Interference Competition and Niche Theory

(population dynamics/adaptive strategies/resource gradients)

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ABSTRACT A linear model of interspecific competition
with separate parameters for exploitation and interference
is deduced. Interference is assumed to have a cost and an
effect. The interfering species realizes a "profit" if some
resources, which the species interfered against would have
utilized, are made available as a result of the interference.
Interference is favored when its cost is small, its effect is
high, and the resource overlap with the species interfered
against is high. Interference is likely to be an alternative
strategy to high exploitation efficiency. The incorporation
of interference into niche theory clarifies the competitive
phenomenon of unstable equilibrium points, excess
density compensation on islands, competitive avoidance
by escape in time and space, the persistence of the "pru-
dent predator," and the magnitude of the difference
between the size of a species' fundamental niche and its
realized niche.

Interspecies competition has long been recognized to be of
two types, exploitation competition and interference competi-
tion (1, 2). Nonetheless, the "niche theory" of competition in
communities (3) assumes that exploitation (or utilization) of
"resources", e.g., prey species or habitat types, primarily
determines ecological segregation. Most actual field or labora-
tory studies of interspecies competition show, however, that
interference was present, and often played the more important
role in determining abundance and distribution.

Interference was the major component of competition in the
classical studies of Gause (4) on yeast and *Paramecium*, and of
Park (5, 6) on *Tribolium*. It was mediated through metabolic
by-products (alcohol) in yeast, through allelochemicals in
Paramecium (7), and by egg predation between species of
Tribolium.

In the field, interspecific interference competition, e.g.,
aggression or poisoning, has been found to be important be-
tween species of birds (8–12), mammals (13–20), and inverte-
brates (21–24). In contrast, most, if not all, evidence for ex-
ploitation competition for food is inferential.

Given this taxonomically broad catalogue of interference
competition, it is imperative that interference competition be
explicitly included in current niche theory. To this end, we
shall develop a mathematical model of competition that sep-
arates the contributions from exploitation and interference.
By considering the effect of interference on population
adaptedness (equilibrium density), it will be possible to pre-
dict the circumstances whereunder interference competition
may evolve from exploitation competition.

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Competition models and the evolution of interference

The differential equations of Lotka and Volterra are fre-
quently used to model competition and they also serve as the
basis of niche theory (25), but this model has some weaknesses.
It does not account for sex, age structure, seasonality, thresh-
olds, time delays, stochastic effects and nonlinearities. None-
theless, the model is simple and general. If its approximate
nature is appreciated, it can serve as an excellent vehicle to
understanding. In the following, we shall assume that this
model holds globally; and we shall modify it to account for
both exploitation and interference.

Consider pure exploitation competition in which two popula-
tions, whose densities are denoted by N_i where $i = 1,2$ ex-
ploit some common resources. When the ith population is
alone, it has a low density exponential rate of growth r_i. As it
increases in population density, it depletes the resources and its
rate of growth is decreased by an amount r_i/K_i with the addi-
tion of each individual, such that its growth rate becomes zero
when N_i equals K_i. If members of the jth population are
present, they will deplete some of the resources used by the
ith population for its growth. In units of r_i/K_i, the rate of
growth of the ith population will be decreased by an amount
α_{ij} by each member of the jth population. (Note that α_{ij} in our
usage is restricted to "resource" overlap.) This yields the
following differential equations for population growth
regulated by resource depletion,

$$\frac{1}{N_i}\frac{dN_i}{dt} = \frac{r_i}{K_i}(K_i - N_i - \alpha_{ij}N_j), \quad i, j = 1,2, i \neq j. \quad [1]$$

With interference competition, the individuals of population
i are of a modified phenotype (and genotype) such that they
interfere with individuals of population j. In general, this will
cost the individuals of population i something in terms of the
rate of resource exploitation and therefore the rate of popula-
tion growth, since they will have to spend some time and
energy in acts of interference which consume time and energy
that could otherwise be devoted to resource exploitation.
Also, these acts of interference could lead to injury or death.
Permanent morphological or physiological modification of
species i may also be a necessary prerequisite for interference;
this would likely impose a fixed cost independent of the num-
ber of acts of interference, since a modification of morphology
or physiology could reduce efficiency in resource exploitation.
The behavioral cost of interference depends on the density of
the population interfered against, whereas the physiological
and morphological cost is independent of the density of this
population. Using an economic analogy, the first is a labor
cost and the second is a capital cost.

