REPRODUCTIVE RESPONSES OF SPARROWS TO A SUPERABUNDANT FOOD SUPPLY

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Do passerine birds raise as many young as they can adequately nourish? Considerable debate has surrounded this fundamental question in evolutionary ecology, particularly as it relates to the determination of clutch size (Wynne-Edwards 1962, Lack 1968, Skutch 1967, Ricklefs 1968, 1970). A clutch of eggs represents the commitment of an individual (or a pair) at one point in time to the production of the next generation. As such, the size of that commitment can be assumed to represent a variable which is very powerfully acted upon by natural selection. Lack (1947) first proposed that clutch size in altricial species of birds is adjusted evolutionarily to produce the maximum number of surviving offspring. He further proposed that food is the primary factor responsible for limiting the number of young that a pair can raise successfully. The clutch size of a species in a particular locality is therefore adapted to reflect the average food supply available for feeding the young in that locality.

Cody (1966) modified Lack's hypothesis by identifying other factors that might impinge on the ability of birds to raise the maximum number of young. The two major factors that he identified, predation and competitive ability, operate particularly in the tropics. He concluded, however, that in temperate regions food is probably of overriding importance in determining the number of young that can be raised.

The hypothesis that in temperate zone passerines reproduction is food-limited has been tested to date principally by artificially manipulating brood size (by the addition and subtraction of young from a brood at hatching) and the comparison of survival rates in normal and manipulated broods. Lack's hypothesis predicts that the mean number of young surviving from the normal-sized broods will exceed that of either larger or smaller broods. The results of these experiments (some with very small samples) have been inconclusive, some supporting Lack's hypothesis (Rice and Kenyon 1962, Perrins 1964), and others finding increased productivity from supernormal-sized broods (Nelson 1964, von Haartman 1967, Hussell 1972, Jarvis 1974). This experimental method, however, fails to distinguish between the possibility that brood size is adjusted to the average food supply and the possibility that the foraging methods and rates of the adults are adapted to the normal brood size (Hussell 1972).

Experimental manipulation of the driving variable in this proposed system, food available to the population for nourishing the young, has posed rather intractable problems. Two studies have been reported on the effects of an artificially supplemented diet on the clutch size and reproductive success of free-living individuals of two passerine species. Nutcracker (*Nucifraga caryocatactes*) females fed by P. O. Swanberg showed an increase in clutch size (Lack 1954). Yom-Tov (1974) reported that Hooded Crow (*Corvus corone*) pairs with experimentally supplemented diets showed no increase in clutch size, but did show improved hatching and fledgling success that he attributed to the indirect effects of the additional food in reducing predation. The present paper reports the results of a natural experiment involving a superabundant food supply available to breeding populations of two species of sparrows.

METHODS

From 1968 through 1973 I studied and compared the ecologies of the House Sparrow (*Passer domesticus*) and the European Tree Sparrow (*P. montanus*) near St. Louis, Missouri (Anderson 1973, 1975, in press). I was primarily attempting to identify factors which limit the distribution of the introduced European Tree Sparrow, which has a very circumscribed range in North America. Concurrent population studies of the two species served as a cornerstone for the comparative study, and these included the determination of various fecundity parameters of the populations.

During the course of the study (in 1972) there was a local emergence of Brood XIX of the 13-year periodical cicadas, *Magicicada tredecim*, *M. tredecassini* and *M. tredecula*. Broods of periodical cicadas emerge synchronously during May and June of every 13th or 17th year, and are present locally in extremely high but uneven densities. They are much more abundant, however, than the "dog-days" cicadas that occur widely every year in late summer. Despite local variations in abundance, periodical cicadas represent a superabundant food supply for insectivorous species during the period of their emergence, assuming that other species of insects have a relatively constant unit-area biomass from year to year. Periodical cicadas are also conspicuous and are described as being "predator-foolhardy" (Lloyd and Dybas 1966), scarcely avoiding predators. They can be captured readily by hand, for instance.

TABLE 1. Comparisons of mean clutch size, fledging success and mean interval between successive clutches (first clutch successful) of the House Sparrow and the European Tree Sparrow between the emergence year of the 13-year periodical cicadas (1972) and non-emergence years.

	House Sparrow		Tree Sparrow	
	1969–71, 1973	1972	1969–71, 1973	1972
Clutch Size				
Number of Clutches	60	25	22[a]	12
Mean Clutch Size	5.10	5.12	5.14	5.83
Difference	$t = 0.1215$		$t = 2.5897$[e]	
Fledging Success				
Number of Broods	32	10	9	4
Proportion Fledging	0.627	0.829	0.591	0.550
Difference	$X^2 = 5.790$[d]		$X^2 = 0.003$	
Interval Between Clutches				
Number of Intervals	36	14	24	10
Mean Interval (Days)	38.0	36.6	36.7	34.2
Difference	$t = 1.5665$[b]		$t = 1.9613$[c]	

[a] Clutches from high density years of 1971 and 1973 only (mean clutch size varied inversely with breeding density in this species [Anderson 1973, in press], and 1972 was also a high density year).
[b] $0.05 < P < 0.10$.
[c] $0.025 < P < 0.05$.
[d] $0.01 < P < 0.025$.
[e] $0.005 < P < 0.01$.

The study area was located in a highly cultivated portion of the floodplain between the Mississippi and Missouri rivers near Portage des Sioux, Saint Charles County, Missouri. The study site (site B in Anderson 1973) was a farmstead with a large breeding population (60–80 pairs) of sparrows of both species. During 1972 the cicadas emerged in the vicinity of the study area as early as 15 May, and were extremely numerous on the study site on 22 May. They remained common there through the first week of June, and were last seen there on 15 June. Periodical cicadas at the study site did not attain the tremendous densities that occurred elsewhere. Samples of nestling food from both species of sparrows, obtained by the "pipe-cleaner" method (see Orians 1966), contained cicadas, and I observed adult sparrows capturing flying cicadas by sallying from a perch.

