Suppose now we are at optimum geometric design. Then, if our vector could suffer arbitrary variations, we could lower all the undesirable quantities by simply decreasing the first two components, keeping the second two components fixed. Such a possibility is in contradiction to our assumption of being at a minimum. We conclude that in the vicinity of the optimum design the vector (L_{Fe}, L_{Cu}, A_{Fe}, A_{Cu}) cannot be varied in an arbitrary manner. In mathematical language, the appropriate Jacobian must vanish:

$$\frac{\partial\ (L_{Fe},\ L_{Cu},\ A_{Fe},\ A_{Cu})}{\partial(a,\ b,\ a',\ b')} = 0. \tag{4}$$

Substitution of relations (3) into (4), and making use of the definitions (1), leads directly to our result (2).

Note added in proof: The authors are indebted to the engineers of our Power Transformer Division for constructive comments. Mr. J. H. McWhirter has pointed out that the rectangularity law may be generalized to the case of fixed clearances between the copper conductors within the iron window. Dr. Stein has pointed out that Reed has obtained (eq. (2)) for that particular design which minimizes the total transformer losses [Reed, E. G., *Essentials of Transformer Practice* (New York: D. Van Nostrand Co., 1927), pp. 94–96.]

COMPETITION, HABITAT SELECTION, AND CHARACTER DISPLACEMENT IN A PATCHY ENVIRONMENT

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It is well known that related species often differ in either habitat[1] or size, and thereby avoid competitive elimination. The way in which they differ is related to the specialized ways they have of using resources, which ways in turn control numbers of coexisting species and other aspects of the evolution of the community. The detailed reasons for these assertions are given in the following paragraphs.[2] Briefly, the argument is as follows. Among species which specialize on a single uniform resource, only the most effective one will survive and that species will be found wherever the resource occurs, in abundance determined by the density of the resource. Other such pure specialist species will be found, one to a uniform resource; these will normally differ in morphology, but will not in general be affected by one another's distributions. On the other hand, species which specialize on a particular *proportion* of mixture of two or more particular resources will be found only where their favored proportion is found, and will be replaced by other species in other habitats where the proportion of the mixture changes to one on which the new species are more effective. Of this mixed-resource type of species there can be as many[3] as there are proportions of the resources which can be counted on from season to season—i.e., very many in stable climates and fewer in unpredictable climates.

To make these ideas more precise, we first consider an imaginary habitat in which there is a scattering of uniform units or grains of resource 1 and another

scattering of uniform grains of resource 2.   In such an environment we can distinguish as "fine-grained" an individual or a species which utilizes both resources in the proportion in which they occur.   (If the actual grain size of the resources were so fine that the species could not discriminate and select, then the species would have to be "fine-grained," hence the terminology.)   An individual or a species will be called "coarse-grained" if it discriminates and selects only grains of one of the resources.   These are the pure specialists of the first paragraph.   Notice that if individuals are sedentary, as trees are, it is possible for individuals to be coarse-grained, spending their lives on soil of a single type, while the species is fine-grained, with individuals not selecting soil types.   Normally, coarse-grained utilization will be expected only where the time and energy lost due to neglecting the other possible resource is slight compared with the benefits of specialization.[4]   Pursuing species with relatively large foods are usually of this sort.

If now we plot the quantity of resource 1 along the abscissa of a graph and the quantity of resource 2 along the ordinate, then each habitat, with a certain quantity of each resource, determines a point in the graph.   We assume here that the resources are consumable and renewing, like prey species.   (Other kinds of resources, like nest sites, can be analyzed similarly.[5])   Then the process of competitive elimination consists in one species reducing the resources to such a low level that the other cannot harvest sufficiently to maintain its population.   As a first approximation, each species will increase when and only when its joint resource supply is sufficiently dense.   Thus, for fine-grained species x and y, and resource populations R_1 and R_2, we might have

$$\frac{dx}{dt} = [i_1(R_1 - c_1) + i_2(R_2 - c_2)]x \qquad \frac{dR_1}{dt} = f(x,y,R_1,R_2)$$

$$\frac{dy}{dt} = [j_1(R_1 - d_1) + j_2(R_2 - d_2)]y \qquad \frac{dR_2}{dt} = g(x,y,R_1,R_2).$$

