

- genetic predisposition, the hypothesis of a purely genetic deviation conflicts with this type of observation. At the same time we know that even when twins grow up in the same family, their experiences can never be identical.
19. See, for example, L. Wing, *Autistic Children* (Constable, London, 1971), p. 8.
  20. Although not all the authors of the following books label their subject as "autistic," I mention them because the descriptions of the initial behavior conform in whole or in part to Kanner's syndrome; and, as I have said, I consider such descriptions the only acceptable starting points: R. d'Ambrosio, *No Language but a Cry* (Cassell, London, 1971); V. Axline, *Dibs—In Search of Self* (reprint of 1964 publication, Penguin Books, Harmondsworth, England, 1971); J. Copeland and J. Hodges, *For the Love of Ann* (Arrow Original, London, 1973); J. M. Hundley, *The Small Outsider* (reprint of 1971 publication, Angus and Robertson, Sydney, 1973); C. C. Park, *The Siege* (reprint of 1967 publication, Penguin Books, Harmondsworth, England, 1972); S. S. Wexler, *The Story of Sandy* (re-

- print of 1955 publication, Signet, New York, 1971); G. Thieme, *Leben mit unserem autistischen Kind* (Hilfe für das Autistische Kind e.V., Lüdenscheid, West Germany, 1971). No two of these seven children received the same treatment, but on the whole one can say that those who were treated primarily at the emotional level rather than at the level of specific skills showed the most striking improvement.
21. The clearest introduction is: F. M. Alexander, *The Use of Self* (Chatterston, London, 1932); but a great deal of interest can also be found in: F. M. Alexander, *Man's Supreme Inheritance* (Chatterston, London, 1910) and *The Universal Constant in Living* (Chatterston, London, 1942).
  22. The history of medical science is full of such examples of breakthroughs due to a reorientation of attention. Compare, for example, Jenner's discovery that milkmaids did not contract smallpox; Goldberger's observation that the staff of a "lunatic asylum" did not develop pellagra; Fleming's wondering about empty areas around the *Penicillium* in his cultures

23. W. Barlow, *The Alexander Principle* (Gollancz, London, 1973).
24. J. Dewey, see, for example, introduction to F. M. Alexander, *The Use of Self* (Chatterston, London, 1932).
25. A. Huxley, *Ends and Means* (Chatto and Windus, London, 1937); "End-gaining and means whereby," *Alexander J.* 4, 19 (1965).
26. G. E. Coghill, "Appreciation: The educational methods of F. Mathias Alexander," in F. M. Alexander, *The Universal Constant in Living* (Dutton, New York, 1941).
27. R. A. Dart, *S. Afr. Med. J.* 21, 74 (1947); *An Anatomist's Tribute to F. M. Alexander* (Sheildrake Press, London, 1970).
28. C. S. Sherrington, *The Endeavour of Jean Fernel* (Cambridge Univ. Press, London, 1946); *Man on His Nature* (Cambridge Univ. Press, London, 1951).
29. E. von Holst and H. Mittelstaedt, *Naturwissenschaften* 37, 464 (1950).
30. N. Tinbergen, *Proc. Roy. Soc. Lond. Ser. B* 182, 385 (1973).
31. This plea is nowadays heard more often: see L. Kanner, *J. Autism Child Schizophrenia* 1, 453 (1971); see also p. 457.

## Resource Partitioning in Ecological Communities

Research on how similar species divide resources helps reveal the natural regulation of species diversity.

Thomas W. Schoener

Biologists have long been intrigued by differences in morphology and habit among closely related species, for to comprehend the manner and extent of such differences is to comprehend much of the natural control of organic diversity. Ecologists especially have concentrated on differences in the way species in the same community utilize resources. Studies of this resource partitioning are currently enjoying great popularity. In fact, in the 12 years since Hutchinson (1) posed his celebrated riddle: "Why are there so many kinds of animals?" such studies have grown exponentially at a rate four times that typical of scientific works (2).

The major purpose of resource-partitioning studies is to analyze the limits interspecific competition place on the number of species that can stably coexist. That such limits exist was suggested by the mathematical models of two early 20th-century theoreticians,

Lotka and Volterra (3). The idea was supported by experiments of Gause (4) and later workers on simple organisms in laboratory containers, in which similar species tended to cause one another's extinction. The infusion of models and data crystallized into the Gause principle, one version of which states that species cannot coexist for long if they too similarly use the same kinds of resources. The application of this idea to natural communities, however, was begun primarily in the 1940's during the time of the New Systematics. Although at first interested in differences between species that might ensure reproductive isolation, evolutionists quickly seized upon the idea of reducing competition as an alternative rationale for those differences (5). So rapidly, in fact, did this idea take hold that David Lack, eventually its principal proselytizer, was placed by a publication lag in the awkward position of

having two quite different explanations for bill differences in Darwin's finches appear simultaneously (6)!

Hutchinson's (7) reformulation of the concept of ecological niche provided a precise language for the description of resource partitioning. In essence, he proposed that a species' population could be characterized by its position along each of a set of dimensions ordering environmental variables such as ambient temperature, prey size, and so on. Ideally, these dimensions would be few and independent. Hutchinson originally conceived of the niche as comprising intervals of population survival along each dimension. Now, however, many ecologists consider the frequency distribution of utilization or occurrence along dimensions as the niche.

What evidence demonstrates that the pattern of resource utilization among species results from competition? Mere presence of differences is not enough, for even if niches were arranged randomly with respect to one another, differences would exist. Hence a sufficiently precise search for differences would be bound to result in their detection, a state of affairs that led Slobodkin (8) to rephrase the Gause principle as a "rule of ecological procedure" rather than a verified or even verifiable proposition.

Ecologists now follow two approaches in their attempts to make a case for the importance of competition in nature. One approach is experimental, the other is observational.

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At its most extreme, the experimental approach argues that a descriptive investigation of the equilibrium state of a process reveals little about what that process is. To prove that a particular dynamics operates, one must perturb the system away from equilibrium by adding or removing individuals. Such experiments, mostly quite recent, have demonstrated that compensatory changes sometimes occur in population numbers and in the condition of individuals (9, 10). When such changes are accomplished at several places along an environmental gradient, they show how competition maintains niche differences in nature (11–13). For example, Connell (11) has shown for barnacles, and Grant and others (12) for rodents, that habitat differences can result from competitive interactions.

Simple perturbation experiments in themselves, however, have several shortcomings. First, while demonstrating the effect of one species on another, they fail to reveal the mechanism of the competition. For example, one species may reduce the abundance of a second in a particular habitat by directly depleting its resources, by interfering with its ability to obtain those resources, or by using up in aggressive encounters energy obtained from those resources. Additional information, both observational and experimental, is required to evaluate these alternatives [for example, see (14)]. Second, they shed little light on the origin of differences. Indeed, if species differences have a strong genetic component, short-term experiments will not result in much niche expansion, even though competition may have caused those differences in the first place. Even long-term experiments, however, may fail to show the evolutionary consequences of competition if it acts rarely but with intense selective pressure (15). Third, perturbation is sometimes impractical—it is best when generation time is short, populations are insular, and only a small number of populations need to be studied.

The observational approach lacks some of these drawbacks but has others. In exchange for a direct demonstration of ongoing competition, it attempts to implicate competition indirectly. This can be done by elaboration of the predictions of competition models in such a way as to rule out other mechanisms that might cause species differences, such as selection for reproductive isolation to avoid interbreeding or for divergence in appearance to

avoid habit-forming predators. In the remainder of this article I examine such predictions in detail. I attempt to show to what extent they are confirmed by patterns of resource partitioning and how they allow a better understanding of those patterns.

The evidence (see Table 1) is drawn from 81 studies that, explicitly or not, bear on resource partitioning in groups of three or more species. The studies heavily favor terrestrial vertebrates, probably reflecting my own interests as well as a real bias in the literature. Autotrophs are not included, because the way in which they partition resources is somewhat different and, in particular, seldom involves food types (16). Table 1 shows, for each group, the number of its species and genera, its location, its trophic position, and the dimensions, ranked according to importance, that separate its species (17–20). Many of these dimensions order continuous variables such as food size. Some, however, such as food taxon, are easier to give as nominal categories, though these could probably be ordered along one or more axes.

Most investigators do not state how they delimit the group studied. Usually species of some taxonomic category, especially the genus, are studied in a small area. This procedure centers on theaters of most intense competition, but it introduces arbitrariness: if a species becomes too different in morphology or behavior, it is taxonomically defined out of the system, and if it becomes too different in habitat, it is geographically defined out of the system. These effects must differ for different kinds of animals and may bias the generalizations made in the following sections.

