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The Problem of Size Gaps in Some Community Arrays**

L. Oksanen; S. D. Fretwell; O. Jarvinen

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INTERSPECIFIC AGGRESSION AND THE LIMITING  
SIMILARITY OF CLOSE COMPETITORS:  
THE PROBLEM OF SIZE GAPS IN  
SOME COMMUNITY ARRAYS

L. OKSANEN,\* S. D. FRETWELL, AND O. JÄRVINEN†

Division of Biology, Kansas State University, Manhattan, Kansas 66506

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Hutchinson (1959) and Diamond (1972, pp. 42–45) discussed species sequences where the ratio of sizes between the closest competitors was found to be constant. They generally interpreted this constant ratio to be a result of resource competition, where the species had achieved the tightest possible packing (see MacArthur and Levins 1967) on the single niche dimension, size of food items. While these species sequences generally show only slight variations in the ratio of sizes of nearby competitors, some irregularities and ambiguities invite analysis. In this paper we treat the patterns that can be found both within and between sequences.

MacArthur (1972, p. 65) suggested that the constancy of size ratios, rather than of absolute differences, is caused by the relative rarity of large food items. According to him this rarity results in broader niche breadths, and so a greater variance in the utilization curves of species feeding on large food items. A greater variance in utilization curves would result in a greater absolute size difference between species. However, if we wish to compare the variability of diets of two species, it is not sensible to think in terms of the same absolute units when studying species feeding on foods clearly differing in their average size. We consider it more meaningful to express the variation of the sizes of food items relative to the mean. Then the variance of the utilization curve should remain constant on a logarithmic rather than on a linear size scale, assuming that the resources of all sizes are equally abundant. The constancy of size ratios between the closest competitors will then result from an even size distribution of resources.

SOME EXAMPLES OF COMMUNITY ARRAYS

Size of food items is just one possible niche dimension; but the frequent existence of consistent size patterns among sympatric competitors suggests that food size is, indeed, an important dimension, and a good correlation between forager and food size often exists. Let us look at some examples.

\* Present address: Kevo Subarctic Research Institute, University of Turku, SF-20500 Turku 50, Finland.

† Department of Genetics, University of Helsinki, P. Tautatiekatu 13, SF-00100 Helsinki 10, Finland.  
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TABLE 1

GROUND FEEDING BIRDS OF REED-CATTAIL MARSHES IN SOUTHEAST PARTS OF CENTRAL EUROPE

Species	Weight (g)	Length (cm)
<i>Botaurus stellaris</i> .....	1,200	76
<i>Ardea purpurea</i> .....	970	79
<i>Nycticorax nycticorax</i> .....	580	61
<i>Ardeola ralloides</i> .....	290	46
<i>Ixobrychus minutus</i> .....	150	35
<i>Rallus aquaticus</i> .....	120	28
<i>Porzana porzana</i> .....	82	23
<i>P. parva</i> .....	55	19
<i>P. pusilla</i> .....	44	18

NOTE.—Length data are from Heinzel et al. (1972) and weight data based on Bauer and Glutz von Blotzheim (1966) and Glutz von Blotzheim et al. (1973). Weights calculated as averages of records of adults, weighted for sample sizes, using 10 as the maximum weighting factor.

We first look at the reed-cattail marshes of southeastern Europe. The list of potentially coexisting species (table 1), with average weights and lengths, was compiled from Bauer and Glutz von Blotzheim (1966) and Glutz von Blotzheim et al. (1973). The weights of species tend to make up a geometric series, with a ratio of about 2. The length data are consistent with the weights. The purple heron *Ardea purpurea*, however, seems to be an extra member in the community array. Its shape differs completely from bitterns and night herons, however, suggesting that there is a second niche dimension on which this community is segregated besides the size of food items. Presumably for the same reason, the rails are too close to the herons and bitterns in the community array. The rails are also very close to each other (especially in the genus *Porzana*), which suggests, by MacArthur's relative abundance arguments, that the smaller end of the resource spectrum might be somewhat more productive than the large end. (Lack [1971] believes that *Porzana porzana* is separated from the two smaller species by size, but the mechanism separating the very similar *P. parva* and *P. pusilla* is unknown.)