(We have included the equations for dR_1/dt and dR_2/dt for completeness; actually, they are not needed in the following analysis.)   Here the c's and d's are the threshold densities of resources below which the species have a net loss of energy and the i's and j's measure the effectiveness with which the species utilize their resources to reproduce.   For coarse-grained species V (specializing on R_1) and W (specializing on R_2), these equations would be of the form

$$\frac{dV}{dt} = [a(R_1 - m)]V \qquad \frac{dW}{dt} = [b(R_2 - n)]W.$$

In either case we can plot the lines $dx/dt = 0$ and $dy/dt = 0$ or $dV/dt = 0$ and $dW/dt = 0$ on the graph, and they might[6] look as in Figure 1 or Figure 2.   Notice x and y can increase in environments lying *beyond* these lines, not within them as in the familiar[7] competition graphs.   Thus, if there were a species z with isocline $dz/dt = 0$ as in Figure 1, it could come to equilibrium with species x at resource level P, but such an equilibrium would be subject to invasion by species y which can still increase with resources at this level.   Then a new equilibrium, Q, will be reached in which y has replaced z.   Notice that since two lines determine a point, two species at most[8] will normally be able to coexist; similarly, with three resources
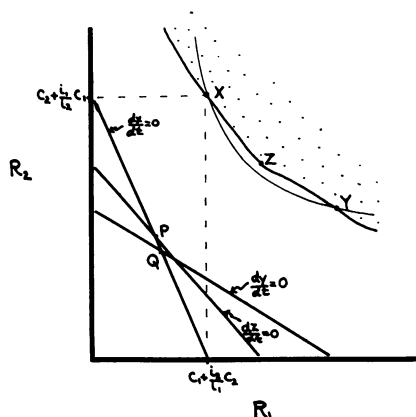
FIG. 1.—The lines, $dx/dt = 0$, $dy/dt = 0$, and $dz/dt = 0$ marking the inner boundaries of the areas in which species x, y, and z can increase. R_1 and R_2 are the quantities of resource 1 and resource 2, respectively. Point x, with coordinates ($c_1 + i_2c_2/i_1$, $c_2 + i_1c_1/i_2$), and points y and z, with coordinates similarly defined by the intercepts of the respective lines, then determine the isoclines $dx/dt = 0$, $dy/dt = 0$, and $dz/dt = 0$, completely. Other possible species might lie at other points in the stippled region. The light curve intersecting the stippled area at x and y is an equilateral hyperbola for reference purposes. See text for further explanation.
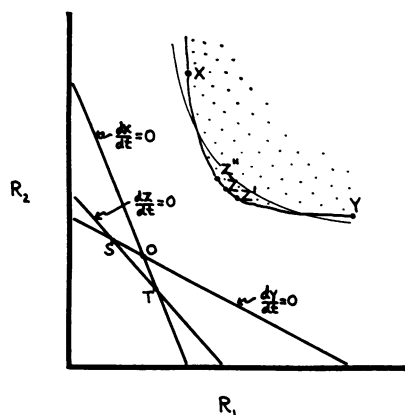

FIG. 2.—The meaning of the lines and stippled area is as in Fig. 1. In Fig. 2 the stippled area is more convex than an equilateral hyperbola, and species z can effectively invade the community consisting of x and y which comes to equilibrium at point O.

and three dimensions it will take three planes to determine a point, so that at most three species can coexist, and so on.[9] Finally, notice that if, as in Figure 2, species z has isocline $dz/dt = 0$ crossing the x and y isoclines inside O, then there will be two alternative equilibria S and T, each resistant to colonization by any of the other species whose isoclines are drawn. Such alternative communities, each resistant to invasion, may be found among islands, but where a large species pool exists, normally one combination is optimal. Thus, when z' and z'' are available, they will replace y and x, respectively, and so on.

To find optimal species combinations and to see how natural selection operates, we construct a set rather like the fitness set described by Levins.[10] We plot on the graphs points whose coordinates are the isocline intercepts (e.g., $c_1 + (i_2/i_1)c_2$, $c_2 + (i_1/i_2)c_1$). Each species then determines a point, and the set of available species—the species pool—determines a cloud of points which, for simplicity, we assume to be fairly solid and continuous in outline (see Fig. 2).