Sometimes it is convenient or necessary to estimate resource differences by using species characteristics, usually morphological, that indicate the position of its utilization on the resource dimension. The commonest *indicator* is the size of feeding structures, which is correlated usually with mean food size, hardness, or depth in some protective medium. But many other indicators (see Table 1) exist, such as body temperature for activity time and hindleg length for habitat (21). Indicators not only short-cut the compilation of data, but they imply strong functional relations between utilization and phenotype, relations which constrain resource partitioning.

## Overdispersion of Niches

Although if species had no influence on each other's resource utilization their niches would still differ, competition should result in an overdispersion of niches in niche-space. Where niches are regularly and widely spaced over one or more dimensions, the alternative or "null" hypothesis of randomly generated differences must be rejected. Overdispersion patterns can be arranged under three headings.

*Regular spacing along a single dimension.* In 1959 Hutchinson (1) called attention to certain groups whose otherwise similar species differed in the size of their feeding apparatus by a constant factor of 1.2 to 1.4. Using this morphological indicator, one may infer that species adjacent on a size scale differ in mean food size by a constant ratio and thereby have their niches regularly spaced. Subsequent work has often, but not always, supported Hutchinson's generalization (19, 22–28). Certain lizards seem regularly to show higher ratios (29). Furthermore, insectivorous birds and lizards sometimes increase ratios with increasing body size (27, 29).

Why should sizes be a constant or increasing multiple of one another rather than be separated by a constant difference? If populations were close to numbers that would make extinction probable, the pattern might result from those species feeding on large items, which are often rare (30), having to be spaced farther apart on the size axis to maintain a viable population size (27). It is likely, however, that the limit of minimum population size is not as important as an increased variance in food-size utilization for large species: the larger the variance for a given distance separating the niches of two species, the greater the overlap and, for a certain set of assumptions detailed below, the more intense the competition. Hence, to hold competition just below a certain intensity, larger species must space more widely (31). The increased variance results from two factors: (i) large individuals usually eat a greater range of food sizes than smaller ones, probably because their optimal food is relatively rare; and (ii) species whose adults are large have a greater diversity of sizes because of their younger, smaller individuals. An increased niche variance is probably also responsible for lizards having greater ratios than birds. Lizard

populations comprise individuals of many sizes, whereas birds mature quickly relative to their life spans and reach a monomorphic size.

*Increase in number of important dimensions with increase in species number.* Levins (32) and MacArthur (33) argue that in a competitive system, as the number of species accumulates, those species will eventually have to segregate on more and more dimensions to preserve minimal resource overlap. This argument assumes an eventual incompressibility of a species niche on any one dimension, an assumption which must be true because of the energy requirements and perceptual constraints of the individuals comprising the species. In contrast, if species were thrown together randomly, there should be no tendency for the number of important dimensions (defined as dimensions separating some minimal percentage of species pairs) to increase with species number. In practice, because of difficulties in ascertaining importance and determining nonindependence of dimensions, it will be hard to disentangle random effects.

Table 1 allows a crude investigation of the dimensionality of species separation.

The Spearman rank correlation coefficient ( $r_s$ ) of number of species in a group compared with the number of dimensions segregating the species is .277 ( $P < .01$ ). Because dimensions within the broad categories of food, space, and time tend to be the most correlated, to reduce the effect of dependence one can recompute the relation using only one dimension from each of the three categories. But the trend is less decisive ( $r_s = .146$ ,  $P < .1$ ). Higher correlations should result from a taxonomically more narrowly defined analysis: our sample includes representatives from slime molds to lions (34, 35).

What is the commonest number of dimensions separating species? For no limit on the maximum, three is the mode, whereas for a maximum of three dimensions, two is by far the commonest value. Even if one admits the imprecise identification of important dimensions, separation appears generally to be multidimensional.

*Separation of species along complementary dimensions.* For groups where more than one dimension is important, similarity of species along one dimension should imply dissimilarity along

another, if resources are to be sufficiently distinct. Such complementarities illustrate especially well the trouble individuals and their genes seem to take to avoid other species' niches, for they often fly in the face of expected functional relationships between phenotype and ecology. For example, small lizards optimally should eat small insects, and they can use small perches. Yet if food were limiting, this arrangement would result in the spatially most overlapping animals competing for the most similar sizes of food. How is this conflict resolved? The dilemma is not imaginary but real, and we can examine the four common lowland *Anolis* lizards of Jamaica to discover their solution (36). Curiously, the four show an inverse correlation between body size and perch diameter: the larger the species, the thinner the perches! The situation is complicated by the fact that the species break down into classes of different-sized individuals (a class is uniquely defined by age and sex, and adult females are usually considerably smaller than adult males). Moreover, within species, larger individuals appropriate larger perches. As Fig. 1 shows, the arrangement whereby there is a direct

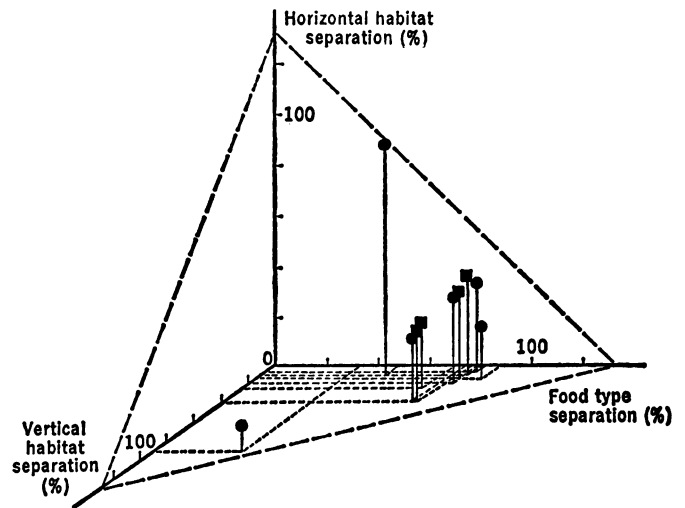
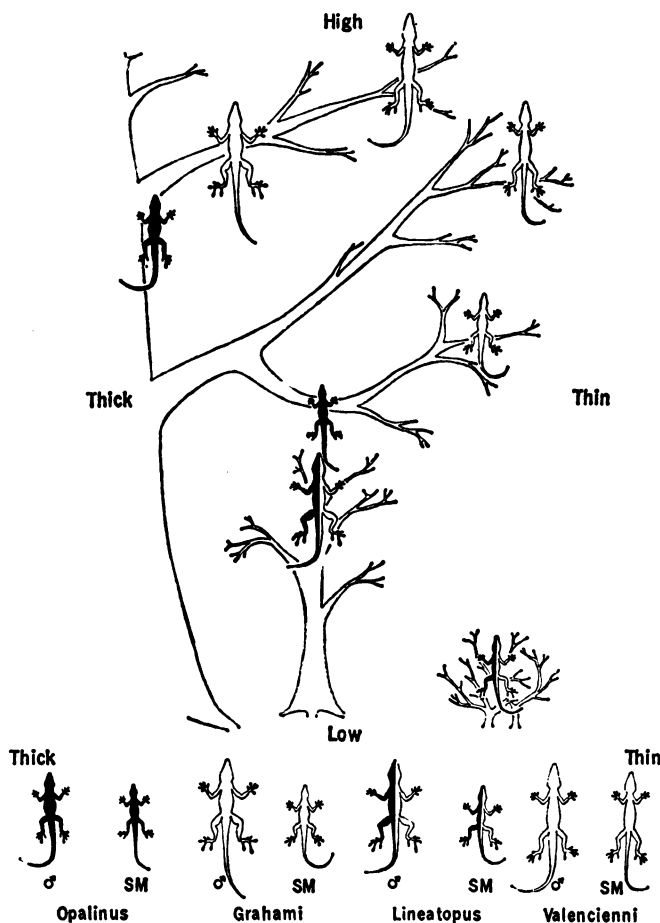


Fig. 1 (left). Spatial arrangement of lowland Jamaican *Anolis* lizards. Bottom line of lizards shows how a direct relation between perch diameter and lizard size within species and an inverse relation between species results in those classes of different species adjacent in perch diameter being of maximally different size. The top of the figure shows the actual spatial placement of lizards at one locality [Mona, see (36)], which is one variation on the theme of the bottom line. Sizes are scaled according to actual mean sizes. Fully shaded lizards denote species found mostly in shaded places, unshaded lizards denote species found mostly in sunny places. Fig. 2 (above). Cody's grassland bird communities, showing how total separation in horizontal habitat, vertical habitat, and food type is constant, but the relative proportion of the three types of separation varies. Squares are South American communities, circles are North American. [From Cody (37); courtesy of the University of Chicago Press]

Table 1. Ecological differences between similar species. Numbers in columns "Macrohabitat" through "Time" denote importance rank of that decision. Abbreviations are as follows. Rank: A, thought to be strictly an aspect of separation on another dimension; b, breeding time; f, feeding time; i, indicator used; n, thought not to be necessarily related to resource partitioning; X, known not to be important dimension. Macrohabitat: Alt, altitude; Aqu, aquatic-terrestrial gradient; Dis, foraging distance from land; For, marine formation; Geo, geographic; Hor, aquatic horizontal zone; Lat, latitude; Soi, soil; Str, stream size or part of stream; Veg, vegetation type; Wat, size or type of water body. Microhabitat: s, used as shelter; structural habitat, food or perch substrate in vegetation. Food type: B, artificial baits; F, feeding type; H, hardness; S, size; T, taxonomic category [letters following T refer to species of food (S), higher taxonomic category (H), life stage of host (L), part of an individual prey (P)]. Indicators: 1, body size; 2, bill size; 3, head size; 4, ovipositor length; 5, bill shape; 6, body temperature; 7, mouth shape; 8, body form; 9, hindleg length; 10, hair quantity; 11, group size; 12, nutrient-utilization ability.