If physiological and morphological cost reduce the exploitation efficiency of the interfering population, then each interfering individual will cause a greater reduction in his own population's growth rate. In units of r_i/K_i, let f_i be the additional reduction of growth rate that a member of an interfering population causes on its own population's growth rate. The single-species growth equation for this population is:

$$\frac{1}{N_i}\frac{dN_i}{dt} = \frac{r_i}{K_i}(K_i - (1+f_i)N_i). \qquad [2]$$

The growth rate becomes zero when N_i equals $K_i/(1+f_i)$; thus, the fixed cost leads to a reduction of a population's carrying capacity.

In addition to the constant fixed cost, each act of interference will also have a cost. Per unit time, the number of interference acts will be proportional to the density of the population that is interfered against. In units of r_i/K_i, let c_{ij} be the reduction of the ith population's growth rate by its interference against a member of the jth population.

Interference by population i will have an effect on the growth rate of population j. This effect must be proportional to the density of the interfering population. In units of r_j/K_j, let e_{ji} be the reduction of the jth population's growth rate by the interference of a member of the jth population.

Putting this together, the growth equations for two exploitation competitors with reciprocal interference, may be compactly expressed as

$$\frac{1}{N_i}\frac{dN_i}{dt} = \frac{r_i}{K_i}K_i - (1+f_i)N_i - (\alpha_{ij} + c_{ij} + e_{ij})N_j \qquad [3]$$

which reduces to

$$\frac{1}{N_i}\frac{dN_i}{dt} = \frac{r_i}{K_i}(K_i - \Sigma_j\alpha_{ij}N_j - \Sigma_j\phi_{ij}N_j) \qquad [4]$$

where

$$\alpha_{ij} \equiv \begin{pmatrix} 1 & \alpha_{12} \\ \alpha_{21} & 1 \end{pmatrix} \qquad [5]$$

and

$$\phi_{ij} \equiv \begin{pmatrix} f_1 & c_{12}+e_{12} \\ c_{21}+e_{21} & f_2 \end{pmatrix} \qquad [6]$$

The α matrix accounts for competition that results from the exploitation of common resources; its elements are relatively easy to measure with an "overlap" approach (3). The ϕ matrix accounts for competition that results from interference interactions; its elements could be very difficult to measure, for these might involve pheromones or allelochemicals that are relatively "invisible" to human observers. The "community matrix," which gives the dynamics of the competitive interaction, is the sum of the α and the ϕ matrices. Inversion of the community matrix gives the equilibrium population densities of the competitors as

$$\bar{N}_i = \Sigma_j(\alpha_{ij} + \phi_{ij})^{-1}K_j \qquad [7]$$

where $\bar{N}_i$ is the equilibrium density of the ith competitor.

Interference competition should evolve when it promotes fitness, or is "profitable" (26, 27). We shall make this precise by assuming that interference competition should evolve when it increases population adaptedness, as measured by equilibrium density, that is, population i will evolve interference if

it can thereby increase its equilibrium density in the community.

This vaguely suggests some form of group selection, since the population is being considered as a whole, but MacArthur (28) has shown that natural selection operating on differences in Darwinian fitness between genotypes ultimately leads to an increase in a population's carrying capacity if resource renewal rates are unaltered. However, it is not generally true that increases in carrying capacity are strictly the result of increases in the average individual fitness, since there is a problem with "altruistic" interference and interference effecting resource renewal rates.

If one or a pair of exploitation competitors interferes with the other, it will reduce the equilibrium density of the other and free some resources the other could have consumed. These freed resources are made available to the interfering population; they may more than offset the cost of its interference and thereby increase its equilibrium density.

