

LETTERS TO THE EDITORS

A BIOGEOGRAPHIC EXTENSION OF THE COMPRESSION
HYPOTHESIS: COMPETITORS IN NARROW SYMPATRY

The compression hypothesis states that when one species invades the range of another, both species should decrease the number of habitat types but increase (or hold constant) the number of prey types utilized (MacArthur and Pianka 1966; MacArthur and Wilson 1967). As originally developed, the hypothesis applies only to short-term, nonevolutionary interactions. Here we extend its application to evolutionarily stable species in narrow sympatry and test this application with data from two species of lizards.

The hypothesis is based on an individual's feeding strategy, as follows. Prey of type x should be included in the diet if and only if

$$\frac{e_x}{t_x} \geq \frac{\sum_{\text{diet}} N_i e_i - C_s K A}{\sum_{\text{diet}} N_i t_i + K A} \quad (1)$$

where e_i is the net energy (potential energy minus pursuit, handling, and swallowing costs) for a single item of type i , t_i is the time to pursue, handle, and swallow a single item of type i , N_i is the number of type i available in an area A , $1/K$ is rate of search, and C_s is cost per unit search time. The notation \sum_{diet} means sum over all item types actually included in the diet; the right-hand side of inequality (1) does not include type x . In inequality (1), $K = DT_s$, where T_s is search time per item of available (encountered) food and D is the number of available items per unit area ($D = \sum N_i/A$). Inequality (1) assumes that potential energy and pursuing, handling, and swallowing costs are item-type specific, whereas search is simultaneous for all items (See Schoener 1974 for details; also see Pulliam 1974 and Charnov 1976). Because the abundance of item type x is not included in inequality (1), changes in that abundance, which might be caused by a competitor, have no effect on the item's inclusion—if true before competition, inequality (1) is true after. (But if the preferred items become rare, they could "disappear" from the diet for short periods of time due to sampling error). However, because a competitor can lower the abundances of other, more preferred items, inequality (1) can be false before but true after competition; then item type x should be added to the diet. Thus diet either expands or remains the same.

Now we reinterpret inequality (1) in terms of habitat types by redefining symbols (N_i becomes the abundance of habitat type i , etc.). By preferentially feeding in a particular habitat type, a competitor can actually lower the value of e_x/t_x (energy per unit time while feeding in habitat type x). Thus inequality (1) may very easily be true before competition but false after, resulting in the dropping of habitat type x from the itinerary. While other habitat types may be added, this divergence should frequently result in a net specialization by habitat.

The contrast between food and habitat hinges on the effect or lack of effect by a competing species on e_x/t_x . For diet, this term is unaffected—any item worth eating in the absence of competition is still worth eating in its presence. The opposite can hold for visitation of habitats. However, the argument for diet assumes little evolutionary change. If phenotypes of the species shift so as to be better able to handle some foods but less able to handle others (remember e_i/t_i contains costs in time and energy of feeding once an item is found), e_x/t_x can change for types of food. This phenotypic modification should ordinarily occur over the long-term, via evolution. Because natural selection should favor those individuals better able to handle food types not preferred by the other species, competitors should eventually diverge and specialize in both food and habitat type.

Thus the compression hypothesis applies only to nonevolutionary stages of competition. Such stages are usually short-lived, and natural (nonexperimental) tests for these are unlikely. However, a situation exists in which competition can remain suspended in its initial stages over evolutionary time; in narrow sympatry, directional selection for phenotypic divergence can be impeded by gene flow. Here, local phenotypes might be more adapted to the area of allopatry than to the much smaller overlap area. Consequently, we have the following, somewhat paradoxical, expectation for situations in evolutionary equilibrium. In narrow sympatry the range of habitats used should frequently be restricted, but the range of food types should actually be expanded (or unchanged) in comparison to allopatry. In broad sympatry, on the other hand, habitats and diets should diverge, and species should often be more specialized.

The compression hypothesis deals with foods and habitats used by individuals. The ideal data for testing it would therefore be observations sufficiently numerous for each individual so as to be representative of its "true" utilization. Such data for habitat can be collected by marking individuals and observing them over a period of time. For diet, however, one frequently cannot discover what is being eaten without gut analyses, and the quantity of items present in the gut at any moment may not be very large. A less direct way to test the hypothesis utilizes the population "niche breadth." This often-computed statistic takes on a variety of mathematical forms, all of which increase with increasing evenness of utilization. Although such a measure is more like the variance than the range (for continuous data, breadth is frequently defined as exactly the variance), the two should be highly correlated. (In the normal and uniform distributions, for example, the expected range is proportional to the standard deviation.) If individuals had identical true utilizations, the sample population breadth may estimate true individual breadth better than would the sample average individual breadth. If individuals were not identical in their utilizations, population and individual breadth may still be closely related. Population variance is formally the sum of between- and within-individual variance (Roughgarden 1972,

TABLE 1
NICHE BREADTH ($1/\sum p_i^2$) IN ALLOPATRY AND NARROW SYMPATRY FOR TWO SPECIES
OF MABUYA SKINKS

	OBSERVED CHANGE				PREDICTED CHANGE	
	<i>M. spilogaster</i>		<i>M. striata</i>		Allo.	Symp.
	Allo.	Symp.	Allo.	Symp.		
Microhabitat*	6.5	← 5.9	6.3	→ 6.8		←
Structural habitat*	8.6	← 6.9	9.1	← 7.6		←
Prey size*†	2.2	→ 3.8	1.6	→ 3.5		→
Prey taxon*†	5.0	→ 7.0	3.7	→ 4.8		→

* All categories and most data in Huey and Pianka (1977); prey taxon by number data available from any of the authors on request.