The effects of a superabundant food supply on the following reproductive parameters of the two sparrows were examined, and comparisons made between 1972 and the four non-emergence years of the study: (1) clutch size, for clutches initiated from 20 May to 3 June (clutch size varies seasonally in both species (Anderson 1975) which allows for comparison only between comparable periods in the different years); (2) fledging success, expressed as the proportion of the young hatched from clutches initiated from 3 May to 18 May which survive to leave the nest (mean clutch initiation—hatching intervals for the House Sparrow and the European Tree Sparrow were 14.1 and 14.9 days, respectively, and nestling periods were 14.8 and 14.0 days, respectively, at the study area (Anderson, in press)); (3) nestling weight; and (4) interval between successive clutches at a nest site, where the first clutch was initiated between 16 April and 10 May and was successful.

Based on Lack's hypothesis that reproduction in altricial species of birds is limited primarily by food, I made the following predictions concerning changes in these reproductive parameters in response to a superabundant food supply:

Clutch size: (1) If clutch size is a more-or-less genetically predetermined trait that is adjusted by natural selection to reflect average conditions of food availability, no change would be expected, or (2) if clutch size is responsive directly to food availability during the egg laying period, it should increase.

Fledging success: Fledging success should increase.

Nestling weight: (1) The rate of development should increase resulting in a more rapid attainment of fledging weight, and/or (2) weight at fledging should be greater.

Interval between successive clutches: If the rate of development of the young is increased and/or if the time to secure sufficient energy to produce a second clutch is reduced, the interval should be shorter.

Because the direction of all the responses can be predicted by the hypothesis, one-tailed *t*-tests and X^2 tests were used in the analysis.

RESULTS

The mean clutch size of the House Sparrow for the emergence year was not significantly different from that for the same period in the non-emergence years (table 1). The mean clutch size of the European Tree Sparrow in the emergence year, however, was significantly higher than that of the two non-emergence years with similar high densities of breeding tree sparrows, 1971 and 1973. Mean clutch size varied inversely with breeding density in this species (Anderson 1973, in press), as has been observed in many other species of birds (see Klomp 1970). The different responses of the two species may be the result of different selective regimes operating on the two species with respect to reproductive commitment. The House Sparrow, with a rather stable, dense population, may be under the influence of *K*-selection (MacArthur and Wilson 1967), which would favor the adoption of a clutch size which is not responsive to temporary fluctuations in the food supply (assuming that the population is not being controlled by predators). The European Tree Sparrow, however, is much less common than the House Sparrow, and its population density is also less stable, at least in parts of its range (Barlow 1973). This species may therefore be under the influence of *r*-selection, with the result that it may exhibit a facultative response in clutch size to variations in the food supply.

Fledging success in the House Sparrow was significantly greater during the emergence year than in the comparable periods of the non-emergence years (table 1). Fledging success in the European Tree Sparrow was not significantly different. The samples for this species were very small, however, with only four broods observed during 1972.

Only five broods of House Sparrows whose nestling periods occurred during the cicada emergence were weighed near the time of fledging. The mean weights of each of these five broods (one with four young, two with five and two with six) are compared in figure 1 with the mean weights ($\pm$ 2 $s_{\bar{x}}$) of young of the same ages weighed throughout the course of the study. In four of the five instances the mean weight of the brood was significantly higher than the mean weight of young raised under normal circumstances. The two broods of six young were the only House Sparrow broods of that size to fledge during the course of the study (in at least 18 other broods in which six young hatched, plus one brood of seven young, less than six young survived to fledge).

The mean interval between successive clutches was significantly shorter in the emergence year than in the non-emergence years in the European Tree Sparrow (table 1). It was also shorter in the House Sparrow, although not significantly so.

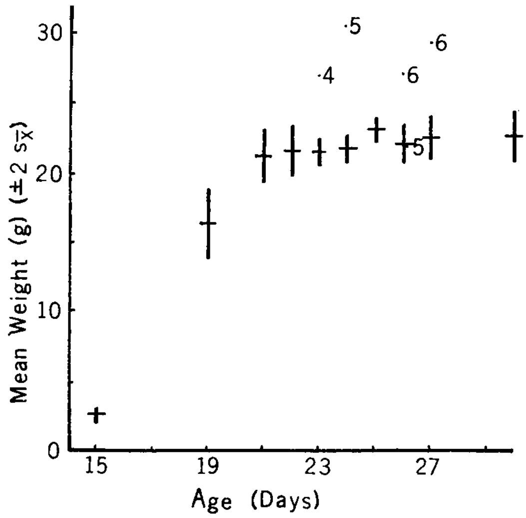

FIGURE 1. Mean weights of five broods of House Sparrows (with the number of young in the brood recorded beside the mean) raised during the emergence period of periodical cicadas plotted with the mean weights of nestlings of the same age raised under normal conditions (age plotted in days from initiation of the clutch [see Anderson 1973]).

DISCUSSION

These results generally conform to the expectations derived from Lack's hypothesis, and hence further support it. They do not, however, constitute conclusive evidence with respect to the validity of that hypothesis for the two species. The question of whether or not feeding rates are adapted to the average brood size is left unanswered, as the superabundant prey in this case were much larger than the average prey fed to the young under normal conditions (Anderson, in press). A carefully designed experiment in which brood sizes were manipulated and feeding rates were monitored in conjunction with a superabundant food supply at the population level, such as an emergence of periodical cicadas, would be most instructive.

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