Consumers			Rank and description of resource dimensions					
Group, location, and reference	No. of species	No. of genera	Food	Macro-habitat	Microhabitat	Food type	Time	
							Day	Year
<i>Simple organisms</i>								
Slime molds, forest, eastern North America (93)	4	2	Bacteria	X		1-TS		
<i>Paramecium</i> , near Ann Arbor, Mich. (94)	5	1	Organic minutia	1-Wat				1
Triclads, shallow littoral zone of lakes, Britain (95)	4	3	Invertebrates		2 (X)-Depth	1-TH; X-S		
Nematodes, psammolittoral, Gulf of Mexico (96)	46	?	Invertebrates, plants	1-Hor	1-Depth	3-F		
Rotifers, small lake, central Sweden (97)	5	1	Flagellates		1-Depth	1 <sup>1</sup> -S <sup>1</sup>		
Tubificid oligochaetes, Toronto Harbor (98)	3	3	Bacteria		X	1-TS <sup>1,2</sup>		
Polychaetes, soft bottom, Beaufort, N.C. (99)	5	3	Deposit feeder		1-Sediment type 2-Vertical zone			
Chaetognaths, Agulhas Current, Indian Ocean (100)	18	4	Mostly copepods	2-Hor	2-Depth	1 <sup>1</sup> -S		
<i>Mollusks</i>								
Gastropods, shallow water, Florida (47)	8	6	Invertebrates			1-TS		2
<i>Conus</i> , Hawaii (101)	25	1	Polychaetes, fish, gastropods	3-For	2-Substrate	1-TSH	4	
<i>Conus</i> , Pacific atolls (102)	17	1	Mostly polychaetes		2-Substrate	1-TSH		
<i>Crustacea</i>								
Crabs, intertidal bench, Tasmania (103)	11	9	Algae, invertebrates, detritus	1-Hor	1-As macrohabitat <sup>10</sup> 2-Cover 5-Vertical zone 1-Shell shape <sup>a</sup> 2-Shell weight <sup>a</sup> 3-Bed and tidepool type <sup>a,n</sup>	3-TH		3 <sup>b</sup>
Hermit crabs, intertidal, San Juan Islands, Wash. (61)	3	1	Detritus					
<i>Diaptomus</i> copepods, Clarke Lake, Ontario (44)	3	1	Plant, animal particles		1-Depth	1 <sup>1</sup> -S	X	1
<i>Diaptomus</i> copepods, Saskatchewan ponds (104)	7	1	Plant, animal particles	1-Geo	4 (X)-Depth	2 <sup>1</sup> -S		2
Amphipods, marine sand beaches, Georgia (44)	5	5	Mostly detritus, algae, protozoa	1-Hor	2-Depth in sand	2-S <sup>1</sup> 5-TH		2 <sup>b,1</sup>
Crustaceans, cave streams, West Virginia (105)	4	3	Leaves, microorganisms		1*-Riffles or type pool	X		
<i>Insects</i>								
Grasshoppers, prairie, northeastern Colorado (106)	14	11	Grasses, forbs			1-TS; 1-TS		2
<i>Melanoplus</i> grasshoppers, grasslands, Boulder, Colo. (107)	3	1	Mostly grasses	2-Veg		1-TS		2
Termites, Savannah-woodland, West Africa (108)	5	1	Grasses	1 <sup>n</sup> -Veg		4-TS; 4-S	3	2
Psocids, larch trees, Britain (109)	9	5	Bark algae, fungi	4-Alt	2-Twig condition	1-THP		3
Butterflies, lowland rain forest, Costa Rica (110)	12	7	Decaying fruit		X-Microclimate	X-B	1 <sup>n</sup>	
Carabid beetles, fen, England (111)	8	2	Mainly scavengers	1-Veg		A-TH; A-S		2 <sup>f</sup>
Whirligig beetles, Michigan (112)	3	1	Predators, scavengers	1-Lat	1-Lake size			3(X) <sup>b</sup>
<i>Euglossa</i> bees, Panama (113)	19	1	Nectar	2-Veg	3 <sup>1</sup> -Microclimate	1 <sup>1</sup> -S	X	
Ants, Colorado (114)	4	3	Animals	1-Veg	3-Type log or cover	2 <sup>1</sup> -S		
Ants, Colorado (114)	5	2	Seeds	2-Veg	3-Type log or cover	1 <sup>1</sup> -S		
<i>Megarhyssa</i> wasps, beech-maple, Michigan (115)	3	1	Parasitoids		1 <sup>1</sup> -Depth of food <sup>4</sup> X-Leaf type <sup>a</sup>	X	2	X
Wasps, <i>Neodiprion</i> , Quebec (19)	11	9	Parasitoids	4-Veg	1 <sup>1</sup> -Depth of host	1-TL; 1 <sup>1</sup> -S 4-TS		
<i>Other arthropods</i>								
Millipedes, maple-oak forest, central Illinois (116)	7	7	Leaf litter, decaying wood		1-Position in log, litter	X-F		
Mites, deciduous forest, central Maryland (117)	7, 9	1	Invertebrates	1-Veg	1-Depth in soil	1 <sup>1</sup> -S		4
Water mites, ponds, central New York (118)	20	1	Parasites	3-Wat		1-TS; 2-P		4
<i>Fish</i>								
Stream fish, dry season, Panama, moist tropics (42)	12	12	Animals, plants	2-Str	2-Depth	1-TH	3	
River fish, River Endrick, Scotland (119)	5	4	Arthropods, algae	1-Str		1-TSH		
Lake fish, eastern Ontario (43)	17	15	Animals, plants	1-Hor <sup>a</sup>	5-Depth <sup>s</sup>	1-TH 5 <sup>2</sup> , S <sup>1,7</sup>	3	3
Intertidal fish, Brittany (120)	13	12	Invertebrates, algae	1-Hor	1-As macrohabitat	2-TH		