A comparable sequence was also compiled from open (or semiopen) boreal peatlands in central Finland (table 2), using the census data of Järvinen and Sammalisto (1976). The smaller body weights approximate a Hutchinsonian series (ratio of species about 2), but the common crane *Grus grus* is a very clear exception—there is a gap of about three species between the crane and the most similar member of the community, assuming that size ratios should be constant. In the southern boreal peatlands a larger species of *Numenius*, about 735 g, replaces the whimbrel, reducing the gap to about two species (see Järvinen and Sammalisto 1976).

A similar gap can be found in the community array of dabbling waterfowl in the ponds of Finnish boreal peatlands. A typical species sequence (U. Häyrinen and O. Järvinen, unpublished data) consists of the teal *Anas crecca* (300 g), the pintail *Anas acuta* (737 g), the mallard *Anas platyrhynchos* (1100 g), and the whooper swan *Cygnus cygnus* (9000 g). (The wigeon *Anas penelope* is also common, but it is a semiterrestrial grazer and was thus excluded.) Again, three species are absent between the largest member of the community and its most similar competitor.

TABLE 2  
GROUND FEEDING BIRDS OF BOREAL PEATLANDS IN FINLAND

Species	Weight (g)	Bill length (mm)
<i>Grus grus</i> .....	5,000	110
<i>Numenius phaeopus</i> .....	360	86
<i>Tringa nebularia</i> .....	180	55
<i>Gallinago gallinago</i> .....	95	67
<i>Lymnocyptes minimus</i> .....	68	40
<i>T. glareola</i> .....	60	28

NOTE.—All species have been included that have their highest frequencies in one of the three middle zones of Järvinen and Sammalisto (1976). The ruff *Philomachus pugnax* has been excluded, as it appears to be at least partially separated by habitat; bill lengths averaged from Haftorn (1971), weight data from von Haartman et al. (1963–1972).

It seems that both of these cases can be extended to the entire Holarctic region. We were unable to find extensive census data from boreal North America, but a community array was constructed on the basis of Robbins et al. (1966) for the wading birds of boreal peatlands: the lesser yellowlegs *Tringa flavipes* and common snipe *Gallinago gallinago* (bill-to-tail 22 cm), which appear to be segregated by vegetation density, short-billed dowitcher *Limnodromus griseus* (24 cm), greater yellowlegs *T. melanoleuca* (28 cm) and sandhill crane (94 cm). This array corresponds to the results reported from central Saskatchewan by Erskine (1974), with the exception of perhaps the solitary sandpiper *T. solitaria* (18 cm). In any case, there is a relatively neat size sequence of several smaller species, and a large gap between the largest and next largest species. The waterfowl sequence is similar in North America and in Europe, for the same dabbling ducks occur in North America as in Europe, but the European whooper swan is replaced in North America by the trumpeter swan *C. buccinator*, which coexists (or at least used to) with the ducks. It is even larger than its European congener (mean weight of males nearly 12 kg; Scott 1972).

#### EXPLAINING THE GAP

We found above that there is a size gap between the waders and the crane, and also a gap between the dabbling ducks and the swan, but no gap in the ground feeding marsh birds. The gaps might be caused by some discontinuity existing in the niche space, but data on the foods taken by swans and cranes (Bauer and Glutz von Blotzheim 1968; Glutz von Blotzheim et al. 1973) do not support this idea. Foraging depth might be more important than food size for the dabbling waterfowl species, but the gap is not explained by the replacement of one continuous niche dimension by another. We thus assume that the two community arrays are ecologically meaningful and will try to explain the size gap as a consequence of some characteristics of the species or their habitat.

According to Walkinshaw (1973), Scott (1972), and Wilmore (1974), most cranes and swans are vigorously territorial. Furthermore, the breeding ranges of different swans or cranes rarely overlap. In case of range overlap, as between *Burgeranus*

*carunculatus*, *Anthropoides paradisea*, and *Balearica regulorum* in South Africa, Walkinshaw (1973, p. 248) reports segregation by habitat and strong interspecific territoriality. Harassment of smaller competitors by these cranes was also reported. Wilmore (1974, p. 61) cites similar observations about mute swans. Interspecific aggression thus appears to be a plausible reason for the gap; presumably the larger cranes and swans would aggressively exclude any smaller competitor which was large enough to compete with them.

