

Fig. 2. Gel scan of secretion after the instillation of [3H]chymotrypsinogen (bovine) into rabbit duodenum. The solid line represents a scan of gel prepared in the manner of Jones (12) and stained by the procedure of Ahlroth and Mutt (12) on which 25 μ l of secretion collected l hour after the injection of labeled enzyme into the gut was layered. The gels were run for 25 minutes at 3.5 amp per tube toward the cathode. The dashed line represents a scan of 10 μ l of the exogenous enzyme run in the same way at the same time. The number at the top represents the dividing line for gel fractions analyzed for tritium content. Fraction 8, the section of a gel of exogenous enzyme (dashed line) contained 70 percent of the label and virtually all of the protein; for secretion it contained 67 percent of the label and less than 5 percent of the total protein.

ture of the fluxes suggests that a wholly probabilistic or random circulation of molecules through a series of membranes with a finite but undifferentiated permeability cannot account for the circulation of digestive enzyme.

CHARLES LIEBOW

Department of Physiology, Cornell University Medical College, New York 10021

STEPHEN S. ROTHMAN Department of Physiology, University of California, San Francisco

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Coexistence of Sparrows: A Test of Community Theory

Abstract. A study of the coexistence of sparrows in grassland and woodland habitats of the Research Ranch in southeastern Arizona supports the predictability of current community theory. For each of the habitats studied, the production of seeds and the abundance of seed-eating, winter-resident sparrows were measured. The theory correctly predicts the number of species supported in each of the habitats. In both cases for which the prediction is that only one species could be supported, the theory correctly predicts which species should be present.

Among the prime goals of theoretical ecology is the prediction of species abundance and species diversity. For this reason a predictive theory of species coexistence is central to the development of the science. In the last decade a sophisticated "community theory" has been developed to predict the composition of equilibrium communities and, thus, the criteria for coexistence. For this theory, ecologists are indebted to Levins, May, and, particularly, MacArthur (1, 2).

This report is a result of an attempt to test predictions of community theory on populations of seed-eating sparrows inhabiting the Research Ranch in the plains grasslands of southeastern Arizona (2). The American sparrows comprise the bulk of the subfamily Emberizinae of the family Emberizidae. Although in many local areas 15 to 20 emberizinine species may occasionally be recorded, there are usually only three to eight winter resident species in the composite of all habitats of a local region.

The probable importance of competition for food among seed-eating sparrows is suggested by the empirical observation

that there is an amazingly constant average ratio of bill sizes (culmen lengths) of adjacent pairs when the species are ranked by size. For the resident species near Turrialba, Costa Rica, this ratio is 1.11 ± 0.15 (S.D.); for the winter residents near Durham, North Carolina, the ratio is 1.10 ± 0.05 ; and for the winter residents at the Research Ranch in southeastern Arizona it is 1.09 ± 0.10 (3). This constant ratio allows one to generate a hypothetical sparrow guild, without reference to specific species, and then to predict which species will be present in a given habitat. To do this, let us start with the smallest North American sparrow, the Brewer's sparrow (Spizella breweri), with a culmen length of 8.8 mm. From the relation C_{r+1} $= (1.1)^{\prime}8.8$, the vector of culmen lengths for the hypothetical guide is C = (8.8, 9.7,10.6, 11.7, 12.9, 14.2, 15.6), and the hypothetical species are referred to as one through seven, respectively. The culmen length for the hypothetical species seven is 15.6 and roughly corresponds to the culmen length of the largest temperate North American sparrow.

Culmen length is important because

Table I. Seed production in the three study sites. On the basis of these data and the utilization matrix for the six hypothetical species, the following vectors of carrying capacity were calculated: for site 1, $k_1 = 505.4$, $k_2 = 512.9$, $k_3 = 515.3$, $k_4 = 512.8$, $k_5 = 500.4$, $k_6 = 489.3$; for oak site, $k_1 = 105.1$, $k_2 = 105.6$, $k_3 = 104.4$, $k_4 = 102.6$, $k_5 = 99.3$, $k_6 = 95.2$; and for riparian site, $k_1 = 84.3, k_2 = 84.9, k_3 = 84.8, k_4 = 85.8, k_5 = 83.4, k_6 = 82.1.$