Consumers				Rank and description of resource dimensions				
Group, location, and reference	No. of species	No. of genera	Food	Macro-habitat	Microhabitat	Food type	Time	
							Day	Year
<i>Salamanders</i>								
<i>Desmognathus</i> , Appalachians (121)	5	2	Arthropods	1-Aqu 2-Alt		2-S <sup>1</sup> A-TH		X
<i>Triturus</i> , ponds, England (122)	3	1	Invertebrates	2?-Alt	2-Temperature	1-S, 4-TH		
<i>Frogs</i>								
Tropical <i>Rana</i> , streamsides, rain forest, Borneo (123)	3	1	Small animals	1?-Wat	1-Distance from stream	3-S 3-TH		X
Temperate <i>Rana</i> , northeastern North America (124)	6	1	Small animals	2-Aqu 3-Lat		3 <sup>1</sup> -S		1 <sup>b</sup>
<i>Lizards</i>								
<i>Ameiva</i> teids, Osa, Costa Rica (40)	3	1	Arthropods, fruit	1-Veg		2-S <sup>1</sup>	2 <sup>1</sup>	
<i>Ctenotus</i> skinks, desert, Australia (21)	7	1	Arthropods		4-Plant cover <sup>a, b</sup>	3-S <sup>2</sup> ; 1-TH	5 <sup>a</sup>	2
<i>Cnemidophorus</i> whiptails, Trans-Pecos (125)	5	1	Arthropods	1-Veg		2-TH		
<i>Cnemidophorus</i> , south and central New Mexico (126)	4	1	Arthropods	1-Veg		2-TH; 2-S <sup>1</sup>	5 <sup>1</sup>	4 <sup>b</sup>
<i>Anolis</i> , Bimini (20)	4	1	Arthropods	5-Veg	1-Structural habitat	2-S <sup>2</sup> ; 2-TH	2	
<i>Anolis</i> , Jamaica (35)	6	1	Arthropods, fruit	3-Veg	1-Structural habitat	1 <sup>1</sup> -S	4	
<i>Anolis</i> , Puerto Rico (127)	10	1	Arthropods, fruit	2-Veg	1-Structural habitat	3 <sup>1</sup> -S	4 <sup>2</sup>	
<i>Phyllodactylus</i> geckos, Sechura desert, Peru (128)	4	1	Mostly arthropods	2-Alt 3-Soi	3-Plant species 5-Foraging substrate	1-TH 6-S	X	
<i>Other reptiles</i>								
<i>Sternotherus</i> turtles, southeastern United States (129)	4	1	Mollusks, arthropods	1-Wat		3 (X)-TH	1	
Garter snakes, Michigan (130)	3	1	Animals	2-Veg		1-TH		3
<i>Birds</i>								
Alcids, Olympic Peninsula (49)	6	6	Fish, invertebrates	1-Dis	2-Feeding depth	2-TH		X <sup>b</sup>
Alcids, St. Lawrence Island, Alaska (131)	3	2	Invertebrates	4-Dis	X-Feeding depth	1-S <sup>2</sup> 1-TH <sup>5</sup>	3	X <sup>b</sup>
Terns, Christmas Islands (23)	5	4	Fish, invertebrates	2-Dis		1-S <sup>1, 2</sup> A-TH	2	
Sandpipers, tundra, Alaska (132)	4	1	Insects	1-Veg		1-TS 3-S		
Hérons, Lake Alice, Fla. (133)	4	4	Animals		2-Feeding place	1-THS; 3-S		
Ducks, Medway Island, Britain (24)	7	3	Plants, animals	3-Veg	2-Feeding method	1-THP		
Hummingbirds, Arima Valley, Trinidad (38)	9	8	Nectar, insects	2-Veg	1-Kind of plant	2-S <sup>1, 2</sup>		
Flycatchers, deciduous forest, south West Virginia (134)	5	5	Insects	1-Veg	4-Feeding height 3-Vegetation density	1 <sup>1</sup> -S <sup>1, 2</sup> A-TH		
Flycatchers, deciduous forest, eastern United States (39)	5	4	Insects	1-Veg		2-S <sup>1</sup>		
Titmice, broadleaved woods, Britain (18)	5	1	Insects, seeds	1-Veg	2-Structural habitat	X-TH 2-S		
Vireos, New World (135)	17	1	Insects	2-Alt 1-Geo	2-Foliage layer	4 <sup>1</sup> -S		
Warblers, boreal forests, Vermont (136)	5	1	Insects	X	1-Part of tree 2-Feeding style	X-TH	X	3
Icterids, channeled scabland, Washington (137)	4	4	Insects (for nestlings)	1-Veg	1-As macrohabitat	2-TH		
Tanagers, Trinidad (138)	10	5	Fruit, insects	2-Veg	1-Structural habitat	2-THS		
Honeycreepers, Trinidad (138)	5	4	Fruits, insects	3-Veg	1-Structural habitat	2-THS		
Finches, southeastern United States (139)	5	5	Seeds, insects	1-Veg	1-Height	3 (A)-S		
Finches, near Oxford, England (140)	10	5	Seeds, insects, buds	3-Veg	4-Ground, air, or foliage	1-TSH <sup>6, 2</sup> 1-S <sup>2</sup>	5	
<i>Geospiza</i> finches, central Galápagos Islands (18)	5	1	Seeds, fruit, buds, insects	2-Veg		1-S, H		
<i>Camarhynchus</i> finches, central Galápagos Islands (18)	4	1	Insects	3-Veg	1-Structural habitat 1-Foraging method	3-S		
Grassland birds, ten sites, New World (37)	2-4	2-4	Seeds, insects	2-Veg	3-Vertical	1 <sup>1</sup> -S	X	X
Foliage gleaners, oak woods, California (25)	5	3	Insects		3-Substrate	1-S		
Upland birds, broadleaved woods, Britain (50)	22	17?	Insects	2-Veg	4-Foraging layer 1-Structural habitat A-holes <sup>a</sup>	1-TH 2-TH		A
<i>Mammals</i>								
Pocket gophers, Colorado (71)	4	3	Plants	1-Soi		X-FT		
Chipmunks, Sierra Nevada, Calif. (141)	4	1	Seeds, fruits	1-Alt				
Rodents, deserts, North America (142)	10	3	Seeds	1-Veg 3-Soi	1-Foliage height	X?-S	X	
<i>Peromyscus</i> , Ozarks, Mo. (143)	3	1	Insects, seeds	1-Veg		X-THP		
Giant rats, western Malaysia (144)	4	3	Plants, insects	1-Alt 3-Veg	2-Height in trees	3-THP		
Carnivores, Serengeti, Africa (145)	7	5	Large animals	2-Veg		1-S <sup>1, 2</sup>	3	
Bats, central Iowa (146)	8	6	Insects	2-Veg			1	
Bats, Central American lowlands (52)	31	21	Animals, plants	2-Veg		1 <sup>1</sup> -S; 2-TH		

intraspecific relation between size and perch diameter, and an inverse interspecific relation, results in maximizing the size difference between adjacent classes from different species. Thus sizes are staggered in space so as to minimize resource overlap between species. The way the lizards solved the awkward problem of balancing heavy animals on thin perches was to evolve elongated body form and short-femured limbs.

More complex examples are provided by the grassland bird communities studied by Cody (37): in each community, the species separate according to various mixtures of differences in vertical habitat, horizontal habitat, and food type. The proportional importance of the three dimensions varies from community to community, but the total separation is remarkably constant (Fig. 2).

Cases of complementarity involve nearly all possible combinations of kinds of dimensions:

1) Food type and habitat: The tendency for species that overlap in habitat

to eat different foods is perhaps the commonest combination. In addition to having been reported for birds (23, 37–39) and lizards (20, 36, 40, 41), it has also been reported for fish (42, 43) and crustaceans (22, 44). The *Anolis* lizards of Bimini provide a precise example of this combination. In Fig. 3, overlap in food size is plotted against overlap in structural habitat (perch height and diameter) for all pairwise combinations of classes of Bimini lizards. For pairs from different species, where structural habitat is similar, food size is not, and vice versa. For pairs from the same species, similarity in one dimension implies similarity in another. This indicates the relative effectiveness of competition in spacing similarly sized individuals, depending upon whether those individuals are in the same gene pool and reproductively attractive to one another.

Many otherwise similar species are separated, often with extraordinarily small overlap, in geographic range. When that separation parallels changes in habitat variables, such as in Dia-

mond's numerous examples (28) of altitudinal separation for New Guinea birds, the situation is similar to those just described. However, other cases of geographic separation do not appear to covary with any dimension and are particularly common in archipelagos, where terrain is fragmented (10, 28, 45).

2) Food type and time: Temporal separation can be on a daily or a yearly basis and both sorts can complement separation by food type. For example, two similarly sized terns feed at different times of the day (23), and similarly sized lizards (46), crustaceans (22, 44), and gastropods (47) reach peak abundance at different times of the year.

3) Habitat and time: Lizards in habitats where climatic factors vary substantially during the day can show nonsynchronous spatial overlap (36, 40, 48).

4) Habitat and habitat: In addition to Cody's birds, other species similar in horizontal habitat often differ in vertical habitat—seabirds partition depth under water (49), while woodland passerines partition foraging height (50).

5) Food type and food type: McNab constructed a matrix whose columns index food size and whose rows index food taxon; members of the Trinidad bat fauna fill this matrix fairly evenly (51, 52).

Despite there being so many cases of complementarity, there are more cases where similarity of species along one dimension implies similarity along another. This is because the dimensions that ecologists recognize are rarely independent: for example, moisture and food size can be correlated (30). The point is not to compare numbers of examples. Rather, given correlations between environmental variables and functional relations between consumer and resource characteristics, one must explain why examples of complementarity should exist at all.

