the evolution of escape behavior diversity, and escape diversity ultimately reduces realized predation pressure.

Although observed data are consistent with the escape-diversity hypothesis, they can also be fitted to another, very different model (fig. 4). Individual lizards could simply learn to be wary after being attacked by a predator. At sites where few lizards have been attacked and most are docile, escape diversity would be low (lizards would use one or a few docile tactics). Likewise, at sites where most individuals have been attacked most would be wary, and escape diversity would again be low with primarily wary tactics. At intermediate levels of predation, escape diversity should be maximal: About half the lizards have been exposed to predators and become wary while the other half remain docile. We cannot discriminate between hypotheses since we have no data for sites where predation

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms

pressure is exceedingly high. However, if this learning hypothesis is valid lizards with broken tails should on the average be more wary than those with intact tails, as they are more likely to have been pursued or attacked by a predator. We tested this at two sites with large samples. Mean number of runs by a fleeing lizard at site C for animals with regenerated tails was 1.5 ($N = 96$), whereas for animals with whole tails the mean was 1.6 ($N = 189$). At site S respective means were 1.3 ($N = 70$) and 1.2 ($N = 130$). The two groups did not differ significantly in wariness at either site (t-tests; P's $> .05$). In laboratory experiments whiptail lizards quickly learn to avoid noxious stimuli (Benes 1969; J. J. Schall and R. Thomas, in prep.); yet, anomalously, above data suggest whiptails do not become more wary after being attacked by a predator. Possible explanations for this anomaly abound. For example, whiptails could in fact become more wary after attack, but those animals without damaged tails may simply have been initially more wary (and thus avoided predators). Further speculation is pointless until more is discovered about the nature of lizard learning.

ESCAPE DIVERSITY AMONG SPECIES AT MULTISPECIES SITES

Cnemidophorus species in southwestern Texas have similar ecologies and behaviors. All are insectivorous, diurnal, widely foraging, and have similar body temperatures, activity times, clutch sizes, and courtship behaviors (Schall 1976, 1977, 1978). Among most species, whiptail dorsal color patterns are relatively similar. Frequently, syntopic species are the most similar morphologically (*C. tigris-C. tesselatus* and *C. exsanguis-C. gularis*) and have in the past been confused by biologists. All five species considered here can occur within a radius of several kilometers and two to five species are easily observable within a day by a mobile predator, such as a shrike, hawk, or roadrunner. Up to four species occur at a single site. Thus, the five species doubtlessly share predators, which may have difficulty differentiating among these species of whiptails.

Because *Cnemidophorus* in southwestern Texas are phylogenetically closely related and have similar ecologies and predators, they might be expected to converge on the most effective escape behavior. However, escape behaviors differ dramatically among species (table 2; χ^2 test for five independent samples, $P < .001$). All pairs of species likewise differ (χ^2 tests, P's $< .01$). Some pronounced differences exist between species most often syntopic. For example, *C. tigris* frequently used fast escapes (classes, 1, 10 = 60%), much less frequently used slow escapes (classes 3, 4, 6 = 12%), and only occasionally utilized burrows (15%). A phenotypically similar species *C. tesselatus* used fast behaviors relatively infrequently (16%), slow behaviors more often (55%), and almost never ran down a burrow (< 1%). Thus, syntopic species often use escapes that differ in physiological costs (fast and/or geographically extensive escapes must be more expensive than slow and/or spatially more limited ones [Bennett and Dawson 1976]).

Parthenogenetic species are descendants of hybrids between bisexual forms, some of which are still present in the assemblage (Cole 1975). However, all-female species do not have escape tactics intermediate between those of their bisexual

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms

TABLE 2

ESCAPE-BEHAVIOR FREQUENCIES FOR FIVE *Cnemidophorus* SPECIES

Behavior	*tigris*	*tesselatus*	*gularis*	*exsanguis*	*inornatus*
1. Shrub to shrub	.38	.09	.12	.006	.06
2. Open to open	.03	.03	.03	.11	.03
3. Into shrub, stay	.03	.19	.15	.13	.26
4. Remained still	.03	.15	.05	.15	.16
5. Down burrow	.15	.007	.02	.03	.03
6. To edge, sat	.06	.21	.14	.25	.18
7. Into shrub, calmed	.01	.19	.03	.08	.04
8. Long straight run	.00	.00	.16	.10	.03
9. Zig zag, open	.02	.007	.006	.00	.004
10. Into veg., ran	.22	.07	.15	.03	.10
11. Shrub to open	.003	.01	.03	.03	.007
12. Into veg., vanished	.08	.04	.11	.08	.10
Escape diversity	4.4	6.5	8.2	7.2	6.5
N	288	143	169	155	268