The isocline analysis shows that the equilibrium species are those whose isoclines have small intercepts. Hence, the optimal combinations consist of some species on the inner boundary of the sets in Figures 1 and 2. To see which these will be, we find that shape of boundary which would have all its species isoclines passing through the same point. All of the species on such a boundary would be equally good competitors. This shape of boundary is an equilateral hyperbola. In fact, an isocline passing through (a,b) with slope m has the intercepts $x = a - b/m$, $y = b - ma$. As m varies, these values of x and y are the coordinates of points in the figures describing species whose isoclines all intersect at (a,b). But for these points $(x-a)/b = -l/m = a/(y-b)$ so that $(x-a)(y-b) = ab$ is the equation of a boundary consisting of equally good competitors. Thus, if the boundary of the set stippled in the figures bulges uniformly more than an equilateral hyperbola, a single, jack-of-all-

trades will be favored (Fig. 2). If the set is flatter—less convex—than the hyperbola, as in Figure 1, then the specialists at either end of the boundary will be favored. In the latter case the species will be coarse-grained; in the former the optimal species is relatively fine-grained. As we change from one habitat to another of slightly differing relative suitability for the two resources, the values of i_1, c_1, i_2, c_2, etc., change, and so the fitness set in Figure 2 becomes transformed into a new one. The same species will still be the best specialists, but in general the optimal jack-of-all-trades will change. Hence this type of species will show habitat selection.

In most real habitats, grains of resource are not uniform. For these, it is still useful to talk about fine- and coarse-grained species, but to be precise we must refer to fine- and coarse-grained *differences* between species. Thus among birds, warblers eat smaller food than temperate zone tanagers, and hence the two groups have coarse-grained differences and suitable habitats will contain representatives of each. However, different warblers eat the same food species, only in slightly different proportions; hence among warblers there are fine-grained differences and habitat selection resulting in each species consuming insects in a slightly different location within a forest or in a slightly different forest type. With these distinctions in mind, all the preceding analysis still holds true.

Since pursuing species with large items of food can efficiently specialize, these tend to be separated by coarse-grained differences. Thus, weasels tend to be found in sympatric forms of many sizes, as do accipiters among the hawks and other pursuing predators. But species which spend most of their time searching, especially for small items, cannot afford to overlook many. For these the fitness set, stippled in the figures, will tend to be very convex, and fine-grained differences with marked habitat selection will predominate. Most small birds, grazing mammals, and, among the hawks, perhaps the buteos fall into this category.

[1] Habitat here includes microhabitat (e.g., layer in a forest), and both small- and large-scale geographic separations.

[2] A fuller account will appear as part of a larger publication by Levins and MacArthur on the evolution of the niche.

[3] The number of such species will be proportional to a spatial diversity divided by a temporal diversity at any point. The amount of overlap has been discussed by G. E. Hutchinson, *Am. Naturalist*, **93**, 145 (1959).

[4] The concept of grain is treated in more detail by R. Levins and R. MacArthur, *op. cit.*

[5] Levins, R., and R. MacArthur, *op. cit.* For such species will be governed by equations of the form $dx/dt = i_1x[K_1 - P_1(x,y,...)] + i_2x[K_2 - P_2(x,y,...)]$; $dy/dt = j_1y[K_1 - P_1(x,y,...)] + j_2y[K_2 - P_2(x,y,...)]$. K_1 and K_2 are the quantities of two kinds of nest sites, and P_1 and P_2 are the number in use. We then plot $dx/dt = 0$ and $dy/dt = 0$, etc. in a graph whose coordinates are P_1, P_2.

[6] If the resources are not alternatives but are both required, or if they alternate in time, then the lines will bow in; see Levins, R., and R. MacArthur, *op. cit.*

[7] Slobodkin, L. B., *The Growth and Regulation of Animal Populations* (New York: Holt, Rinehart and Winston, 1961).

[8] At most two because it is infinitely improbable that three or more independent lines will pass through the same point. Even if three did pass through the point, the two most closely parallel to the coordinate axes will alone persist.

[9] This theorem does not depend upon the specific form of the equations.

[10] Levins, R., *Am. Naturalist*, **96**, 361 (1962).