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Migration and Species Diversity in the Tropics

(birds/temperate zone)

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ABSTRACT If the young of a dominant species are subjected to disproportionately heavy predation, this, together with a limitation on food, can promote a high species diversity. This is seen among tropical birds, which are simultaneously exposed to both conditions to a far greater degree than are Temperate Zone species. Migration to the Temperate Zones during the spring provides a release from these restraints, while also precluding breeding in the Tropics.

The clutch size for most tropical passerine birds is smaller than that of related species of the Temperate Zone. Lack (1) proposed that this increase was due to greater day length during the breeding season in temperate as compared to tropical areas. In early summer a bird north of the Arctic Circle may have nearly 24 hr of daylight in which to feed nestlings (and birds in temperate latitudes will have considerably more day than night hours), while in the Tropics the amount of daylight does not vary significantly from 12 hr. Corroborative evidence is provided by studies of several species (e.g., *Corvus corax* and *Loxia curvirostra*; in ref. 2). However, this is not to say that day length is the sole factor regulating clutch size. Other factors are certainly involved, and some species do not show this latitudinal gradient [e.g., nocturnal birds, which might even be expected to show a reverse correlation (3)].

It also appears that in addition to usually having smaller clutches, tropical birds take longer to develop than those from the north, that is, incubation times and age at fledging are greater (4, 5). It has not been clear why this should be so, particularly since predation on nestlings in the Tropics is very much more intense than it is at higher latitudes. Ricklefs (6) has demonstrated that 75% or more of many tropical passerine nests fail to produce any young. Whatever the effects of predation on clutch size, one would expect it to shorten or accelerate developmental times (7).

Let us assume that the longer day length during the breeding season at higher latitudes produces a temporarily higher supply of whatever food resources the birds depend upon. This does not necessarily imply a higher annual productivity in temperate areas, merely a greater concentration of available energy during the late spring and early summer. The sharper the peak of resources, the greater the pressure for shortening developmental times, irrespective of clutch size or of multibroodiness (multibroodiness permits exploitation of an unusually favorable season without sacrificing the ability to withstand an unfavorable one). It is thus reasonable that growth should take less time north or south of the Tropics than within them. Conversely, in the Tropics, where a relatively more uniform pattern of abundance prevails, the populations of adult birds have, we may assume, ex-

panded to the upper limit supportable by the available resources. When the young birds hatch, therefore, there can be available for them only a small amount of the high protein resources beyond what is normally required to support the population of adult birds. The developmental period of the young must as a consequence be stretched out in the Tropics.

Morton has recently (8) shown that part of this increase in developmental periods for some species of tropical birds may also be a result of differences in the types of food available to the birds. Many adult tropical birds feed exclusively on fruit, which is more abundant in the Tropics than in temperate latitudes, especially during the breeding season in the latter. However, it would be disadvantageous for those fruit-eaters to feed their growing young a diet composed only of fruit, which is relatively low in protein. In fact, they also feed insects to their young.

As autumn approaches in temperate latitudes, waning food resources compel some species to return to the Tropics (i.e., those areas where mean monthly variations in temperature are less than the mean daily variations). Why don't these migrants breed again while in the Tropics? We propose that the resources available in any one day in the Tropics are insufficient to maintain the more rapid developmental rates of birds adapted to the seasonally richer temperate zones. Hence these species are compelled to continue an annual movement north or south from the Tropics if they are to breed successfully. The key implication of our assumption regarding differences in springtime resources between the Temperate Zone and the Tropics is that in the latter the absolute amount of energy available on a daily basis does limit fledgling developmental rates.

In addition to necessitating the return of temperate passerines to the north (or south) to breed, the meager tropical peak of protein resources available to feed avian young also has an important effect on fledgling predation which, we claim, generates a community whose species diversity is simultaneously limited by both resources and predators.

Predation is one of the major selective forces involved in reducing nestling periods; it follows that longer nestling periods will result in greater nestling losses (9). For instance, in Costa Rica, more nests of the red-winged blackbird (*Agelaius phoeniceus*) fail to fledge any young than do those in the United States (Orians, in ref. 10). Ricklefs (6) has shown that the failure to fledge any young is the result of predation. Such large reductions in the total number of nestlings must certainly liberate some food resources. Yet, it seems certain that competition among the parents of the remaining young (which would favor any acceleration in the

growth of their nestlings) will almost immediately eliminate this surplus.

Predation, however, may alter the competitive pattern by which the various species garner any liberated resources. Assuming, in the absence of predation, that the most common bird species is also the best competitor (highest alpha coefficients), it follows that it would succeed in obtaining the highest proportion of the new resources. Since the fledging period of its young would then be shortened, it would recruit a larger proportion of young into the adult population. Mathematically this is illustrated by the Lotka-Volterra equations

$$dN_i/dt = r_i N_i [(K_i - N_i - \alpha_{ij} N_j)/K_i]$$

$$dN_j/dt = r_j N_j [(K_j - N_j - \alpha_{ji} N_i)/K_j]$$

where the recruitment rate (dN_i/dt) is expressed as a function of N_i , the number of young of species i at time t ; K_i the carrying capacity of the environment for the young of species i ; r_i the intrinsic growth rate of the young of species i ; and α_{ij} , the competitive effect of the young, as determined by the parents, of species j on species i . If α_{ji} is greater than α_{ij} , over time N_i will approach K_i while N_j will approach zero.

Consider now the effect of predation when it disproportionately reduces the young of the dominant species. The overall competitive influence of this species will be reduced, even through the competitive abilities (α) of the individuals of the species will not be altered. In terms of the Lotka-Volterra equations, selective predation will reduce the N_i of the dominant species and thus reduce the recruitment rate of that species; more importantly, however, it will lower the value $\alpha_{ji} N_i$, a measure of interspecific competition. This reduction leads to an increase in the recruitment rate of the competitor species, with a resulting increase in species diversity in the community (11, 12).

Disproportionate predation on the young of the dominant species, therefore, interacting with limited food resources, can provide a mechanism that maintains an avian community of high species diversity. The seemingly disparate phenomena of migration of temperate passerines and avian species diversity in the Tropics are thus shown to be related by the more uniform patterns of food available to feed avian young in the Tropics.

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