If one species (A) has individuals of a particular genotype which are capable of overexploiting the shared resources and thereby lowering resource renewal rates for all genotypes, e.g., when resources grow logistically, then this genotype will replace the alternatives if one assumes no overdominance. However, the resulting equilibrium density of species A in the 2 species competitive system may become lower. The incorporation of interference into this system is complex and beyond the scope of the present paper. Interference is altruistic when some members of a population pay the cost of interspecific interference but the resources they free are shared equally by all members. This puts the interfering individuals at a selective disadvantage within their own population, yet increases the total population density. Such interference could only evolve through selection at the level of groups. In most cases of interference, however, it is expected and necessary by Darwinian selection that the interfering individuals would get the greater share of the "profits", i.e., the freed resources, from their individual acts of interference. This would be the case for organisms that are sessile, relatively immobile, or occupy a home range or territory. It would also be the case for organisms that use predation as the mechanism of interference. Since most cases of interference fall in these categories, individual selection accounts for most interference competition.

The evolution of interference competition may be mathematically related to the model of competition developed in this paper. Assume that two populations are engaging in exploitation competition. Initially, their community matrix is just the α matrix. Now assume that the first interferes with the second. This will add to the α matrix, a ϕ matrix of the form

$$\begin{pmatrix} f_1 & c_{12} \\ e_{21} & 0 \end{pmatrix}.$$

This will produce a change in the equilibrium densities of the two populations so that

$$\Delta\bar{N}_i = \Sigma_j[(\alpha_{ij} + \phi_{ij})^{-1} - \alpha_{ij}^{-1}]K_j \qquad [8]$$

where $\Delta\bar{N}_i$ is the change in the equilibrium density of the ith population. If $\Delta\bar{N}$ is positive for the interfering population, the interference will increase fitness and should evolve; if this quantity is negative, the interference is maladaptive and should not evolve.

The $\Delta\bar{N}_i$ are functions of the α and ϕ matrices and the K vector. Thus they are functions of seven parameters. It is
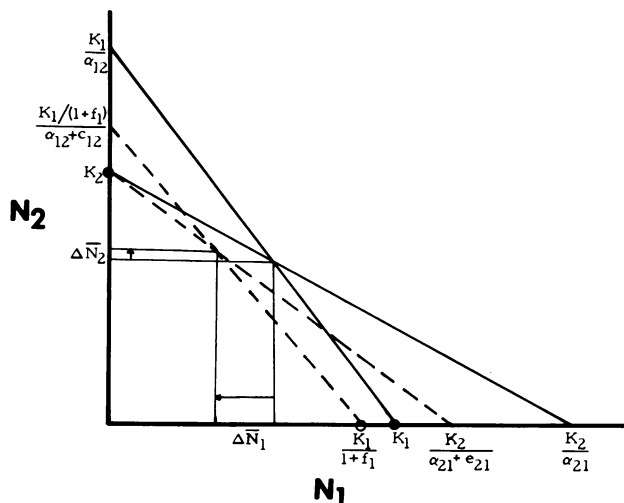
FIG. 1. A hypothetical exploitation competition system that develops interference competition. The *solid circles* represent the carrying capacities under exploitation competition. The *solid lines* are the zero isoclines under exploitation competition. Population 1 interferes with population 2. This lowers the carrying capacity of population 1, represented by the *open circle*. It also shifts the zero isoclines of both populations, represented by the *dashed lines*. The 2 species equilibrium point under exploitation competition is the intersection of the two solid lines. With the addition of interference competition, the 2 species equilibrium point shifts to the intersection of the two *dashed lines*.

possible to use Eq. 8 to map out the region of this seven-dimensional parameter space where the ΔN of the interfering population is positive.

Equivalently, the foregoing algebraic analysis may be carried out graphically. Fig. 1 shows how interference by population 1 against population 2 changes the zero isoclines and thus the equilibrium densities of the two populations. In this particular case, interference is maladaptive and therefore would not evolve, i.e., ΔN_i is negative.