### Importance of Particular Dimensions in Resource Partitioning

The data just reviewed raise the questions of which dimensions are important for which groups and why some kinds of animals show greater dimensionality than others. To approach these questions, we need to answer two others: (i) What is the absolute heterogeneity of resources and, in particular, what resource kinds renew as separate popu-

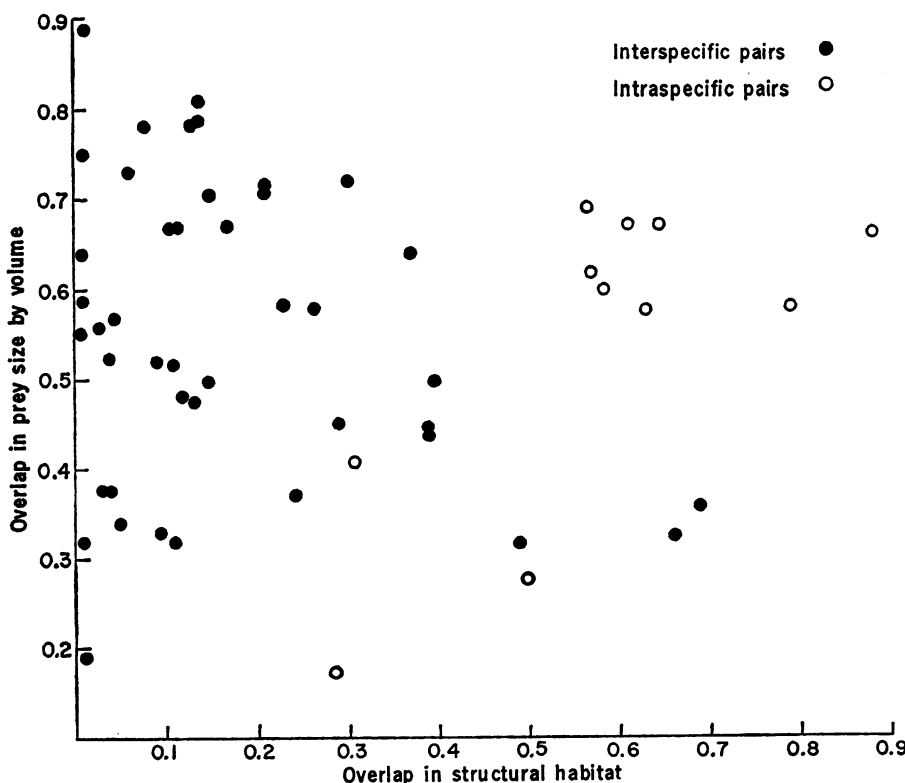


Fig. 3. Similarity in prey size (weighted by prey volume) plotted against similarity in structural habitat for all pairwise combinations of classes of Bimini *Anolis* lizards. Overlap is expressed as percentages. For interspecific pairs, similarity in habitat implies dissimilarity in prey size and vice versa, whereas the reverse is true for intraspecific pairs. More exactly, divide the plot into four sections bounded by the axes and two lines corresponding to 0.5 overlap for habitat and 0.5 for food. Then 25 interspecific pairs fall into the top left or lower right sector, whereas no pairs fall into the top right sector. In contrast, the same figures for intraspecific pairs are 0 and 8 ( $P < .001$ , in either separate or combined binomial tests).

lations, and (ii) to what degree is it adaptive or necessary for consumers to distinguish that heterogeneity?

Phrased another way, we need a theory of the feasibility of resource partitioning as it relates to particular dimensions. This theory is now in a formative stage, in which the qualitative sorting out of biologically important effects is critical. To obtain suggestions about the directions that such a theory might take, we can examine the data of Table 1. Five major generalizations emerge.

*Habitat dimensions are important more often than food-type dimensions, which are important more often than temporal dimensions.* There are two ways to show the considerable magnitude of these differences. First, we can give the percentage of groups where the most important dimension falls into one of the three categories. The result is as follows: 55 percent of the groups fall into the habitat category, 40 percent into the food category, and 5 percent into the time category. Second, we can give the percentage of groups where each kind of dimension is known to separate species. The result is: in 90 percent of the groups the species are separated by habitat; in 78 percent, the species are separated by food; and in 41 percent, the species are separated by time.

We can begin to assess the likelihood of partitioning by habitat as compared to food type with MacArthur and Pianka's (53) foraging-strategy scheme. Picture a set of habitat patches between which individuals of a given species travel and within which they forage, and suppose that individuals of a second species invade and reduce food density in certain kinds of patches. Then it may no longer be worth the while of the given species to visit patches of that habitat kind, since the time spent there might better be spent traveling to and feeding in less depleted places. However, picture now the situation within such a habitat patch, where a competing species reduces the density of certain kinds of items. The yield per unit time spent there for individuals of the original species must go down, but if those individuals still find it optimal to feed in that kind of habitat patch, they should at least eat all the types of food that they ate before competition and should probably eat other kinds of food as well. In short, competition changes the value, per unit time, of feeding in kinds of patches

once they are entered, but does not affect the per-unit-time value of eating types of food once they are found (54).

Thus, at first, species will partition habitats. However, evolution should eventually redistribute phenotypes of the consumers, those phenotypes better at extracting energy from the more abundant food types becoming more prevalent. Unless the competing species eliminate the possibility of such evolution by their separating into nonoverlapping habitats and quickly becoming genetically fixed in them, the result can be a narrowing of diet with consequent specialization. Hence, the MacArthur-Pianka argument may not be sufficient to explain the preponderance of separation by habitat.

Perhaps a more critical factor relates to the contrasting ways in which habitat and food are distributed in space and encountered by consumers. An individual must encounter many food items (and to a lesser extent microhabitats) in its foraging and if it skips too many it will lose too much energy and time in searching relative to its energy input. However, because macrohabitat patches are more continuously distributed and are large relative to the need and ability of individuals to range through them, it is feasible for an individual to spend most of its time in a single macrohabitat. Thus, when it becomes impossible to specialize further on food types, species can continue to partition macrohabitats.

Despite these arguments, there is no statistically significant overall trend for habitat rank to increase or food-type rank to decrease with increasing species number in an assemblage. Certain kinds of animals, such as lizards [for their microhabitats, see (35)], do seem to show an overall trend, but others, such as terrestrial mammals, do not. Indeed, in the latter group, separation by macrohabitat is more important than it is in any other group and species often seem to be separated only in this way. This is in contrast to groups such as birds, which are able to partition space vertically and which often show greater horizontal overlap (13).

Should the partitioning of time be more like habitat or food type? As for habitats, competitors reduce the value of foraging in certain time periods by lowering the density of available food. However, there is a fundamental difference. In deciding not to forage in a particular type of habitat, a consumer

is simultaneously deciding instead to forage in or travel between other habitat types; he is weighing one positive energy gain against what is nearly always another. But in deciding to omit certain time periods, the consumer is usually trading something—a lowered but positive yield in the time period frequented by competitors—for nothing, no yield at all. Only where ability to process food is limited relative to risk of being eaten during feeding should temporal specialization be marked. A similar argument can be made for seasonal activity, where what is at stake is some reproduction as opposed to no reproduction. No wonder temporal partitioning is relatively rare (55).

The importance of seasonal differences between species decreases with increasing species number ( $r_s = .377$ ,  $P < .05$ ). So does the importance of diel differences ( $r_s = .313$ ). Although the latter is not quite statistically significant, both of the temporal correlations are substantially greater than those for other dimensions. Hence it seems that the possibility for temporal partitioning is rapidly exhausted as species are added to an assemblage.

*Predators separate more often by being active at different times of the day than do other groups.* Of the 63 groups for whose species no differences in daily activity were noted, 49 percent are primarily predators, 27 percent are primarily herbivores or scavengers, and 24 percent are primarily omnivores. Of the 17 groups showing partitioning by daily activity, 82 percent are predators and 12 percent herbivores [ $P < .025$  (56)].

The most likely hypothesis for this pattern gives a second reason for the rarity of temporal partitioning: resources cannot often be separated into independently renewing populations by their own daily activity. This is obviously true for plants and most plant products—a leaf not eaten during the day can be eaten at night. It is least likely to be true for animal foods, which themselves often show peaks of activity. Therefore, predators will be more likely to partition resources by being active at different times of the day than will other animals.

*Terrestrial poikilotherms relatively often partition food by being active at different times of the day.* Of the 23 such groups, 43 percent segregate by having different periods of daily activity, whereas only 12 percent of other animals do [ $P < .005$  (56)]. Those ani-

mals most sensitive to diel climatic variation are poikilotherms, because they are less buffered against external temperature change. And such changes are greater on land than in water. Therefore, both consumer-perceived and absolute temporal heterogeneity is high for terrestrial poikilotherms.

*Vertebrates segregate less by seasonal activity than do lower animals.* Forty-four percent of invertebrates but only 13 percent of vertebrates differ in seasonal activity or breeding ( $P < .01$ ). The obvious explanation for this trend is that animals whose generation times are relatively long cannot partition the year as finely as those that mature in shorter time periods. What is more, even when there is unusual opportunity for vertebrates to stagger breeding, as for birds in tropical climates, the species simply expand their breeding periods so that overlap is no less than for temperate species (57).