† By number.

1974), so if between-individual variance is constant, population and individual variance are exactly linearly related; otherwise (again) they would usually be highly correlated.

Data from two species of skinks (*Mabuya*), narrowly sympatric in the Kalahari semidesert of southern Africa, are suitable for testing our biogeographic version of the compression hypothesis. (Details of the species are in Huey and Pianka [1977]). Their sympatry does not appear to be particularly recent. Characteristics of their niches suggest a crucial role for food competition. Four dimensions of resource partitioning can be distinguished: microhabitat (sun/shade and plant type), structural habitat (perch height and diameter), food size, and food taxon. Our compression hypothesis predicts that in narrow sympatry breadth for habitat dimensions should decrease, whereas breadth for food dimensions should increase. These predictions are realized in seven of eight possible comparisons (table 1). If the four dimensions were totally independent, the probability of this or a more extreme result in a binomial test would be .035; the true probability is somewhat greater because of probable slight correlation among dimensions. The only exception to the trend is microhabitat for *M. striata*, but the difference in breadth between allopatry and sympatry is slight relative to the seven consistent differences.

Two possible problems besides the more general one discussed above may characterize our application and may require consideration in most other applications as well.

First, we assume that differences in resource availability between sympatry and allopatry are not responsible for the observed changes in breadth. We have no data on availability per se. However, for *M. spilogaster* plant-height diversity is lower in sympatry than in allopatry (Pianka and Huey 1971). This alone might account for the lower structural-habitat and microhabitat breadth in sympatry. Conversely, the anomalous result for microhabitat breadth of *M. striata* might reflect the greater plant-height diversity in sympatry. Unfortunately, even directly measured data on availability might not ensure the correct interpretation of the compression hypothesis; the model would have to be quantified from its presently qualitative state.

Second, we assume that little local evolutionary change has taken place in the

area of narrow sympatry. In fact, both species increase snout-vent length slightly but significantly in sympatry (mean prey size also increases). However, size differences between the species are apparently small enough so that no significant correlation with prey size exists, even when head length rather than body length is the measure used (Spearman rank correlation coefficient = .40). Moreover, distributions of prey sizes eaten are not very different in sympatry, and the smaller species actually eats significantly larger prey by the Kolmogorov-Smirnov 2-tailed test ($P < .05$; maximum cumulative difference = 8.4%; $N_1 = 1250$; $N_2 = 559$). Thus, any evolutionary change is not a divergence (both species increase, though a greater net size difference results), and prey distributions in sympatry differ little.

In summary, we argue that in narrow sympatry the compression hypothesis should hold in the long term. Using data from natural lizard populations, we illustrate how its rather paradoxical predictions can account for some unusual results. Because we have not demonstrated gene flow, nor entirely supported the other assumptions mentioned above, the proposed mechanism remains of course hypothetical for these data.

LITERATURE CITED

- Charnov, E. L. 1976. Optimal foraging: attack strategy of a mantid. *Am. Nat.* 110:141-151.
- Huey, R. B., and E. R. Pianka. 1977. Patterns of niche overlap among broadly sympatric versus narrowly sympatric Kalahari lizards (Scincidae: *Mabuya*). *Ecology* 58:119-128.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *Am. Nat.* 100:603-609.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.J.
- Pianka, E. R., and R. B. Huey. 1971. Bird species density in the Kalahari and the Australian desert. *Koedoe* 14:123-129.
- Pulliam, H. R. 1974. On the theory of optimal diets. *Am. Nat.* 108:59-74.
- Roughgarden, J. 1972. Evolution of niche width. *Am. Nat.* 106:683-718.
- . 1974. Niche width: biogeographic patterns among *Anolis* lizard populations. *Am. Nat.* 108:429-442.
- Schoener, T. W. 1974. The compression hypothesis and temporal resource partitioning. *Proc. Natl. Acad. Sci. USA* 71:4169-4172.

THOMAS W. SCHOENER

DEPARTMENT OF ZOOLOGY
UNIVERSITY OF WASHINGTON
SEATTLE, WASHINGTON 98195

RAYMOND B. HUEY

MUSEUM OF VERTEBRATE ZOOLOGY
UNIVERSITY OF CALIFORNIA
BERKELEY, CALIFORNIA 94720

ERIC R. PIANKA

DEPARTMENT OF ZOOLOGY
UNIVERSITY OF TEXAS AT AUSTIN
AUSTIN, TEXAS 78712
October 10, 1977