It can be shown that low f_i and c_{ij} and high e_{ji} favor the profitability (increase ΔN_i) of nonreciprocal interference by population i against population j. This profit also increases sigmoidally with increases in α_{12} and α_{21}. The effect of K_i and K_j on the profit of interfering is more complex. A high value of K_i also favors nonreciprocal interference by population i against population j; but at very high values of K_i, this tendency is reversed and the change in the increase of equilibrium starts to drop. This happens because very high values of K_i allow the ith population to exclude or drastically reduce the jth population purely by exploitation efficiency, making the cost of interference an extra burden. Thus, for either interference or exploitation, a high K_i is always favorable in competitive systems. At low values of K_j interference by i is equally unnecessary, and at much higher values of K_j the density of j is so high that the profit of interference declines precipitously. The maximum profits from interference occur at intermediate values of K_j. Under certain conditions interference can still be profitable even when $c_{ij} = e_{ij}$.

Interference competition works by freeing resources for the interfering population. Obviously, a population that interferes against a population that is not a resource competitor pays a cost that returns nothing. Such interference will not evolve. Yet it is possible that interference may exist in the

absence of exploitation competition. Elephants step on ants and beaver ponds may flood the burrows of smaller rodents. Such "unintended" interference may be termed "gratuitous."

Interference works best when its costs are low and its effects high. Preadaptations may influence the cost–effect ratio. For example, a species which had evolved morphological weapons for prey capture or predator defense, such as horns, teeth, claws, large size, or great swiftness, could easily employ these for aggression interspecific interference with low cost and great effect. A population that interferes intraspecifically may be highly preadapted for interspecific interference.

Predation interference against the eggs or immature forms of a resource competitor has low, or negative cost, and great effect. This is particularly common in non-territorial species. For example, *Tribolium* beetles eat the eggs of other species (29), and aquatic invertebrates and fish frequently consume the young of their competitors.

The incorporation of interference competition into niche theory helps to explain other competitive phenomena. First, unstable competitive equilibrium points, such as those that occur in laboratory *Tribolium* systems, are impossible to explain with the resource or niche overlap approach (3). If the elements in the community matrix are solely the α's from resource overlap, it is impossible for the product $\alpha_{12}\alpha_{21}$ to exceed unity, a necessary condition for the existence of an unstable equilibrium point. By adding interference competition to the competitive interaction this necessary condition may be satisfied, since

$$(\alpha_{12} + c_{12} + e_{12}) \cdot (\alpha_{21} + c_{21} + e_{21})$$

may clearly exceed unity.

Second, the ecological literature is replete with statements that species avoid competition by operating in different spaces or at different times. In regard to resource competition, these are absurd. If the species are exploiting the same resource at different times and in different species, then they have not escaped resource competition. Whereas, if they are exploiting different resources, then it is more straightforward to state simply that they have escaped resource competition by exploiting different resources. With interference competition, however, escape in time or space is more meaningful since species using common resources but at different times and places, avoid direct interactions, and therefore interference. When potential resource overlap is high, mutual interspecific interference may evolve, leading to interspecific territoriality. The separation of individuals of the two species within a continuous habitat patch may benefit both, by allowing individuals of each species to avoid the cost of interference, yet still reap a portion of the profits (30). Interspecific territoriality may also allow individuals of each species to better predict the particular nuances of resource microdistribution and renewal rates within their specific territories. When interference is unilateral between two species with broadly overlapping fundamental niches, individuals of the subordinate species may become restricted to habitats or activity periods in which interference is unprofitable to the dominant species. This situation could result in abutting distributions and divergence in each species' resource use.

Third, consider the trade-offs involved in competitive fitness. It is adaptive for a population to be good at resource exploitation, and also adaptive for it to be good at interference competition. However, a species cannot be superior at
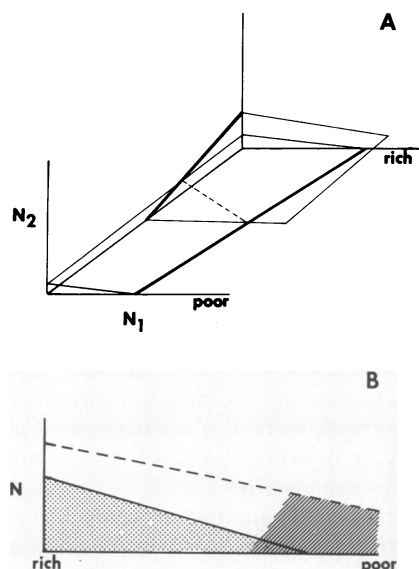
FIG. 2. (*A*) A hypothetical case of competition along a re-source density gradient. The *heavy lines* are the carrying capacities of the two species; these are higher at the rich end of the gradient. Population 1 is an exploitation competitor; it has high K but is greatly affected by the interference of population 2. Population 2 has low K, but it can interfere with low cost and great effect. Population 2 excludes population 1 at the rich end of the re-source gradient. The *dashed line* represents coexistence of the two populations. At the poor end of the gradient, population 1 excludes population 2. (*B*) Population density along the re-source gradient. The *dashed line* represents the single species equilibrium (the carrying capacity) of population 1; the *solid line* represents the single species equilibrium of population 2. The *stippled area* represents the equilibrium density of population 2 in the presence of 1, and the *lined area* represents the equilibrium density of population 1 in the presence of 2.