Aggressive behavior and strict allopatry are clearly most pronounced in the breeding season in cranes and swans, implying that we have to assume breeding-season limitation (see Fretwell 1972). This assumption is supported by life-history data. Both mute swans and trumpeter swans tend to remain within their breeding territories even in rather adverse winter conditions, and the migratory species arrive at breeding grounds very early (Wilmore 1974). This suggests that keeping the breeding territory in possession has a high priority. Among winter-limited species, the ones breeding farthest away from the breeding grounds generally have the largest clutches (Royama 1969; Fretwell 1972). On the basis of maximum clutch sizes (Kear 1972), this pattern is reversed among the swans wintering in western Europe (*Cygnus columbianus*, *C. cygnus*, *C. olor*). A further point suggesting breeding-season limitation is the strong tendency of the fledglings of sandhill cranes to kill their siblings if not kept in check by the parents (Walkinshaw 1973, p. 121). For precocial fledglings this would hardly make sense if there were not a frequent shortage of breeding resources.

Two observations weaken the suggested interpretation of the size gaps. The interpretation is based on the apparent aggressivity of the largest species, but the Australian black swan *C. stratus* is colonial and generally nonaggressive. However, the species is also relatively small (males 6.2 kg, females 5.1 kg; Frith 1967), and an especially large duck (*Tadorna tadornoides*, male 1.6 kg, female 1.3 kg) breeds in similar habitats (Frith 1967). Thus the gap is not very large (one species), either.

The generally low abundance of cranes and swans is also in apparent contradiction of the proposed mechanism, as our explanation implies that the largest species has gained a monopoly over a wide range of resources by its aggression. This rarity may well be caused by human activities, however. A large and conspicuous animal is an easy target, and the destructivity of modern man to this kind of species was well demonstrated during the conquest of America by white men. The present size of the mute swan population in Denmark (Ogilvie 1972, p. 39) and the population explosion of mute swans in southwest Finland (Tenovuo 1976) show that, when protected and adapted to human presence, at least certain swan species can become quite numerous. The numbers of sandhill cranes are also increasing after the protection of the species has become efficient (Walkinshaw 1973).

As such, the interspecific aggression is not a sufficient explanation for the gaps in size sequences. The behavior of a species is a result of natural selection and interspecific aggression can be expected to occur whenever the aggressor expects to gain from it (MacArthur 1972; Morse 1974). The problem is, then, to find the factors determining the costs and gains of interspecific aggression and to study how they could be related to the characteristics of the species and its environment.

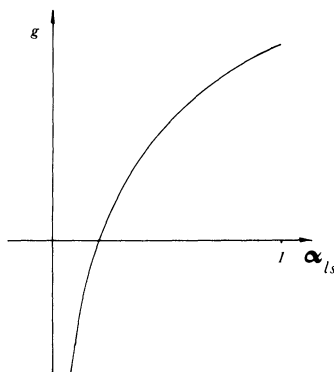


FIG. 1.—Gain of interspecific aggression ( $g$ ) as a function of the resource competition coefficient of the smaller species against the larger one ( $\alpha_{ls}$ ).

BALANCED COSTS AND GAINS OF INTERSPECIFIC AGGRESSION

Assume that we have an array of competing species separated by size alone. Each species is territorial (in the ideal-despotic sense; Fretwell 1972) and has the capacity of being interspecifically territorial against its smaller competitors. If behaving in an optimal way, it will use this capacity whenever the overall cost-gain balance will be positive.

The gain will be a reduction in resource competition. Thus, the magnitude of the gain considered here depends on that part of the competition coefficient of the smaller species on the larger one which is strictly due to resource depletion or “depression” (Charnov et al. 1976). We call this  $\alpha_{ls}$ . When  $\alpha_{ls}$  approaches one, aggression against the individuals of the smaller species whenever they are seen within the territory becomes almost as advantageous as corresponding behavior against conspecific individuals. When  $\alpha_{ls}$  decreases, the maximum gain of the individuals of the larger species from aggression against the individuals of the smaller species must decrease as well.