NOTE.—Escape behaviors are listed in text; escape diversity and sample size (*N*) are also given; veg. = vegetation.

parental species. For example, *C. tesselatus* in southwestern Texas is a descendant of *C. tigris* × *C. septemvittatus*. Both bisexual species are very wary, elusive animals compared to *C. tesselatus*. Because genetic variability in parthenogenetic whiptail species is very low or absent, they are presently unlikely to be capable of significant evolutionary change. However, escape behaviors of unisexual species must have arisen during formation of these species, when genetic variability within hybrid swarms of whiptail lizards must have been very high. Each species' modal escape behavior can be briefly described.

1. *Cnemidophorus tigris* relies on speed, darting very rapidly from shrub to shrub, often in a wide arc returning the animal to near its original site of activity, Long hind legs and tail are important in lizards for rapid locomotion (Urban 1965), and *C. tigris* has relatively the longest hind legs and tail of any species considered here (Schall 1976).

2. *Cnemidophorus tesselatus* typically runs into a shrub's base, quickly calms down and soon begins to forage again. Frequently, individuals do not run at all or bolt only a few meters.

3. *Cnemidophorus gularis* very often runs in a long straight line, often through grass or other vegetation. In southwestern Texas it is a very wary animal, similar to *C. tigris*. Notably, *C. gularis* and *C. tigris* are never found syntopically, although they sometimes do occupy abutting habitats (desert-grassland boundaries).

4. *Cnemidophorus exsanguis* is by far the most easily approachable species, often not fleeing even when an observer came very close. Characteristic flight behavior is short, sudden runs often to the edge of vegetation or from one open area to another. Many runs are less than 1 m. The animal then "freezes" and looks back at the intruder. The dorsal pattern is very cryptic, making it difficult to

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms

see even after such a short run. This temerarious species is very often syntopic with the extremely wary *C. gularis*, which it closely resembles.

5. *Cnemidophorus inornatus* often runs into a shrub's base and does not leave even when the shrub is disturbed. It may not be worthwhile for a predator to exert much effort in attempting to extract these small lizards from tiny crevices in tangled shrub bases. Also, *C. inornatus* is strongly striped and is cryptic in a tangle of grass and twigs. Interestingly enough, juvenile whiptails of other species use this escape tactic more frequently than do adults (for example, 12% of juvenile vs. only 3% of adult *C. tigris*). Many whiptail species which are not striped as adults are strongly striped as juveniles.

Some escape tactics are rare or difficult to quantify and therefore are not included in table 2. Nonetheless, they may be important; several examples follow. (1) Dorsal coloration varies from strongly striped (*C. inornatus*) to blotched (*C. tesselatus*). Such differences between striped and blotched dorsal pattern can be important in threshold velocity for detection of movement (Jackson et al. 1976) and flicker fusion (Pough 1976). *Cnemidophorus tigris*, for example, appears striped when running but mottled when immobile. (2) Very often a *C. tigris* darting into a shrub would flush out one to six other whiptails which would in turn begin darting from shrub to shrub. A single lizard's sighting a human could result in an entire area being devoid of whiptails within a few seconds. Such weak sociality may be a predator escape mechanism in that the sudden appearance of many fleeing lizards presents a confusing image to predators. This behavior is effective in limiting capture by humans, and *C. tigris* has the lowest tail-break frequency of any whiptail in our study.

In this *Cnemidophorus* assemblage overall escape diversity is 9.04, higher than for any single species. Novice human observers are confused by the diversity of escape tactics and collecting success is low. With experience, the first identification of an individual whiptail is often based on its escape behavior, although behavioral overlap among species results in errors. A very experienced nonhuman predator (say, an aging roadrunner) might also recognize species by their escape behavior, although this would presumably be of limited help in making a capture since most predators rely on predicting behavior in advance to catch prey effectively.

Escape behavior differences among whiptail species could be a result of random historical effects rather than coevolution. If *Cnemidophorus* escape behavior is a product of coevolution, escape behaviors of species within the observed assemblage should be less similar to one another and more evenly distributed in escape space than randomly generated assemblages. That is, mean overlap and variance in overlap values should be lower in the observed than random assemblages. Observed mean overlap in escape behavior among the ten pairs of species is compared with 100 random assemblages using each of four randomization routines in table 3. The observed assemblage, as predicted, appears to overlap less among species and the overlap values are more evenly distributed.

