The GAD activity of cortical gray and white matters of human cerebrum was differentially affected by the addition of $10^{-3}M$ AOAA to the regular assay medium. The GAD of cortical gray matter was inhibited 70 percent, and that of white matter was stimulated 80 percent by $10^{-3}M$ AOAA (Table 1). Glial cells grown in culture and gliomas of human brain removed at surgery had lower GAD activities than cortical gray matter. These activities, however, were stimulated approximately fourfold by $10^{-3}M$ AOAA (Table 2).

To date, all the evidence favors the existence of at least two forms of GAD in mammalian tissues. It has been shown that glial tumors contain both γ-aminobutyric acid (GABA) and GAD activity (*8*) and that the GABA system is present in normal glial cells as well (*9*). Now we have shown the presence of GAD activity stimulated by AOAA in human glial cells grown in culture, in gliomas, and in white matter. The magnitude of stimulation by AOAA was consistent with the suggestion of a glial localization of GAD II, which is present in several nonneuronal tissues and in developing chick embryo brain (*2*). Further studies are being made of the functional significance of the presence of GAD II in glial cells. The rapid isotopic GAD assay may be a useful adjunct in helping distinguish at surgery glial tumors metastasizing from other sites if GAD II should be found to be higher in the glial tumors.

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2 January 1970

Clutch Size in Birds: Outcome of Opposing Predator and Prey Adaptations

Abstract. *A model is proposed to explain clutch size in birds as the outcome of the interaction between predatory adaptations of birds to increase their feeding efficiency and adaptations of their food resources to avoid predation. Variations in clutch size are consistent with the model. A modification that incorporates the seasonality of food resources is also discussed.*

Although Lack focused attention on the problem over 20 years ago (*1*), variation in clutch size among birds remains inadequately explained (*2*). Songbirds (Passeriformes) exhibit several patterns. (i) Hole-nesting birds generally lay one to two more eggs per clutch than those which build nests in less-protected locations (*3*). (ii) Clutch size generally decreases as one approaches the equator; from five to seven eggs for open-nesting birds in arctic areas and four to five in temperate localities, to two to three eggs in tropical latitudes. (iii) Within the tropics there are local gradients with respect to rainfall (*4*); however, clutch size does not change as one moves up mountains into cooler climates (*5*). Within temperate areas, birds inhabiting stable "coastal" climates tend to have smaller clutches than those exposed to more variable "continental" climates (*6, 7*).

Currently favored to explain variations in clutch size is Lack's "food-limited" hypothesis (*7*) which treats food availability, or the rate at which adults can gather food, as the factor which limits clutch size. Cody (*8*) modified the theory to incorporate the allocation of time and energy between foraging behavior, which affects clutch size, and other behavior involving predator avoidance, self-maintenance, and competitive ability. Murphy (*9*) and Williams (*10*) have pointed out that the intensity of reproduction, which is reflected in clutch size, may alter the survival of the adults, hence the probability of future reproduction. Such compromise must be incorporated into any complete theory of clutch size. Lack's theory, even as currently modified, postulates that clutch size is adjusted to the optimum rate at which the parents can gather food. Thus, if this rate is maximized through natural selection, clutch size is limited by the abundance, or availability of the food resource.

If Lack's hypothesis is true, we must ask what determines the absolute availability and variations of food resources which produce the diversity of clutch sizes among birds. Differences in local primary productivity cannot be solely responsible because, for example, species of arid and humid regions in the temperate zone have similar clutch sizes although productivity of desert vegetation is but a small fraction of that of eastern forests (*11*). Moreover, the ability of adult birds to gather food resources cannot be treated as a simple function of prey availability but must be considered as the outcome of evolutionary responses of the predator and prey to each other. Birds evolve to maximize the efficiency with which they can exploit food resources. Equally important, and generally neglected in considerations of clutch size, prey evolve to minimize the efficiency of their predators.

These considerations lead to a simplistic model of evolutionary interactions whose outcome is reflected in clutch size. The efficiency with which environmental food resources, or prey, are converted into offspring of the predator depends on the balance between predator and prey adaptations. Evolutionary changes in the foraging strategy of the predator will alter the environment of the prey and select for an evolutionary response, which tends to restore the original rate of exploitation of prey. The equilibrium which determines the mortality of the prey and the rate at which food is gathered by the predator will depend, in the final analysis, upon potential rates of evolutionary change and also upon constraints which limit the adaptability of the predator and prey.

We measure the outcome of the adaptive system from the standpoint of the predator by its clutch size (we assume all species to be equally efficient at converting gathered food into offspring). Perhaps most striking is not that clutch size varies among species, but that it is so constant. Among small passerines, for example, most of those which breed in the United States raise broods of four young. Yet these include flycatchers, foliage gleaners, ground

scratchers, bark probers, and others with very different feeding behavior; or they may inhabit eastern deciduous forests, mountain coniferous forests, midwestern grasslands, southwestern deserts, and so forth, over which net primary productivity varies tenfold or more (*11*). Similar uniformity of outcome resulting from systems of predator-prey adaptation of diverse species has been noted elsewhere (*12*).