The minimum cost will be energy spent in contests plus the energy that could have been obtained if the time spent in contests would have been spent feeding. These costs are likely to increase as  $\alpha_{ls}$  decreases: The smaller competitor is probably more numerous, and more time must therefore be spent in contests. Also, driving an individual out of the territory may become quite costly if the individual is small enough to be difficult to chase. Thus, when  $\alpha_{ls}$  gets very small, the gain of interspecific aggression approaches zero and we suppose that the costs will rise without an upper limit. Figure 1 presents the smoothest possible curve that fills the above conditions. The most simple equation that would produce a curve with this shape would be

$$g = \log (k\alpha_{ls}) = \log k + \log \alpha_{ls} \tag{1}$$

where  $g$  = net gain from antagonistic behavior and  $k$  = a constant related to the aggressive characteristics of the species involved. The curve will intersect the  $\alpha_{ls}$ -axis

when  $\alpha_{ls} = k^{-1}$ ; the net gain will be positive to the right of this point and negative to the left, approaching  $-\infty$  when  $\alpha_{ls}$  approaches zero.

The aggression we have thus far discussed may or may not be identical with interspecific territoriality. The model has been concerned with the question: How should an individual of the larger species behave toward the individual of the smaller one after having observed it? Aggressive behavior upon sight is probably enough to prevent the smaller species from nesting in those parts of the territory of the larger one that are frequently visited by its owner. But we wish to consider complete interspecific territoriality, which would altogether prevent the smaller species from nesting within the territories—and, consequently, within the habitat—of the larger one. This must require some amount of active searching on the part of the larger species, which will bring in a new cost factor. We now consider how large the cost factor will be.

An individual of a territorial species must spend some time and energy in order to detect the presence of possible conspecific trespassers. The question is, What additional searching costs are needed if all individuals of the smaller species are also to be detected? If the species are very similar ( $\alpha_{ls} \simeq 1$ ) the same surveying method will be good for both, and the extra costs will be very small. This comes from our assumption that the size is the only distinguishing characteristic between the species. The principle of character convergence (Cody 1969) reduces the limitations of this assumption. With an increasing size difference between the species ( $\alpha_{ls}$  approaching zero) it must become increasingly costly for the larger species to survey its territory thoroughly enough in order to find all individuals of the smaller species present there. Again, there is no upper limit to the costs as  $\alpha_{ls}$  approaches zero. We can thus describe the relation between the searching costs and  $\alpha_{ls}$  by a family of leftward rising curves (fig. 2). The equation

$$c = -\log \alpha_{ls}^u = -u \log \alpha_{ls} \quad (2)$$

would produce a curve with this shape. The variable  $u$  is to be interpreted as an environment-dependent constant, large in environments where surveying is difficult (e.g., in densely covered ones) and small in easily surveyed (e.g., open) ones.

Now we can calculate the net gain from complete interspecific territoriality ( $G$ ) using equations (1) and (2).

$$\begin{aligned} G &= g - c = \log k + \log \alpha_{ls} - (-u \log \alpha_{ls}) \\ &= \log k + (u + 1) \log \alpha_{ls}. \end{aligned} \quad (3)$$

The graphical presentation of equation (3) is simple (fig. 3).

If we set  $G = 0$  and solve for  $\log \alpha_{ls}$ , we get  $\log \alpha_{ls} = -(1/(1 + u)) \log k$ . When  $\log \alpha_{ls}$  exceeds this quantity it will be advantageous for an individual of the larger species to exclude the smaller one from its territory. In order to apply this in making and testing predictions we need to know what the constants  $k$  and  $u$  stand for, and whether there is any way to measure or estimate them.

The constant  $k$  comes from equation (1) and thus can be interpreted as the aggressive capacity of the species involved. There does not appear to be any easy way to estimate or measure it, but certain kinds of qualitative statements can be made.

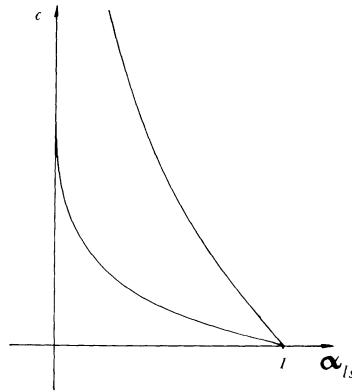


FIG. 2.—Additional searching costs ( $c$ ) as a function of  $\alpha_{ls}$ , with two different values of  $u$ . The most simple curves filling the boundary conditions discussed in the text have been chosen.