Differences among species in southwest Texas could simply be a result of different patterns of microhabitat usage. That is, the frequency with which each species utilizes escape classes listed in table 2 could be determined, or at least

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms

TABLE 3
OVERLAPS IN BEHAVIOR FREQUENCIES FOR OBSERVED AND RANDOM ASSEMBLAGES OF WHIPTAIL SPECIES

	Observed	RM1	RM2	RM3	RM4
Mean Overlap	.665	.770	.755	.684	.707
GO Mean Overlap	...	98	91	65	79
GO Mean s^2	...	100	100	95	100

NOTE.—The single observed assemblage had five species (10 species pairs) whereas each randomization method generated 100 assemblages. The no. of random communities for each method (see text) which had greater than the observed (GO) mean overlap and overlap s^2 are also given; RM = random method.

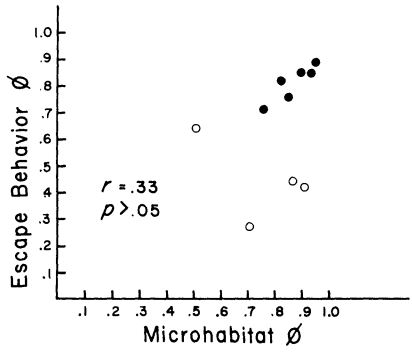

FIG. 5.—Overlap in escape behavior plotted against microhabitat overlap among pairs of whiptail species in southwestern Texas. Open circles = pairs involving *C. tigris*.

markedly influenced, by the frequencies of use of differing microhabitats. In figure 5 escape behavior overlap is plotted against microhabitat overlap for the 10 pairs of species (data from Schall 1976). The correlation is not significant; however, excluding *C. tigris* overlap pairs improves the relationship. Although escape behavior can vary greatly among syntopic species at a site, such variation could result mainly from evolution of modal escape behaviors in differing microhabitats. Other reported cases of aspect diversity in communities could be similarly explained (for example, the moths studied by Ricklefs and O'Rourke 1975). Alternatively, evolution of escape behavior could have influenced or even constrained microhabitat use. Obviously, interpretation of these enigmatic results is difficult.

The escape-diversity hypothesis predicts that in the southwestern Texas whiptail assemblage *C. tigris* should have reduced escape diversity compared to conspecific populations faced with similar predation pressures at single-species sites. However, *C. tigris* in southwestern Texas has about the escape diversity expected for a solitary population with the same percentage of broken tails (fig. 3). Also, community-wide escape diversity is very high for the assemblage's overall tail-break frequency. Tail-break frequency for *C. tigris* is about half what is expected at the latitude of southwestern Texas (fig. 2). Unfortunately we have no quantitative data on predator abundance at Texas study sites, but predators are quite abundant, approximately comparable to those at Sonoran sites A and B.

This content downloaded from
fff:ffff:ffff:ffff:ffff:ffff on Thu, 01 Jan 1976 12:34:56 UTC
All use subject to https://about.jstor.org/terms

West Texas *Cnemidophorus* thus appear to have reduced tail-break frequencies, perhaps as a result of the effectiveness of escape-behavior diversity as an anti-predator mechanism.

SUMMARY

Predators which form search images or learn to predict prey escape behavior should be hindered by diverse prey morphologies and escape behaviors. Thus, among conspecific prey populations, escape tactic diversities should vary positively with predation pressure and escape tactics should diverge among similar sympatric species that share predators. Escape behaviors were quantified for whiptail lizards at sites with only one species (*Cnemidophorus tigris*) scattered over the western North American deserts and for an assemblage of five species of sympatric whiptails in southwestern Texas. Relative predation pressure was estimated by frequency of broken tails. Several factors confound use of this index; however, percent broken tails is correlated with actual density of potential whiptail predators seen at sites. Escape-behavior diversity is positively correlated with percent of tails broken at single-species sites and is also correlated with three estimates of predator abundance, although not significantly. These results also fit another hypothesis, namely, that lizards become wary after being attacked by a predator. However, lizards with broken tails are not more wary than unharmed lizards. Sympatric whiptail species differ significantly in escape behavior. Escape behaviors are more divergent than if each species evolved its escape tactics independently of others in a random fashion. Behaviors of each whiptail species are described; syntopic species frequently differ greatly in escape behaviors. However, differences among species in escape behaviors may be related to differences in microhabitat selection, a possibility that is difficult to discount. *Cnemidophorus tigris* in southwestern Texas has a reduced frequency of broken tails compared with populations at more westerly sites where this species occurs without congeners but with presumed similar predation pressures, perhaps as a result of the protection offered by the assemblage of species with diverse escape behaviors.