Organism	Seed production (mg/m ²)		
	Site 1	Oak site	Riparian site
	Class 1 (0.0 to 0.5 n	nm)	
	Class 2 (> 0.5 to 1.0	mm)	
Aristida hamulosa	48.06	6.03	
Erichloa gracilis			105.76
Panicum sp.			26.15
Setaria macrostachya			40.55
Trichachne California	83.92		
	Class 3 (> 1.0 to 1.5	mm)	
Andropogon barbinoides	141.00	46.72	6.30
Aristida divaricata	484.22	31.46	
Bouteloua gracilis	246.51	30.39	6.67
Bouteloua hirsuta	156.26	24.22	
Bouteloua sp.	39.60	29.40	
Chloris virgata			15.48
Leptochloa dubia	24.28	228.40	48.52
Lycurus phleoides	112.72	1.51	3.34
	Class 4 (> 1.5 to 2.0	mm)	
Aristida ternipes	1036.56	43.76	67.20
	Class 5 (> 2.0 to 2.5	mm)	
Bouteloua curtipendula		30.93	151.33

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mean seed size in the diet of a sparrow species is linearly related to it. Of the approximately 20 sparrow species which I have recorded at the Research Ranch, information is available for nine species from the food habits files at the Patuxent Wildlife Center near Laurel, Maryland (4). The regression equation for mean seed size (M)on culmen length (C) for these species is M = 0.108 + 0.120 C (r = .814; P < .01).This relationship defines a vector of mean seed sizes for the seven hypothetical species corresponding to the vector of culmen lengths. The variance of seed sizes in the diet of a species shows no simple trend with culmen length and can be treated as homogeneous (Bartlett's test for homogeneity of variance, $\chi^2 = 12.75$; .75 < P < .90), with σ^2 = .99. The actual distribution of seed sizes in the diet of a sparrow species is closely approximated by a normal distribution (5). Thus, for a given vector of culmen lengths for the seven hypothetical species, a set of seven utilization curves is uniquely determined and can be represented by the seed size utilization function for the i^{th} species

$$f_i(x) = 0.402 \exp\left[-(M_i - x)^2/2.0\right].$$
 (1)

There is considerable evidence that population sizes of sparrows are determined by the availability of seeds in winter (6). If we assume this we can model the annual change in population size as dependent on (i) the number of births in the breeding season, which is a function of population size and (ii) the percentage of winter survivorship, which depends on the carrying capacity (k) of the winter seed supply. Combining these, we obtain the simple difference equation of annual change in population size as

$$\Delta N_i = f(N_i) \left[k_i - \sum_j \alpha_{ij} N_j \right]$$
(2)

The α_{ij} , called competition coefficients, measure the relative effect per individual of species *j* on the survivorship of species *i*. The *m* by *m* matrix of the competition coefficients is called the competition matrix, *A*. For sparrow species competing on the one-dimensional resource spectrum of seed size, the competition coefficients measure the overlap of the utilization curves for pairs of species. Mathematically, this is given by the convolution of two utilization curves as given by Eq. 1 or

$$\alpha_{ij} = \int_{0}^{\infty} f_i(x) f_j(x) dx / \int_{0}^{\infty} f_i^2(x) dx \quad (3)$$

The values of α_{ij} for the 7 by 7 sparrow competition matrix were obtained by numerical integration of the equations on a computer by means of a Runge-Kutta technique. The value of k_i in Eq. 2 is determined both by the utilization function,

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Table 2. Pairwise coexistence matrices. Pairs marked with a plus can coexist and pairs marked with a minus (-) cannot. A plus mark below the diagonal indicates a pair which is resistant to invasion by all other species.



 $f_i(x)$, and the seed production function, P(x), which is the production of seeds along the gradient of seed size (7). The value of k is given by the convolution of the production function and the utilization function, that is

$$k_i = \int_0^\infty P(x) f_i(x) \, dx \tag{4}$$

For the actual calculations of k for this report, a discrete approximation to 4 was used. The seeds produced in each habitat were divided by weight into five seed size classes (0 to 0.5 mm, >0.5 to 1.0 mm, ..., >2.0 to 2.5 mm), represented by the vector P as shown in Table 1. For each of the seven hypothetical sparrow species, the percentage of diet that falls into the same five size classes was calculated, resulting in a 7 by 5 utilization matrix U. The actual vector of the k's was then calculated as k = UP.