*Segregation by food type is more important for animals feeding on food that is large in relation to their own size than it is for animals feeding on relatively small food items.* This trend holds separately for predators and for other trophic types. For the groups whose food items are relatively large, the combined totals are as follows: 71 percent separate by food type and 33 percent separate by habitat; for groups whose food items are small, 28 percent separate by food type and 72 percent by habitat [ $P < .05$ ;  $P < .01$  (58)].

The reasons for this pattern may be several. First, unless some kind of small food is abundant, a necessary condition for individual specialization is that the animal eat only a few items, as do those animals feeding on relatively large foods. Many herbivorous insects, for example, spend most of their lives on a single "item." Second, animals that eat relatively large prey are often pursuers, and several models of foraging strategies argue that pursuers should specialize on food of a limited size range (53, 59).

In addition to these five patterns, there are others which are not quite statistically significant but which may be real.

For example, animals that mature in size quickly relative to their life span, or whose adults are ecologically dissimilar to their young, partition food by size more often than do others (59 percent as opposed to 39 percent). A striking exception is mammals, and if these are deleted, the result is sta-

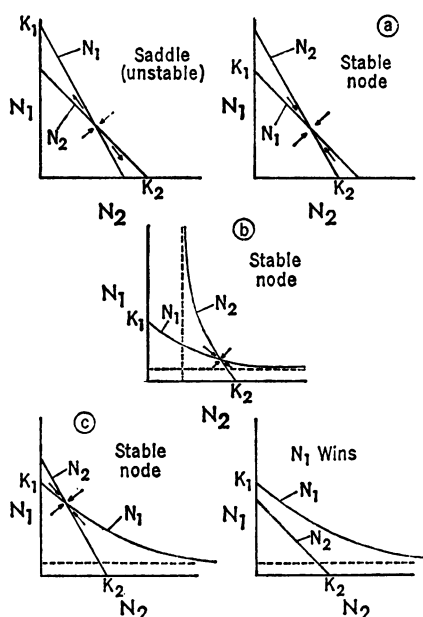


Fig. 4. (a) The two kinds of equilibria for Lotka-Volterra competition equations. (b) Equilibrium in a competition model where each species has exclusive resources (Eq. 3). (c) The two possible outcomes of competition in an "included niche" model, where one species has exclusive resources but the other does not. Either the first species wins, or there is stable coexistence.

tistically significant ( $P < .025$ ). The pattern supports the idea that specializing on food size is difficult for consumer species whose populations at any one time comprise many sizes because, for a given range of available food sizes, overlap must be greater among such species.

There is another rough tendency shown by the data in Table 1. Habitat is less often the most important dimension in aquatic animals than it is in terrestrial animals (43 percent as opposed to 65 percent). A striking exception to this pattern is terrestrial arthropods. If real, the pattern is hard to explain except on the basis of a lower absolute habitat heterogeneity in aquatic systems. As a terrestrial ecologist, I fear this hypothesis may be near-sighted. Yet there is agreement among ecologists working on benthic marine systems (60) that spatial heterogeneity there is often low. In addition, because of the high specific heat of water compared to air, spatial climatic variation in aquatic systems should often be less severe. Finally, because of greater resource mobility, spatial dimensions may characterize resource kinds less well in aquatic than in other systems [for example, see (61)].

## Limiting Similarity

Although niche overdispersion falsifies the hypothesis of randomly placed niches, it fails to rule out alternatives to competition, such as predation and reproductive isolation, that can cause species differences. Analysis of the particular dimensions used by particular kinds of animals may to some extent enable us to discriminate among the hypotheses. For example, instead of the divergence in time of activity or in time of reproduction that would be expected from competition, predation might sometimes result in these times becoming synchronized so as to saturate the predators, as in the case of periodical cicada species (62). However, an entirely different approach is through a theory specifying quantitatively just how similar species could be and yet coexist. This number, called the limiting similarity, could then be checked against differences in hypothetically equilibrated communities. The theory, only begun during the last several years, links properties of the niche to dynamical models that specify the outcome of competition between populations.

The dynamical system that has served as the basis for models of limiting similarity is that of Lotka-Volterra for  $n$  competing species:

$$\frac{dN_i}{dt} = (r_i N_i / K_i) (K_i - N_i - \sum_{j=1, j \neq i}^n \alpha_{ij} N_j) \quad i = 1, \dots, n \quad (1)$$

where  $N_i$  is the population size of the  $i$ th competitor,  $r_i$  is its intrinsic rate of increase,  $K_i$  is its carrying capacity (the number of individuals at equilibrium with no competing species), and  $\alpha_{ij}$  is a competition coefficient (the effect of an individual of competitor  $j$  on the growth of competitor  $i$  relative to the effect of an individual of competitor  $i$ ). Depending upon the  $K$ 's, the  $\alpha$ 's, and (for  $n > 2$ ) the  $r$ 's, Eq. 1 can give mathematical equilibrium with some nonpositive  $\hat{N}_i$ , in which case those species are excluded from the community (63). When equilibrium occurs with all positive  $\hat{N}_i$ , it can be stable or unstable. Figure 4a illustrates the two possible kinds of equilibria for two competitors: a stable node (64) and a saddle (the "unstable equilibrium" of some texts). Both positivity and stability are necessary for coexistence.



Conditions for coexistence were investigated with deterministic models first by MacArthur and Levins (65) and then by Roughgarden (66) and May (67). These investigators assumed that competitors separate along one dimension and obey Eq. 1. To incorporate niches into the differential equations, they calculated competition coefficients as

$$\alpha_{ij} = \sum_k p_{ik} p_{jk} / \sum_k p_{ik}^2 \quad (2)$$

or the continuous analog. Here,  $p_{ik}$  is the percentage of utilization of resource  $k$  by competitor  $i$ . Thus the  $p$ 's specify the niche of competitor  $i$  along the dimension indexed by  $k$ . They also assumed that species have niches with the same shape and variance ( $w^2$ ) and with means differing from those of adjacent niches by a constant amount,  $d$ . Not only does this last assumption collapse the algebra, but it also sets the stage for predictions about how variation in  $d$ ,  $w$ , and niche shape affects  $\alpha$  and thereby affects coexistence.

MacArthur and Levins dealt with the survival of a species trying to wedge its niche between the niches of two species that were already established. For bell-shaped niches and equal  $K$ 's, limiting  $d/w$  for invasion is 1.56, and this decreases as the invader's  $K$  increases. Roughgarden dealt with the survival of the peripheral as well as the "sandwiched" species and determined how variation in niche kurtosis (a shape parameter) affects limiting similarity. As utilization curves with constant  $w$  vary from normal to back-to-back exponentials, limiting similarity decreases. He speculated that concave niches may characterize species whose resources show little long-term dependability. He also predicted a bimodality in the distribution of  $d/w$  in nature. Species with  $d/w$  larger than the upper bound of a certain interval can always coexist. Below the lower bound, successful invasion can often result in one of the peripheral species becoming extinct, giving a small  $d/w$  between the two survivors. May examined limiting similarity for arbitrary numbers of species and showed that the more species along the resource dimension, the less tightly they can be packed. It is interesting that Pianka (41) has evidence from desert lizards for this "diffuse competition," that is, the aggregate competition from many species rather than just from neighboring ones. He finds that niche overlap decreases with

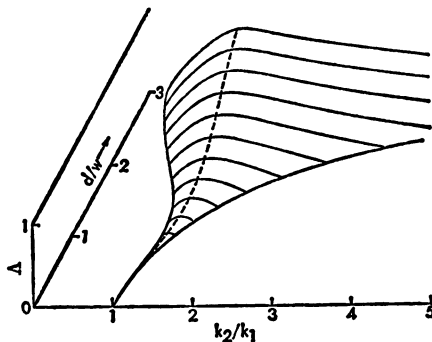


Fig. 5. Conditions of coexistence for three species arrayed along a resource dimension. The  $K$ 's of peripheral species (1 and 3) are equal; species with  $d/w$  and  $K_2/K_1$  within the limiting curves will coexist;  $\Delta$ , the eigenvalue that determines stability in May's stochastic model and sets the rate of return to equilibrium in the deterministic model, is plotted as a third dimension (contours spaced 0.2  $d/w$ -units apart). Note the rapid rise of  $\Delta$  past  $d/w = 1$ . Dashed line shows  $\Delta$ 's for which all equilibrium populations are equal. [From May (147); courtesy of the American Mathematical Society]

increasing species diversity of an assemblage.