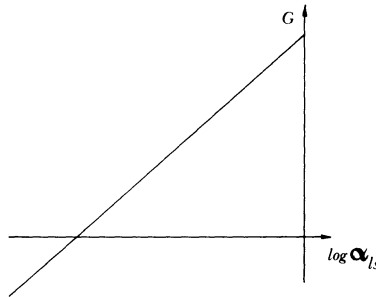


FIG. 3.—Net gain of interspecific territoriality ( $G$ ) as a function of  $\log \alpha_{ls}$ .

For example, we suppose that those animals that need to struggle with their prey would have a greater  $k$  than ones feeding on more passive or vulnerable prey. As we deal with groups of species where the size is the main distinguishing characteristic, we expect  $k$  not to vary much between the species.

The constant  $u$  represents the ease of surveying the territory. This constant depends, as already suggested, on the openness of the environment. The better the visibility, the less additional energy is needed in order to achieve a comparable level of effective search. The absolute costs of intensifying the searching also depend on the area: a surveying method that increases the surveying costs by a certain percentage can have widely different effects on the energy budget of the animal, depending on the area to be surveyed. For the present we assume that the size of the territory remains a constant proportion to the size of the animal, which is to be expected if resources of different sizes are equally abundant.

Thus, the constant  $u$  appears to be able to generate predictions; so, we examine how the abscissa of the  $G = 0$  point in figure 3 changes as a function of  $u$ . The analytical form of this function was already noted to be

$$\log \alpha_{ls} = - \frac{1}{1 + u} \log k. \tag{4}$$

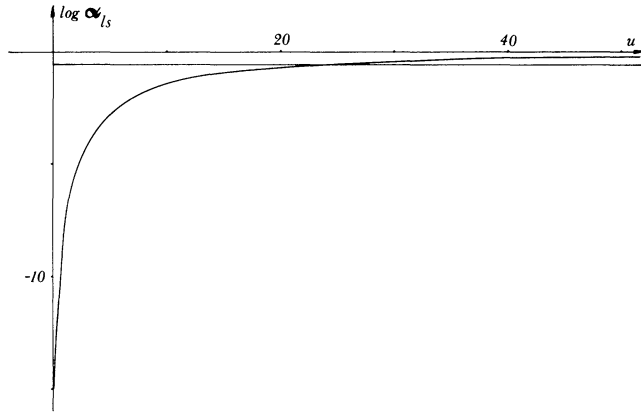


FIG. 4.—The abscissa of the  $G = 0$  point in figure 3 as a function of  $u$ , when  $a = 1$  and  $k = e^{15}$ . Above the  $\log \alpha_{ls} = \log 0.54$  line the coexistence of the species would normally not be possible due to resource competition alone.

The graphical presentation of this function is in figure 4.

When  $u$  approaches 0 (e.g., the environment becomes so open that even relatively small items are easy to observe), the minimum value for  $\alpha_{ls}$  which still makes interspecific territoriality feasible approaches a value solely dependent on  $k$ , as one would expect. From this point the curve rises rapidly and asymptotically approaches the  $u$ -axis. Species with a resource competition coefficient much larger than  $\frac{1}{2}$  cannot coexist anyway. (MacArthur and Levins 1967; their calculations showed that the limiting value for the resource competition coefficient is about 0.54 when the resource utilization curves are normal and have an equal variance.) Thus there will be some maximum value for  $u$  beyond which interspecific aggression plays no role in determining the limiting similarity of coexisting competitors.

In making predictions and more detailed biological interpretations, both axes should be expressed in units that can be measured and that have a readily understandable biological interpretation. Unfortunately,  $\log \alpha_{ls}$  does not fill these conditions very well. A quantity which is easier to measure and to understand is the size of an organism. If the ordinate could be converted from logarithms of resource competition coefficients to ratios or differences of body sizes, we would be rather well equipped to test the model.

MacArthur and Levins (1967, p. 380) concluded that if the resource utilization curves of species are normal, with equal height and equal variance, the resource competition coefficient of two species could be expressed as  $\alpha = e^{-D^2/2H^2}$ , where  $D$  is the distance between the peaks of the utilization curves and  $H$  is a parameter related to the variance. Then  $\log \alpha = -(1/2H^2)D^2$ , where  $-(1/2H^2)$  is a constant. If we call this constant  $-a^{-2}$ , then  $D = a\sqrt{-\log \alpha}$ .