When the left-hand side of Eq. 2 is set to zero, one obtains the equilibrium relationship

$$k_i = \sum_{j=1}^m \alpha_{ij} N_j^*$$

Representing the simultaneous equations of m species in vector notation gives

$$N^* = A^{-1}k \tag{5}$$

The predicted equilibrium number of individuals (N^*) can thus be calculated by Eq. 5 by use of the competition matrix and the utilization matrix, both associated with the seven hypothetical sparrow species and the empirical production vector P. However, Eq. 5 gives no guarantee that the elements

of N^* are positive. Obviously negative values are meaningless in the real world. For pairwise (two species) coexistence, the following positivity condition must hold

$$1/\alpha_{ji} > k_i / k_j > \alpha_{ij}$$
 (6)

This criterion allows the construction of a pairwise coexistence matrix. For each pair of the hypothetical sparrows and for an empirically determined production vector P, the criterion can be tested. If the pair can coexist, a plus mark (+) is entered above the diagonal in the matrix for that pair; if the criterion is not fulfilled, a minus mark (-) is entered. Below the diagonal a plus mark indicates that a given pair which can coexist is resistant to invasion by other species. A given pair of species was determined as not resistant to invasion if the growth of any third species could be positive when the first two species were at their equilibrium numbers with respect to each other. This procedure is equivalent to finding all stable, positive subcommunities using Cramer's rule (8).

From September 1972 through March 1973, I measured grass seed production and sparrow abundances in each of three distinct habitats at the Research Ranch. Seed production was measured with 15 to 33 seed traps placed on a regular grid pattern in each of the habitats. The surface of each trap was 10 by 10 cm and caught the seeds falling from plants produced after summer rains in July, August, and September. Traps were emptied once every 2 weeks. Loss from vertebrate seed eaters was prevented by half-inch mesh hardware cloth guard placed approximately 35 mm above the nylon floor of the trap. Loss to seed-eating ants was negligible since most seed production occurred during the cold months when no ants were active. The standard error of the number of seeds produced per plant species per square meter was usually less than 5 or 10 percent of the mean. A census of the sparrows in each habitat was taken biweekly for 7 months by walking slowly through each habitat and recording all birds seen. All census counts were made between sunrise and 2 hours past sunrise.

Table 1 shows the seed production by plant species and seed size for site 1 (dense short-grass prairie) and the vector of carrying capacities (k) for this site. With the criterion given in Eq. 6, a pairwise coexistence matrix was constructed and is shown in Table 2 (site 1). Either hypothetical species 1 or 2 could coexist with 4, 5, or 6; but species 3 has the highest value of k, hence it would always win in pairwise competition. Thus, the prediction for site 1 is that hypothetical species 3 alone would be present. Hypothetical species 3 has a culmen length of $(1.1)^2$ by 8.8 = 10.6 mm. The only sparrow species present on site 1 was the grasshopper sparrow (*Ammodramus savannarum perpallidus*) with a culmen length of 10.8 mm.

The pairwise coexistence matrix for the oak site is shown in Table 2. The only pairs that could coexist consist of hypothetical species 1 with either 3 or 4 but both of these pairs can be invaded by species 2. Hypothetical species 2 has the highest k value of all six species and could coexist with none. Thus, the prediction is that it should be the only sparrow species present. Hypothetical species 2 has a culmen of 9.7 mm. The only resident species in the Oak site was the chipping sparrow (*Spizella passerina arizonae*), with a culmen of 9.6 mm.

Table 2 (riparian site) gives the pairwise coexistence matrix for the riparian site. Hypothetical species 1 or 2 could coexist with 3, 4, 5, or 6; but only the pair consisting of hypothetical species 2 and 3 is resistant to invasion. Actually present were the chipping sparrow with a culmen of 9.6 mm and the brown towhee (*Pipilo fuscus mesoleucus*), with a culmen of 15.2 mm. These correspond most closely to hypothetical species 2 (9.7 mm) and 7 (15.6 mm). Using Eq. 6, one predicts the ratio of abundance for hypothetical species 2 and 7 to be 93 : 7. The observed ratio of chipping sparrows to brown towhees was 94 : 6.

Though not resident, the rufouscrowned sparrow (Aimophila ruficeps scottii) was frequently seen in the riparian site. This sparrow is the resident species in the nearby sacaton (Sporobolus minor) habitats and apparently occasionally utilizes the riparian habitat.