A second approach to limiting similarity, developed by May and MacArthur (31) and May (67), incorporates stochastic variation. For competition coefficients given by Eq. 2, equilibria involving all positive  $\hat{N}_i$  are necessarily stable for the deterministic version of Eq. 1. Hence, as far as stability is concerned, there is no limiting similarity, so that the deterministic approaches just discussed deal with positivity. However, the situation is different for a stochastic analog. By incorporating environmental fluctuations (white noise) into the competitors'  $K$ 's, May showed that over a wide range of the fluctuations' amplitude, limiting  $d/w$  is close to one (Fig. 5). Again, the more species along a resource dimension, the less tightly they can be packed, although this effect diminishes rapidly for  $n > 4$ .

There are many cases in nature of species separating on one dimension having  $d/w \approx 1$ . Examples are birds separating by prey size and feeding height, and parasitic wasps separating by depth of prey in wood. There are also cases in which limiting similarity appears to be much less than 1, for example, tropical frugivorous birds (66, 68). According to the theory just presented, such exceptions may occur in extremely stable environments or among species whose niches are con-

cave rather than bell shaped. Most of these new and exciting ideas have yet to be tested in detail.

## Other Mathematical Approaches to Resource Partitioning

While providing the gateway to the current theory of limiting similarity, the Lotka-Volterra equations (Eq. 1) are less than ideal for modeling resource utilization. This is because they fail to incorporate explicitly the mechanism of that utilization. Indeed, interpreted literally they seem better to model competition by direct interference (69, 70), though if considered a Taylor series, they can approximate a variety of more complex equations. Alternatives to Eq. 1 now exist for both one and several trophic levels, and I shall review three examples.

Without much explicit justification, Eq. 1 is sometimes said to model the situation where each competing species has an exclusive set of resources, this resulting in the stable node of Fig. 4a. However, if competition were effected purely through exploitation of resources, it would be difficult to imagine how, as Eq. 1. implies, one species could reduce the other's abundance to zero, much less how this reduction could be linear. A model (70) for one trophic level that incorporates resource partitioning explicitly is

$$\frac{dN_1}{dt} = R_1 N_1 \left( \frac{I_{E1}}{N_1} + \frac{I_{01}}{N_1 + \beta N_2} - C_1 \right) \quad (3)$$

where  $R_1$  is the number of individuals of consumer 1 produced from a unit of processed energy,  $C_1$  is the cost in energy of the death and maintenance of an individual of competitor 1,  $I_{E1}$  is the energy extractable from competitor 1's exclusive resources per unit time,  $I_{01}$  is the energy that individuals of competitor 1 can extract from resources used by both species per unit time, and  $\beta$  is the relative likelihood of an individual of competitor 2 getting a unit of the overlapping resource relative to an individual of competitor 1.

The equation for competitor 2 is similar to Eq. 3 but has a  $\beta$  multiplying the second term; the format easily generalizes to  $n$  species. Equation 3 is not appropriate where the  $\hat{N}$ 's are small relative to the  $I$ 's but is better close to equilibrium. Figure 4b shows the equilibrium solutions for two competing spe-

cies, neither of which can be reduced below the level of that population size supportable on its exclusive resources.

When two competitors are mimicked by equations such as Eq. 3, there is always a single stable equilibrium. By including more resources, the equations can be made more complicated and less tractable. However, they can also be simplified so as to model coexistence or extinction for Miller's (71) "included niche" phenomenon. Here one species has its resource kinds contained entirely within those of the other, whereas the other has resource kinds not used by the first. The appropriate model for the broad-niched species is Eq. 3, and for the included species,  $dN_2/dt = R_2 N_2 \{ [I_2 \beta / (N_1 + \beta N_2)] - C_2 \}$  is the appropriate model (70). The broad-niched species always persists, but the narrow-niched species survives if and only if  $K_1 C_2 < I_2 \beta$  (Fig. 4c). Among other things, this condition requires that individuals of the narrow-niched species be sufficiently better than those of the broad-niched species at appropriating the overlapping resources, and that those resources be sufficiently abundant and calorically worthwhile. This model thus conditions coexistence on parameters more directly related to resource utilization than  $K$  and  $\alpha$ .

Instead of fluxes through the food processing machinery of competitors, resources can be modeled as reproducing populations. MacArthur's (72) two-level system is the best-known example:

$$\begin{aligned} dN_i/dt &= R_i N_i \left( \sum_i a_{ik} b_{ik} F_k - C_i \right) \\ dF_k/dt &= r_k F_k - (r_k F_k^2 / K_k) - F_k \sum_i a_{ik} N_i \end{aligned} \quad \begin{matrix} i = 1, \dots, n \\ k = 1, \dots, m \end{matrix} \quad (4)$$

where  $F_k$  is the number of resource  $k$ ,  $a_{ik}$  is the consumption rate of resource  $k$  by competitor  $i$ ,  $b_{ik}$  is the net energy per item of resource  $k$  extractable by an individual of competitor  $i$ ,  $r_k$  is the intrinsic rate of increase of resource  $k$ ,  $K_k$  is the carrying capacity of resource  $k$ , and other symbols are as before. At equilibrium, Eqs. 1 and 4 are structurally equivalent, whence

$$\alpha_{ij} = \left[ \sum_{k=1}^m \frac{a_{ik} a_{jk} b_{ik} K_k}{r_k} \right] / \left[ \sum_{k=1}^m \frac{a_{ik}' b_{ik} K_k}{r_k} \right] \quad (5)$$

A second two-level system (73) has consumers the same as in Eq. 4 but resources growing according to

$$dF_k/dt = S_k - F_k \sum_i a_{ik} N_i \quad k = 1, \dots, m \quad (6)$$

where  $S_k$  is the number of resource  $k$  entering the system per unit time (15, 69, 70). At equilibrium, Eq. 6 is structurally the same as models of the type of Eq. 3.

Two-level models show explicitly how many key variables affect competition. For example, Eq. 5 says that the larger a resource kind's net caloric value to consumers and the smaller its intrinsic rate of increase (a measure of recovery), the greater that resource's contribution to the magnitude of the competition coefficient,  $\alpha$ . When resources have a one-to-one correspondence with habitats, Eq. 5 shows that the more similar the habitat preferences (reflected in the  $a$ 's), the greater  $\alpha$ . This interpretation of resources provides an approximate justification for the form of Eq. 2, since the  $a$ 's are proportional to the  $p$ 's. When dietary utilizations are known,  $a_{ik}$  in Eq. 5 must be replaced by  $n_{ik}/f_k$ , where  $n_{ik}$  is the number of items of resource  $k$  an individual of competitor  $i$  eats per unit time, and  $f_k$  is the standing relative abundance of resource  $k$  (74). Then the more similar the diets, the greater  $\alpha$ ; the smaller the standing frequency of a resource kind relative to its utilization, the greater its contribution to  $\alpha$ .

While yielding intriguing results, to achieve tractability the mathematical theory of resource partitioning has had so far to ignore major kinds of biological variability. Most of its restrictive assumptions are too technical to give here. Rather, we can condense the major ones by stating that the theory is one of species with static niches or abilities. That is, the utilizations ( $p$ 's), consumption rates ( $a$ 's), and efficiencies ( $b$ 's) vary neither with abundance of the resources nor with time. Yet often in reality individuals saturate with too much food (75), restrict the kinds of resources eaten when food is abundant (59), and apparently change their ability to perceive (76) and digest (77) resource kinds, depending on abundances. Aside from these adjustments of individuals, natural selection, with some lag, should change a species' utilization and efficiency parameters by

redistributing its phenotypes (78). Niches that change in tandem with abundance of consumers and resources could lead to highly complicated systems behavior, including multiple equilibria and periodic rather than point equilibria. Nonetheless, in situations of tightest species-packing the niches themselves may approach some limiting form.

The most critical problem in applying the models is identification of resources in nature. Theorems have appeared for various model-systems stating that a necessary condition for coexistence of  $n$  consumers is that there be at least  $n$  resources (79). In what may well become a classic paper, Haigh and Maynard-Smith (80) examine the question of when population units can act as resources in the theorems. They conclude that, to act as resources, populations need only not be functionally dependent (81); for example, different parts of the same plant and different life stages of an insect species could be separate resources even if their abundances were highly correlated. One way to determine such units is to examine demographic properties of the prospective resources themselves. Another is to demonstrate or assume resource competition, then employ statistical techniques such as discriminant or multiway-contingency-table analysis (36, 82) to determine what axes and categories best separate consumer niches. Incidentally, the hoopla over resource identification has obscured what, from a resource's viewpoint, is an equivalent problem, and that is consumer identification. Indeed, in certain pollination systems, plants and insects seasonally reverse the roles of competitors and resources (83)!