ACKNOWLEDGMENTS

Our field assistants were indispensable, especially N. Pianka, W. Shaneyfelt, M. Thomas, and R. W. Schall, who also drew the figures. Comments and criticism from C. J. Cole, V. Maiorana, and the ecology lunch groups at the University of Texas, Universities of California, Berkeley and California, Davis were helpful as were comments from readers: J. Endler, J. A. Joern, L. R. Lawlor, R. Ricklefs, T. Schoener, M. Soulé, and M. Stewart. Financial assistance came from NSF grant GB-42239, The American Museum of Natural History (Theodore Roosevelt Fund) and the Society of the Sigma Xi (to J. J. S.) and NSF grant GB-43349 (to E. R. P.). Final preparation of the manuscript supported by an N.I.H. postdoctoral to J. J. S.

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms

LITERATURE CITED

Benes, E. S. 1969. Behavioral evidence for color discrimination by whiptail lizard, *Cnemidophorus tigris*. Copeia 1969:707–722.

Bennett, A. F., and W. R. Dawson. 1976. Metabolism. Pages 127–223 *in* C. Gans and W. R. Dawson, eds. Biology of the Reptilia. Vol. 5, Physiology. Academic Press, London.

Blest, A. D. 1963. Relationships between moths and predators. Nature (Lond.) 197:1046–1047.

Burt, C. E. 1931. A study of the teiid lizards of the genus *Cnemidophorus* with special reference to their phylogenetic relations. Bull. U.S. Natl. Mus., no. 154.

Cain, A. J., and P. M. Sheppard. 1954. Natural selection in *Cepaea*. Genetics 39:89–116.

Chance, M. R.A. 1959. Polyethism-cryptic behavior. Proc. 15th Int. Congr. Zool., Sect. 11(1):834–836.

Chance, M. R., and W. M. S. Russell. 1959. Protean displays: a form of allaesthetic behavior. Proc. Zool. Soc. Lond. 132:65–70.

Clarke, B. 1962*a*. Balanced polymorphism and the diversity of sympatric species. Syst. Assoc. Publ. 4:47–70.

———. 1962*b*. Natural selection in mixed populations of two polymorphic snails. Heredity 17:319–345.

———. 1969. The evidence for apostatic selection. Heredity 24:347–352.

Cole, C. J. 1975. Evolution of parthenogenetic species of reptiles. Pages 340–355 *in* R. Reinboth, ed. Intersexuality in the animal kingdom. Springer-Verlag, Berlin.

Emlen, J. M. 1973. Ecology: an evolutionary approach. Addison-Wesley, Reading, Mass.

Fisher, R. A. 1958. Polymorphism and natural selection. J. Ecol. 46:289–293.

Gilbert, L. E. 1975. Ecological consequences of a coevolved mutualism between butterflies and plants. Pages 210–240 *in* L. E. Gilbert and P. H. Raven, eds. Coevolution of animals and plants. University of Texas Press, Austin.

Humphries, D. A., and P. M. Driver. 1970. Protean defence by prey animals. Oecologia 5:285–302.

Jackson, J. F., W. Ingram III, and H. W. Campbell. 1976. The dorsal pigmentation pattern of snakes as an antipredator strategy: a multivariate approach. Am. Nat. 110:1029–1053.

Joern, J. A. 1977. Guild and community structure in primary consumers: resource utilization in arid grassland grasshopper communities (Orthoptera: Acrididae). Ph.D. diss. University of Texas at Austin.

Jones, J. S., B. H. Leith, and P. Rawlings. 1977. Polymorphism in *Cepaea*. Annu. Rev. Ecol. Syst. 8:109–143.

Li, C. C. 1962. On reflexive selection. Science 136:1055–1056.

MacArthur, R. H., and R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. Am. Nat. 101:377–385.

MacArthur, R. H., and E. R. Pianka. 1966. An optimal use of a patchy environment. Am. Nat. 100:603–609.

May, R. M. 1975. Some notes on estimating the competition matrix α. Ecology 56:734–741.

Milstead, W. W., A. S. Rand, and M. M. Stewart. 1974. Polymorphism in cricket frogs: an hypothesis. Evolution 28:489–491.