The theory is upheld well by the observed results. Nevertheless, the discrepancies between predictions and observations are worthy of comment. There were a number of stragglers of other sparrow species and these occasionally showed up in every habitat. The theory, of course, does not predict these. They accounted for less than 2 percent of the total number of individuals seen and are, thus, probably unimportant to the dynamics of the total system. The rufous-crowned sparrow accounted for approximately 4 percent of the individuals in the riparian site. This indicates the importance of neighboring habitats on the diversity within habitats, as previously mentioned. The habitats chosen for this study were large and relatively uniform. In North Carolina and Costa Rica, I have studied sparrows in areas composed of a patchwork of habitats (3). In both places, as many as 4 species were seen in a single habitat. Coexistence in these situations is doubtlessly explained by a combination of seed-size allocation within habitats and habitat utilization differences.

For two of the habitats studied the theory correctly predicts which of the seven hypothetical species should be present. For the riparian site, the pairwise coexistence matrix correctly predicts that one smallbilled (hypothetical species 1 and 2) and one large-billed (hypothetical species 3 through 7) species could coexist. However, the theory predicts that the species pair actually present is invisible but that another pair, not present, is not invasible. This result indicates that the theory may be useful in predicting when two species may coexist but not precisely which pairs may coexist.

Sparrows in the grasslands were in many ways ideal for testing these predictions. They are easy to observe, their diets are relatively easy to quantify, and the production of grass seeds is easy to measure. The constant ratio of culmen lengths and the normal distribution of seed sizes in sparrow diets made things easier. The models themselves require none of these luxuries and are, conceivably, applicable to a great variety of organisms.

H. RONALD PULLIAM Department of Ecology and

Evolutionary Biology,

University of Arizona, Tucson, 85721

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- 1972); references listed under 3. 8. See R. H. May (2) for a discussion of calculating k's. The measurement of seed size used throughout is $(l \cdot h \cdot w) \lor$, where l is the length in millimeters of the longest axis, h is the greatest height perpendicular to the longest axis, and w is the width perpendicular to the first two axes.
- See C. Strobeck, *Ecology* 54, 650 (1973).
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Nectar Fluorescence under Ultraviolet Irradiation

Abstract. Nectar, which fluoresces in the visible and absorbs in the ultraviolet spectrum when irradiated by ultraviolet light, occurs in many bee-pollinated plants. It is suggested that these characteristics function as direct visual cues by which bees can evaluate the quantities of nectar available. Thus, they assume an important role in pollination of the flowers and foraging efficiency of bees.

We observed a brilliant aquamarine fluorescence in the nectar of *Prunus amygdalus* (L.) Batsch., the cultivated almond, and suspected its possible function in pollination ecology and foraging efficiency of bees. Fluorescent nectar had been described previously only by Frey-Wyssling and Agthe (1). While studying the mechanism of nectar secretion, they found that both the phloem sap and nectar fluoresce blue. They did not suggest a potential function for the substance.

Cruden (2) showed that central areas of *Nemophila* flowers which absorb ultraviolet (UV) light, also fluoresce in the visible spectrum. Indeed many fluorescent compounds are known to absorb UV (3). Thus, when we photographed a spot of almond nectar on filter paper using a UV light source with appropriate filters (2) (Fig. 1, a to c), we found that it not only fluoresced in the visible, but absorbed in the UV spec-

trum. Nectar of *Allium cepa* L., cultivated onion, behaved similarly (4). None of the nonfluorescent nectar tested (*Aloe, Fuchsia*, and *Mandevilla*) absorbed UV. Sugar solutions (sucrose and glucose) placed on filter paper did not fluoresce or absorb UV.

Patterns of color contrasts in flowers due to differential absorption and reflection of UV wavelengths (300 to 400 nm) were demonstrated about 50 years ago (5). Since then many flowers have been shown to exhibit contrasting patterns in the UV spectrum (6). Similar guide marks (7) in the visible spectrum serve as visual cues directing floral visitors to the nectar reservoir (8). The UV patterns, although invisible to man, can be perceived by honeybees and some other insects (9) and are important cues to foraging honeybees (6, 10).

Some flowers, after pollination or fertilization, undergo changes in visible coloration [for example, *Phyla* (11) and *Lupinus*