Finally, an entirely different approach to interspecific habitat separation is to consider the habitat kinds as units within which species come to competitive equilibrium separately. This assumption would certainly be true were the habitat patches completely isolated from one another. But if individuals distributed their utilizations among habitats so as to balance their habitat-specific caloric benefits and costs, the assumption could be approximately met. Then spatial niches would not be static in population-dynamics time. The  $\alpha$ 's could be estimated by regression, with habitat-specific  $K$ 's and  $N$ 's being used as variables. Complementary occur-

rences of species among the habitats then could indicate the outcome of strong competition rather than the weak competition that Eq. 2 implies (70).

### Cross-Community Comparisons

Another way to assess the importance of competition is to examine changes in properties of single species across communities. When such changes correlate with presence or absence of especially similar species, one may infer a causal relationship. When the properties are morphological, the changes are labeled character displacement (84); when they are ecological, the changes are labeled ecological shift (85).

Unfortunately, such simple comparisons fail to discriminate between changes resulting from competition and changes resulting from other mechanisms, such as reproductive isolation. Again, elaboration of predictions are required. For example, one can examine the modality of character change: characteristics especially effective for reproductive isolation, such as voice and plumage for birds, should differ from those most facilitating resource partitioning, such as bill and body size. Or one can ask whether the various mechanisms should always produce displacement. Interestingly, the answer for competition is no. Several models using population-dynamics equations like Eqs. 1 and 4 predict convergence for generalized feeders or homogeneous resources (33, 65). Another model, based on an optimal-feeding argument, predicts that a generalist species should shrink in size when contacting another, whether that other is larger or smaller. Thus, convergence should be associated with and only with shrinking, a prediction verified for *Anolis* lizards (see 59).

### Interaction of Predation and Competition

The theory of how predation affects species differences and diversity is much less well-developed than is the theory for competition. Several major elements for the former have already appeared, however. (i) Predation in which the consumption rates per unit prey (the  $a$ 's in Eqs. 4 and 6) are constant can reverse the outcome of competition among prey, whether that out-

come be extinction or coexistence. For a wide range of parameters, however, such predation has no effect (86). (ii) Predation in which prey-specific consumption rate ( $a$ ) monotonically decreases as that prey's relative abundance decreases and goes to zero as that prey vanishes allows prey species to coexist with greater  $\alpha$ 's and correspondingly lesser ecological differences (87). (iii) Prey when rare may evolve differences in appearance so as to escape predators whose prey-specific consumption rates vary with that prey's abundance (88). (iv) The premium placed on the consumer gaining energy quickly while feeding is set in part by the likelihood of the consumer being eaten while feeding (59). Hence predators may reinforce selection for feeding efficiency, including resource specialization, rather than obviate it.

To disentangle the possible effects of predation and to show how these effects interact with competition is now one of the major challenges of ecology. To discriminate between the effects described in (ii) and (iii), for example, again requires an examination of the modality of differences: differences relating to resource partitioning should decrease, whereas those relating to predator avoidance should increase. And whether competition or predation is dominant will depend on size and trophic position: herbivores (89) and small animals (90) are more likely to be regulated by predation than are secondary consumers and large animals. Most of the classical examples of slight ecological differences, such as Ross' leafhoppers (91), do seem to fit one or both of the two former categories. And large predatory animals, such as *Accipiter* hawks, kingfishers, and mustelids, provide classical cases of resource partitioning (15, 27, 92). But the tendency has yet to be investigated in detail.

### Conclusion

To understand resource partitioning, essentially a community phenomenon, we require a holistic theory that draws upon models at the individual and population level. Yet some investigators are still content mainly to document differences between species, a procedure of only limited interest. Therefore, it may be useful to conclude with a list of questions appropriate for

studies of resource partitioning, questions this article has related to the theory in a preliminary way.

1) What is the mechanism of competition? What is the relative importance of predation? Are differences likely to be caused by pressures toward reproductive isolation?

2) Are niches (utilizations) regularly spaced along a single dimension?

3) How many dimensions are important, and is there a tendency for more dimensions to be added as species number increases?

4) Is dimensional separation complementary?

5) Which dimensions are utilized, how do they rank in importance, and why? How do particular dimensions change in rank as species number increases?

6) What is the relation of dimensional separation to difference in phenotypic indicators? To what extent does the functional relation of phenotype to resource characteristics constrain partitioning?

7) What is the distance between mean position of niches, what is the niche standard deviation, and what is the ratio of the two? What is the niche shape?

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$$(e_x/t_x) > (\sum_{\text{diet}} e_i p_i - C_x T_x) / (\sum_{\text{diet}} t_i p_i + T_x)$$
 where  $p_i$  is the environmental frequency of food type  $i$ ,  $e_i$  is the net energy gained from an item of type  $i$  once found,  $t_i$  is the time it takes to eat an item of food type  $i$ ,  $T_x$  is the search time between two items of encountered food,  $C_x$  is the caloric cost per unit search time, and summations are over those item kinds actually eaten. Since the inequality does not contain  $p_x$  (nor in rearranged form does it contain the absolute abundance of type  $x$ ), competitors that reduce item  $x$ 's abundance do not affect choice. But if  $i$  indexes types of habitat patches, the situation is different. Then competitors by eating in particular patches can change the value of the  $e$ 's and  $t$ 's and thereby change the inequality's direction.
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## NEWS AND COMMENT

# Killian Committee: Report Urges Advisory Council in White House

The scientific community has reacted to the abolition of the science advisory machinery in the White House rather like an amputee whose phantom foot continues to hurt long after the leg is gone. No doubt propinquity to the President has a heavy symbolism for scientists, but many are also convinced of the merits of the case for making room at the top for a science adviser and his staff. And in recent months an increasing number of voices calling for restoration of a science adviser to the White House have been heard, although not, it should be noted, from the direction of the White House.

More on the issue is sure to be said in hearings before the House Astronautics and Space Committee scheduled to run well into July. These hearings on federal policy, planning, and organization of science and technology began on 20 June with an appearance by Senator Edward M. Kennedy (D-Mass.), who is the senator most strategically placed to influence science policy issues on that side of Capitol Hill. The Kennedy appearance was essentially a courtesy call, although his opinion was politely solicited on several matters. The committee should get down to more specific cases on 26 June when it is scheduled to hear former presidential science adviser James R. Killian, Jr., discuss a recently completed report by a blue-ribbon committee he chaired\* (*Science*, 8 February). The Killian committee was formed at the behest of the council of the National

Academy of Sciences "to look into the question of scientific and technical advice to the government, including the advisory and coordinating functions previously carried out by the White House science advisory complex."

The report is likely to have considerable impact, not only because of the prestige of the committee members and the academy's imprimatur, but also because the attention it will get in the hearings is likely to make the report a bench mark in future discussions about science policy arrangements. (This issue of *Science* went to press before the report was scheduled to be discussed at the hearings on 26 June, and this article is based on a conversation between Killian and reporters the previous week.)

The committee's principal recommendation is that a "Council on Science and Technology" be created in the Executive Office of the President along the lines of the Council of Economic Advisers and be designed to interact effectively with the other staff units in the White House and to provide close links with the scientific community.

Killian and his committee were acutely aware that they might be accused of special pleading in behalf of science, and he says they "didn't want to cry over spilt milk or try to reconstitute PSAC" (the President's Science Advisory Committee, which was based in the Executive Office until PSAC was abolished in the reorganization of a year ago). The report concentrates on what science can do for government rather than what the government can do for science in terms of funding and otherwise.

The committee, however, leaves no doubts about its position, beginning the outline and summary of the report with the flat statement, "The committee concludes that the office of the President could benefit from a scientific and technological presence." This presence the committee sees quite clearly in the form of a Council for Science and Technology in the Executive Office of the President. The report describes the council only in general terms, recommending that it have the following major features. The council should have at least three, perhaps more, full-time members drawn from science, engineering, and related areas. The council members, one of whom would serve as chairman, would be appointed by the President subject to the advice and consent of the Senate and would serve at the President's pleasure. The committee would prefer to see the council established by legislative action but leaves the matter open. A staff of 25 to 30 is suggested as appropriate.

Effective working relations between such a council and the major White House staff offices are given heavy emphasis in the report. The committee thinks that the council chairman should sit as a member of the Domestic Council in the White House and that the council should participate actively in the workings of the National Security Council and cooperate closely with the Office of Management and Budget (OMB).

Stress is also put on the role the council would play in areas of foreign policy strongly affected by scientific and technological considerations. It is recommended that the Council for Science and Technology make an annual report to the President and through him to the Congress. The presumable model is the annual report of the Council of Economic Advisers, but Killian hopes that such a report would not be simply a survey of activity in science and technology, but would be devoted to the analysis of trends which represent major opportunities or problems

\* Science and Technology in Presidential Policy-making: A Proposal. Individual copies are available from the Printing and Publishing Office, National Academy of Sciences, 2101 Constitution Avenue, NW, Washington, D.C. 20418.