Moment, G. B. 1962*a*. Reflexive selection: a possible answer to an old puzzle. Science 136:262–263.

———. 1962*b*. Reply to Li. Science 136:1055–1056.

Mueller, H. C. 1977. Prey selection in the American kestrel: experiments with two species of prey. Am. Nat. 111:25–29.

Owen, D. F. 1963. Polymorphism and population density in the African snail *Limicolaria martensiana*. Science 140:666–667.

Parker, W. S. 1972. Ecological study of the western whiptail lizard, *Cnemidophorus tigris gracilis*, in Arizona. Herpetologica 28:360–369.

Parker, W. S., and E. R. Pianka. 1973. Notes on the ecology of the iguanid lizard, *Sceloporus magister*. Herpetologica 19:143–152.

Paulson, D. R. 1973. Predator polymorphism and apostatic selection. Evolution 27:269–277.

Pianka, E. R. 1967. On lizard species diversity: North American flatland deserts. Ecology 48:333–351.

———. 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. Ecology 51:703–720.

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms

———. 1973. The structure of lizard communities. Annu. Rev. Ecol. Syst. 4:53–74.

Pough, F. H. 1976. Multiple cryptic effects of crossbanded and ringed patterns of snakes. Copeia 1976: 834–836.

Pough, F. H., and L. P. Brower. 1977. Predation by birds on great southern butterflies as a function of palatability, sex, and habitat. Am. Midl. Nat. 98:50–58.

Rand, A. S. 1954. Variation and predator pressure in an island and mainland population of lizards. Copeia 1954:260–262.

———. 1967. Predator-prey interactions and the evolution of aspect diversity. Atlas Simp. Sobre Biota Amazonica 5:73–83.

Ricklefs, R. E., and K. O'Rourke. 1975. Aspect diversity in moths: a temperate-tropical comparison. Evolution 29:313–324.

Sargent, T. D. 1975. Legion of night, the underwing moths. University of Massachusetts Press, Amherst.

———. 1978. On the maintenance of stability in hindwing diversity among moths of the genus *Catocala* (Lepidoptera: Noctuidae). Evolution 32:424–434.

Schall, J. J. 1975. Factors influencing the distribution of the Aruban whiptail lizard, *Cnemidophorus arubensis*. Stud. Fauna Curacao, Other Caribb. Isl. 153:94–108.

———. 1976. Comparative ecology of sympatric parthenogenetic and bisexual species of *Cnemidophorus*. Ph.D. diss. University of Texas, Austin.

———. 1977. Thermal ecology of five sympatric species of *Cnemidophorus* (Sauria: Teiidae). Herpetologica 33:261–272.

———. 1978. Reproductive strategies in sympatric whiptail lizards (*Cnemidophorus*): two parthenogenetic and three bisexual species. Copeia 1978:108–116.

Scudday, J. F., and J. R. Dixon. 1973. Diet and feeding behavior of teiid lizards from Trans-Pecos, Texas. Southwest. Nat. 18:279–289.

Shaffer, H. B. 1978. Relative predation pressure on salamanders (Caudata: Plethodontidae) along an altitudinal transect in Guatemala. Copeia 1978:268–272.

Simpson, E. H. 1949. Measurement of diversity. Nature (Lond.) 163:688.

Skutch, A. F. 1972. A naturalist in Costa Rica. University of Florida Press, Gainesville.

Smith, C. C. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecol. Monogr. 40:349–371.

Smith, H. 1946. Handbook of lizards. Comstock, New York.

Tinbergen, N. 1960. The natural control of insects in pine woods. I. Factors influencing the intensity of predation by song birds. Arch. Neerl. Zool. 13:265–336.

Urban, E. K. 1965. Quantitative study of locomotion in teiid lizards. Anim. Behav. 13:513–529.

Vitt, L. J., J. D. Congdon, and N. A. Dickson. 1977. Adaptive strategies and energetics of tail autotomy in lizards. Ecology 58:326–337.

Vitt, L. J., J. D. Congdon, A. C. Hulse, and J. E. Platz. 1974. Territorial aggressive encounters and tail breaks in the lizard *Sceloporus magister*. Copeia 1974:990–993.

Zweifel, R. G., and C. H. Lowe. 1966. The ecology of a population of *Xantusia vigilis*, the desert night lizard. Am. Mus. Novit. 2247:1–57.

This content downloaded from
132.198.50.13 on Sat, 17 Jul 2021 14:07:32 UTC
All use subject to https://about.jstor.org/terms