everything. A generalist may be adequate is a number of areas. A specialist will totally sacrifice many talents for excellence in a single area. Since modifications in physiology, morphology, and behavior are probably necessary for interference competition, it is likely that most populations will specialize in either interference or exploitation. We assume this to be true. Exploitation competitors will have high K. Interference competitors will have low K but will be able to interfere with low cost and high effect.

This may help explain why many predators do not over-exploit their prey, i.e., the problem of the prudent predator. If interference competitors sacrifice ability in exploitation competition and if the limiting resource is a prey species, then the prey species will benefit from interference competition at a higher trophic level. Gilpin and Case (31) have demonstrated this with a two prey and two predator model. Of course, prudence is also likely to be the result of predator–prey co-evolution or group selection (32).

Density compensation occurs when one population leaves a competition community and the other populations increase their density. From niche theory, we expect the total density of all competitors to go down when one population leaves, since the remaining populations are assumed to be less efficient at exploiting the resources previously consumed by the absent population.

Sometimes, however, the total density of a competition community increases when a member disappears. This is especially common on island ecosystems (36, 37) and is readily explained if the missing member of a competition community is an interference strategist. The populations that then exploit the freed resources may be more efficient, and the total community density may increase. It is also easy to see how this would happen on islands. Interference competitors among vertebrates are likely to be large and relatively immobile, with low dispersal abilities. Thus, they would be less likely than exploitation competitors to colonize islands.

Interference competition also clarifies competitive relations in nature along resource and habitat gradients. Assume that an exploitation specialist and an interference specialist coexist in such an arena. Alone, the exploitation competitor would everywhere be able to maintain a higher population density than the interference competitor. If the interference competitor is to be able to dominate or exclude the exploitation competitor, it must do so in those regions where resources are richest, i.e., where both populations have their highest K. Such a situation is depicted in Fig. 2*A*. The interference competitor excludes the exploitation competitor at the rich end of the resource gradient; the reverse is true at the poor end of the gradient.

If "fundamental niche" is indicated by the carrying capacity of a species along a resource gradient and if "realized niche" is indicated by the equilibrium density of a species in the presence of its competitors along a resource gradient, then the contraction from the fundamental niche to the realized niche is likely to be small for an interference competitor and high for an exploitation competitor. That is, populations that are dominant by virtue of interference competition are likely to suffer little niche contraction in the presence of competitors. This is illustrated in Fig. 2*B*. Empirically, Morse (33) found that subordinate bird species adjusted their foraging behavior in the presence of larger dominant species; however, the converse did not appear to be true. He found a similar situation for warblers on small islands off Maine (34), indicating that the insular niche expansion observed by Crowell (35) and others may simply be an immediate effect of release from interference by dominant competitors. Willis' (8–12) observations on tropical birds following army ants also support our predictions. He found that plain-brown woodcreepers (*Dendrocincla fuliginosa*) forage more frequently in a narrow but productive region near the ground in the absence of the large and dominant ocellated antthrushes (*Phaenostictus meleannani*). When antthrushes are present, woodcreepers move to higher or to peripheral and less productive zones.