Because the model of MacArthur and Levins (1967) was built exclusively on resource competition, their  $\alpha$  is equivalent to our  $\alpha_{ls}$ . The typical presence of constant size ratios in an array of coexisting and structurally similar species was already noted to indicate that the shape of the utilization curve tends to remain constant on a logarithmic scale. This means that we need to make a square root transformation of

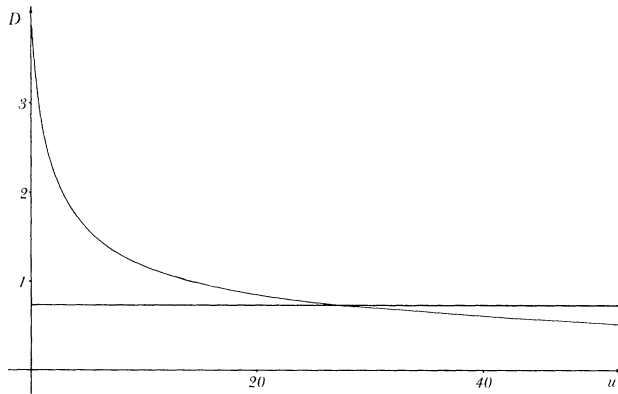


FIG. 5.—The expected relative size difference between the closest competitors (the maximum of the two curves) as a function of  $u$ . The constants  $a$  and  $k$  have the same values as in figure 4.

the ordinate to get from the logarithm of the resource competition coefficient to  $D$ , the difference between the peaks of utilization curves on a logarithmic scale. This should in turn be in some simple relation to the difference between the sizes of the species. We specifically assumed that the optimum food size is a constant proportion to the body size (see also Hespeneide 1973). Then  $D$  also represents the difference of the body sizes on a logarithmic scale. Thus the equation

$$D = a\sqrt{-\log \alpha_{ls}} = a\sqrt{[1/(1 + u)] \log k} \tag{5a}$$

gives the difference of sizes at the point when interspecific territoriality begins to be feasible. By taking the maximum of this curve and the constant function

$$D = a\sqrt{-\log 0.54}, \tag{5b}$$

we get a general statement of the limiting size similarity between coexisting competitors.

The functions (5a) and (5b) are presented in figure 5. When (5a) < (5b), the limiting size similarity will be determined by resource competition alone. Then, interspecific territoriality can occur only at the contact zone between the ranges of two allopatric species and at the boundaries of habitats of two species that do not normally occur together.

The constant  $a$ —relating the functions to the variance of the resource utilization curves—is only a scaling factor. It affects both functions in a similar manner and thus can have any value without affecting the biologically interesting features of figure 5. Changing the value of  $k$  would change the location of function (5b) relative to the function (5a) upward when  $k$  is decreased, downward when it is increased. Doing this, one can see that the range of environments where interspecific territoriality is predicted to have bearing on the limiting size similarity is an increasing function of  $k$ . This would indeed be expected without any modeling. What would not be equally easy to see by intuitive thinking alone is that the response pattern is also predicted to depend on  $k$ . When  $k$  is small, interspecific territoriality is expected to be important only within a narrow range of open environments. The transition from a situation

where resource competition is the sole factor determining the limiting similarity to a situation where interspecific territoriality is important should then be sharp and distinct. With large values of  $k$  there is expected to be a wide range of environments where interspecific territoriality will have some bearing to limiting similarity, but the increases in differences in relative size due to such aggression should be small. As the environment becomes more easy to survey, the contribution of interspecific territoriality increases in an accelerating manner. Distinct changes in differences in relative size should be caused by this acceleration, but the point where the interspecific territoriality begins to affect the limiting size similarity should be difficult to detect.