If clutch size reflects the outcome of predator and prey adaptations, which is similar for many species, how may variations in clutch size be explained? If populations of hole-nesting birds were limited by the availability of nest sites, their overall effect on populations of their prey would be lower than that of open-nesting birds on their prey. Consequently, selection for antipredator adaptations of the prey would be reduced, which would result in a high rate of exploitation by individual hole-nesting birds. However, average rates of exploitation by hole nesters on the entire prey population may be similar to those exerted by open-nesting species (*9*). Significantly, breeding populations of hole-nesting birds are often increased considerably when an area is saturated with artificial nest boxes (*13*).

The decrease in clutch size toward the equator may be explained (i) by a shift in the outcome of predator and prey adaptations in favor of the prey in the tropics, (ii) by a relative increase in the intensity of interspecific competition among predators in the tropics compared to temperate regions, or (iii) increased allocation of food resources to maintaining large populations rather than to supporting high productivity. Several lines of evidence suggest that prey do not have an adaptive advantage in the tropics. First, antipredator adaptations seem more highly developed in the tropics than in temperate and arctic regions, which suggests that predation is a very strong selective force. Second, energy probably travels through the ecosystem more rapidly and with a higher efficiency in the tropics than in temperate regions (*14*). In a specific case, rates of predation on the eggs and nestlings of birds is about twice as high in tropical as in temperate regions (*15*).

Low clutch size of tropical birds could stem from a relatively high diversity of competitors. Accordingly, the exploitation of prey by several predators is likely to be more difficult for the prey to adapt to than equivalent exploitation by a single species because of the variety of predation strategies employed (*16*). This would account for a high mortality of prey species as well as a low productivity of predators. Increased competition would also require greater niche overlap. The reduction of niche size to avoid competition is not consistent with the relationship between predator diversity and rates of exploitation, because an increase in the diversity of predators exploiting individual prey species is required. Moreover, it is necessary that the diversity of predator strategies increase, rather than simply the number of predator species. If tropical predators shared as little of their resources with others as do temperate species, one would expect smaller populations of each tropical species raising nearly as many young as temperate birds. The model relates the reduction in clutch size nearing the tropics to increase in the diversity of competitors, which are postulated to be greater for predator species than for prey species. This suggests that measurements of the relative diversity of adaptations in certain groups of predators and prey may be used to test the hypothesis.

The model, as stated, assumes that clutch size is directly proportional to exploitation of resources. One may argue that the allocation of resources to breeding changes instead, or additionally. The availability of food resources in the tropics is thought to exhibit less seasonal fluctuation than in temperate areas, which may permit the maintenance of larger adult populations throughout the year. This population-maintenance requirement must then be subtracted from the resources gathered during the breeding season, which leaves less surplus available for feeding young in the tropics. Accordingly, we would predict that populations of individual species of predators are relatively greater than their resource populations in the tropics. This would not be expected if variations in clutch size were due to variations in exploitation rather than allocation. The model may bear on the observation that birds of tropical highlands, which have a diversity characteristic of temperate regions, but are exposed to tropical seasonality, lay small clutches, as do their lowland counterparts. Also, arid areas within the tropics and continental climates within temperate regions are generally characterized by being relatively seasonal, and species inhabiting such environments generally lay relatively large clutches.

Species in which the female alone raises as many offspring as species where both parents feed the young present a problem for Lack's "food-limited" hypothesis (*16*). This exception may be incorporated into the "counteradaptation" hypothesis presented here by considering the family group as the exploiting unit which interacts with prey populations. A family group requires a given amount of resources whether one or both parents feed the young. When the female is sole provider, prey adaptation may be relaxed sufficiently so that the one parent alone can obtain enough food for herself and the young. Hence food gathering must impose very little effort on the male. This model also requires that all similar species employ the same unbalanced division of labor, for presumably if males of one species fed the young, twice as many could be raised (and their prey exploited at a higher rate). The trait would then become so prevalent that antipredator adaptations of the prey would increase, and the foraging rates of species with overlapping food resources would be reduced. Among all neotropical hummingbirds (Trochilidae) and manakins (Pipridae), the female alone provides the young with food. Moreover, the males have evolved elaborate and time-consuming courtship behavior which suggests that they require little foraging time (*17*).

These ideas differ from, or elaborate upon, current views on the variation in clutch size in birds. To test these hypotheses will necessarily involve new analyses of adaptations and community organization.

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26 January 1970; revised 4 March 1970