

interesting to know whether other mimicked species are similarly unable to distinguish the copied from the model vocalization.

My thanks to R. Chariff for bringing the Mockingbird imitation of Red-wing song to my attention and to J. Gulledge for providing access to recordings in the Cornell Library of Natural Sounds. D. Koutnik and D. Dobkin made helpful comments on the manuscript. R. Capranica allowed me to use facilities supported by NIH grant NS 09244. This work was partially supported by a grant-in-aid from the national division of Sigma Xi.

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### Reproductive Synchrony and Predator Satiation: an Analogy Between the Darling Effect in Birds and Mast Fruiting in Plants

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Breeding synchrony characterizes many taxa. Some factors impose or select for synchrony, while others entrain it on a more immediate, proximate basis. Observed synchrony in a population represents a compromise between synchronizing and desynchronizing factors. Avian ecologists trace discussion of synchrony to F. Fraser Darling (1938), who proposed that, in gulls, synchrony was adaptive in minimizing predation on young. He assumed that a predator has a finite appetite and that there is no recruitment of predators (Gochfeld 1980: 256). As long as the number or biomass of young was below this predation threshold (a term he did not use), all might be consumed. Synchronous hatching would yield a superabundance of young for a brief period,

allowing some to survive as predators became satiated. Darling's model is attractive in linking evolution and ecology (selection via reduced predation) with behavior and physiology (social facilitation in large groups enhancing neuroendocrine stimulation leading to increased synchrony). Despite this attractiveness, few studies have found support for the model. A relation between synchrony and group size or improved productivity is demonstrable in some studies (Hall 1970, Collias et al. 1971, Burger 1979, Gochfeld 1979), while Nisbet (1975) found evidence for timing and predator satiation. Some studies have found no evidence for the model (Orians 1961, MacRoberts & MacRoberts 1972).

The complexities of studying these interrelated

factors in wild birds have led to frustration. Logistic problems arise in documenting reproductive success over a range of colony sizes, densities, and degrees of synchrony. Also, predation is seldom witnessed and must be measured indirectly. In particular cases, desynchronizing factors may operate more strongly, leading to low synchrony, or alternative synchronizing factors (e.g. weather, seasonal food variation) may operate (see Gochfeld 1980).

It is heartening to find analogies among other taxa, for example the apparent role of synchronous calving of ungulates (Estes 1966) or the metamorphosis of anurans (Arnold and Wassersug 1978) vis-a-vis predator satiation. An important analogy seemingly overlooked by ornithologists is the mast fruiting of plants discussed in detail by Janzen (1969, 1971, 1976). Many plant seeds are subject to intense predation, and many chemical and dispersive strategies have evolved to minimize predation. Janzen (1969) hypothesized that synchronous or mast fruiting achieved predator satiation. Among the critical assumptions are (1) seeds are available to the predator for a short time in superabundance, and (2) predators cannot maintain high populations in the absence of the food source. These assumptions underlie the Darling Effect as well. If predator populations build up as food increases, satiation will not occur; in fact, increased predation pressure might render synchrony maladaptive in some cases.

Janzen's (1971) scenario on the evolution of mast fruiting involves plants storing energy for one or more years and then producing a massive crop. Plants fruiting out of synchrony would be quickly selected against, and predators might find years when the food source is not available. By analogy, chicks hatching outside the peak would be vulnerable to predation (Nisbet 1975), and chick-predators would not linger at a colony when chicks were unavailable (unhatched or too large to eat). The analogy between mast fruiting and the Darling Effect seems a good one, though the time scale may be years in the former and weeks in the latter.

Judging from the numerous papers that open by citing Darling (1938), one must assume that his model has had heuristic value in challenging ornithologists to investigate a complex interaction of factors. Failure to find supporting evidence in some cases, or the operation of alternative synchronizing factors in other cases, cannot be taken as evidence that pred-

ator satiation is unimportant. The analogy of mast fruiting should encourage ornithologists to search for avian systems suitable for studying the Darling Effect in general and predator satiation in particular.

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Received 22 October 1981, accepted 7 January 1982.