The expected pattern of size differences with large values of  $k$  is further complicated by limited similarity due to resource competition, as discussed by MacArthur and Levins (1967) and May (1973). They were concerned with the value of the competition coefficient at which a permanent coexistence of all species is barely possible. Obviously, the minimum value of the competition coefficient that suffices to preclude the intrusion of an additional species between two established ones must be smaller than actually existing values, and so the distance between actually coexisting species has a maximum value as well as a minimum one. Thus, situations where species are slightly less similar than the  $\alpha = .54$  limiting similarity of MacArthur and Levins (1967) can occur due to resource competition and random factors affecting the optima of the species. For example, three species arrays are stable with the overlaps between adjacent species ranging from  $\alpha = .54$  to  $\alpha \simeq .84$ . The function (5b) is therefore to be interpreted as a family of lines, all having zero slope, ranging from the one presented in figure 5 to ones somewhat above it. With large values of  $k$  there should be a comparably wide range of environments (to the left of the intersection of functions [5a] and [5b]) where interspecific territoriality is just a potential eliminator of species compositions that could—but might or might not—exist on the basis of resource competition alone.

#### PREDICTIONS AND TENTATIVE TESTS

The first thing a model must do is to explain the kinds of observations that stimulated its development. First, we noted two wetland communities, the marsh and the boreal bog. In the marsh the community of rails and herons showed no gaps, while gaps were found in two boreal communities. The model explains this by noting that since the marsh grasses are as tall as the tallest heron, and hence make the environment indefensible with no aggression possible, intermediate sized species coexist in a complete Hutchinsonian sequence.

We have also noted two cases in which a habitat has small to medium-sized species with a dense packing and a single very large species that appears to belong to the same ecological group. The model leads us to expect that the small ones live in an at least moderately covered environment, whereas for the larger species the environment must represent the open type. This is plausible. On open peatlands, there is a layer of *Sphagnum* hummocks, sedges, and occasional brush which provides cover for the smaller species but not for the cranes, nor for a bird half of its weight if such a bird were present. An analogous argument seems valid also for dabbling ducks and the swan in their habitat.

Our figure 5 is itself a testable prediction of the model. It is necessary only to find habitats which have similar resources but differ with respect to coverage. Heath and shoreline habitats differing in the degree of stoniness meet this requirement.

Dow's (1977) study of *Manorita melanocephala*, an Australian bird, is a case study relating aggression to competitive exclusion and habitat characteristics. The species was found to be aggressive against all other passerines in the community. In sparse woodlands with little understory the behavior was successful, resulting in monopoly, but in denser habitats the smaller passerines escaped aggression. According to Dow, the competition by the smaller species and the expenditure of energy in futile aggression had a depressive effect on the population density of *Manorita*. A similar mechanism might be included in the relations between bird species diversity and foliage height diversity (MacArthur and MacArthur 1961) or total vegetation cover (Blondel et al. 1973; Willson 1974).

The effectiveness of interspecific aggression may also depend on habitat characteristics in small mammals. Terman (1974) showed experimentally that *Sigmodon hispidus* can, by aggression alone, exclude *Microtus ochrogaster* from open and easily-surveyed habitats, but the two species coexist in highly structured experimental conditions. The voles *Clethrionomys rutilus* and *C. rufocanus* may follow a similar pattern in Finland (H. Henttonen, personal communication). Both species reach peak densities synchronously in most of northern Finland, covered by coniferous forest, but in the very northern stunted mountain birch forests *C. rutilus* reaches peak densities only if the density of *C. rufocanus* is low. Of these species, *C. rufocanus* has been observed to be aggressively dominant in test situations.

These cases encourage further testing of the model. The model may also provide some insight to patterns in species diversity. For instance, Järvinen and Väisänen (1976) found that nonforested habitats were generally very heterogeneous compared with different forests in northern Finland, as judged on the basis of the composition of the bird community. It is possible that the observation is related to the present model; the forests apparently represent the covered habitats, but the nonforested ones include several habitats where resource monopoly may be important.

#### SUMMARY

Starting from MacArthur's hypothesis that interspecific aggression will occur whenever one of the species can expect to gain from this behavior, a model is built explicating the circumstances under which the limiting size similarity cannot be expected to be solely caused by resource competition. We develop the model from considerations of shorebird and waterfowl communities which inhabit open defensible terrain and in which gaps occur in the sequence of size similarities. In shorebird communities there exists a gap of two or three species between the cranes and the sandpipers; in waterfowl communities the gap is three species. In both communities natural history data suggest that interspecific aggression by the largest member of the sequence has eliminated intermediate sized species. Similar gaps do not occur in the rail-heron community, which inhabits an indefensible habitat.

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