In conclusion, it appears from the foregoing that when a species is faced with a situation in which it must compete for common resources either by increasing its exploitation efficiency or else by eating, killing, poisoning, or otherwise interfering against its competitor, it frequently evolves in the direction of this second strategy. One consequence of this is that the relative abundance of a community of competitors will probably not be that which maximizes the use of available resources (38). This does not imply that there will not be selection for greater efficiencies of resource utilization, in both dominant and subordinate species, but only that under many circumstances the profits may be small compared to the more rapid returns of interference competition.

1. Birch, L. C. (1957) *Amer. Natur.* **91**, 5–18.

2. Miller, R. S. (1967) *Advances in Ecological Research*, ed. Cragg, J. B. (Academic Press, London), Vol. 4, pp. 1–74.
3. Levins, R. (1968) *Evolution in Changing Environments* (Princeton University Press, Princeton, N.J.).
4. Gause, G. F. (1934) *The Struggle for Existence* (Williams and Wilkins, Baltimore, Md.).
5. Park, T. (1954) *Physiol. Zool.* **27**, 177–238.
6. Park, T. (1962) *Science* **138**, 1369–1375.
7. Gill, D. E. (1972) *Amer. Natur.* **106**, 461–471.
8. Orians, G. H. & Willson, M. F. (1964) *Ecology* **45**, 736–745.
9. Morse, D. H. (1971) *Wilson Bull.* **83**, 57–65.
10. Willis, E. O. (1966) *Ecology* **47**, 667–672.
11. Miller, A. H. & Bock, C. E. (1972) *Condor* **74**, 284–294.
12. Terborgh, J. & Diamond, J. (1970) *Wilson Bull.* **82**, 29–52.
13. MacMillen, R. E. (1964) *Univ. Calif. Publ. Zool.* **71**, 1–66.
14. Miller, R. S. (1964) *Ecology* **45**, 256–272.
15. Lidicker, W. Z. (1966) *Ecol. Monogr.* **36**, 27–50.
16. Cameron, G. N. (1971) *J. Mammal.* **52**, 288–296.
17. Murie, J. O. (1971) *J. Mammal.* **52**, 181–186.
18. Heller, H. G. (1971) *Ecology* **52**, 312–319.
19. Schaller, G. B. (1972) *The Serengeti Lion* (Univ. Chicago Press, Chicago and London).
20. Teleki, G. (1973) *The Predatory Behavior of Wild Chimpanzees* (Bucknell Univ. Press, Lewisburg, Pa.).
21. Gubler, D. J. (1970) *J. Med. Entomol.* **7**, 229–235.
22. Colwell, R. K. (1973) *Amer. Natur.* **10**, 737–760.
23. Dingle, H., Highsmith, R. C., Evans, K. E. & Caldwell, R. L. (1973) *Oecologica* **13**, 55–64.
24. Preston, E. M. (1973) *Ecology* **54**, 469–483.
25. Vandermeer, J. H. (1972) *Annu. Rev. Ecol. Syst.* **3**, 107–132.
26. Emlen, J. M. (1973) *Ecology: an Evolutionary Approach* (Addison-Wesley, Reading, Pa.).
27. Hutchinson, G. E. & MacArthur, R. H. (1959) *Amer. Natur.* **93**, 133–134.
28. MacArthur, R. H. (1962) *Proc. Nat. Acad. Sci. USA* **48**, 1893–1897.
29. Sokoloff, A. & Lerner, I. M. (1967) *Amer. Natur.* **101**, 261–276.
30. Cody, M. L. (1974) *Annu. Rev. Ecol. Syst.* **4**, 189–211.
31. Gilpin, M. E. & Case, T. J. (1974) *Amer. Natur.*, submitted for publication.
32. Gilpin, M. E. (1974) *The Theory of Group Selection in Predator-Prey Communities* (Princeton Univ. Press, Princeton, N.J.).
33. Morse, D. H. (1970) *Ecol. Monogr.* **40**, 119–168.
34. Morse, D. H. (1971) *Ecology* **52**, 216–228.
35. Crowell, K. L. (1962) *Ecology* **43**, 75–88.
36. MacArthur, R. H., Diamond, J. & Karr, J. (1972) *Ecology* **53**, 330–342.
37. Case, T. J. (1974) *Ecology*, in press.
38. MacArthur, R. H. (1970) *Theor. Pop. Biol.* **1**, 1–11.