

EXPERIMENTAL MANIPULATION OF BROOD SIZE IN RED-WINGED BLACKBIRDS

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ABSTRACT.—We increased the brood size of Red-winged Blackbirds to determine whether females could raise more young than they normally do. Despite greater within-brood losses, experimental nests produced more young than did natural and control nests. Females with enlarged broods made significantly more feeding trips to their nests; both male and female nestlings from enlarged broods, however, were significantly lighter than young from natural and control broods at the time they left the nest. Lighter young from enlarged broods probably experienced lower survival rates as fledglings than heavier young from natural and control broods. We interpret these results as being consistent with the hypothesis that selection produces clutch sizes that maximize the number of young that ultimately survive to breed and that the upper limit is set by the amount of food the parents can obtain for their young. *Received 5 November 1979, accepted 15 January 1980.*

THE number of eggs that birds lay in their clutches is an important component of reproductive effort, so natural selection will produce clutch sizes that maximize the fitness of females. Consideration of the constraints that environments place upon the allocation of resources to reproduction has led to Lack's (1954, 1968) view that natural selection produces clutch sizes that maximize the number of young surviving to breed, with the upper limit set by the amount of food that parents can provide to their offspring. Other potential selective forces affecting clutch size include the impact of the number of young raised on adult survivorship and on the likelihood that a predator will find the nest (Cody 1966, Williams 1966, Charnov and Krebs 1974, Perrins and Moss 1975).

If clutch size is limited by the amount of food that parents can provide to their offspring, the modal clutch size should produce the largest number of future breeders each year and thereby maximize the parents' fitness. Alternatively, parents might maximize their fitness by reducing clutch size below the food-limited maximum if this (1) increased significantly their chances to survive to breed again, or (2) decreased the probability that their nestlings would be taken by predators.

Experiments in which brood size is manipulated can be used to investigate the potential importance of these selective forces in determining clutch size. This paper reports the results of an experiment in which broods of Red-winged Blackbirds (*Agelaius phoeniceus*) were enlarged.

STUDY AREA AND METHODS

The experiment was performed from May through mid-August 1977 within the Conesus Inlet Wildlife Management Area, Livingston County, New York (42°42'N, 77°42'W) on a 20-ha tract consisting of five small ponds with cattails (*Typha* spp.) and of wet areas dominated by grasses, low shrubs, and scattered deciduous trees.

Most nests were found during construction or egg laying. Clutches were considered complete when no

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TABLE 1. Reproductive success of Red-winged Blackbirds in relation to nest category.

	Natural	Control	Experimental
Number of nests	15	10	17
Number (%) of successful nests	8 (53.5)	6 (60.0)	9 (52.9)
Number of young hatched	39	26	88
Number (%) of successful young	21 (53.8)	14 (53.8)	35 (39.8)
Number of young/successful nest	2.6	2.3	3.9

eggs had been laid for 2 consecutive days. A daily record was kept of each nest's contents. In western New York, the clutch and brood size of the redwing is usually three or four eggs and young (see Case and Hewitt 1963). We created broods of 5 or 6 by placing 2 additional young in experimental nests on the day of hatching. All nestlings in a nest were within one day's age of one another to eliminate competitive differences attributable to size. Added nestlings came from eggs laid in other nests in the Conesus Lake marsh and were from eggs incubated in the laboratory or were taken upon hatching from other nests. Three categories of nests were studied: (1) experimental nests in which brood size was increased by 2 to 5 or 6; (2) control nests in which nestlings were exchanged but in which brood size remained the same; and (3) natural nests in which brood size was not increased and nestlings were not exchanged.

Each of 42 completed clutches surviving the incubation period was assigned by a random process to 1 of the 3 categories. Nestlings were individually marked at hatching by coloring their tarso-metatarsus with a felt-tipped pen; when 7 or 8 days old, they were banded with a U.S. Fish and Wildlife Service aluminum band and colored plastic bands. Nestlings were weighed at approximately the same time each morning to the nearest 0.1 g on a triple-beam balance, and the following measurements were made: (1) bill length, from the middle anterior end of the nostrils to the tip of the maxilla; (2) body length, from the tip of the bill to the tip of the pygostyle; (3) eighth primary, from the point of emergence of the shaft from the skin to the tip of the shaft; (4) tarsus, from behind the middle of the joint between the tibio-tarsus and tarso-metatarsus to the lower edge of the last undivided scute of the tarso-metatarsus; (5) wing, from the radial region to the tip of the phalanges (see Baldwin et al. 1931). A one-way analysis of variance, ANOVA (Nie et al. 1975), was used to test for the influence of brood size on weight and length of body parts among young of the three groups from the 1st through the 9th day of the nestling period. To insure that the data met the assumptions of the ANOVA, we tested for homogeneity of variances and for kurtosis and found for most comparisons no significant departures from the requirements of the test. Growth rates of nestlings in the three groups were compared by fitting data to the logistic growth curve using Ricklefs' (1967) graphic method.

The frequency of trips by females carrying food to experimental, control, and natural nests was recorded during 3-h periods on the 3rd and 6th days of the nestling period. The fate of individual nestlings was followed to determine whether or not there were differences among nests in the numbers of young lost to predators or abandonment (whole-brood loss) and starvation (partial-brood loss). In the absence of direct evidence of the fate of missing young, we assumed that predators were responsible when all young disappeared from the nest before the 8th day of the nestling period (see Thompson and Nolan 1973: 160–161, Nolan 1978: 411) and that abandonment had occurred when nestlings that seemed to be healthy and vigorous the day before died in the nest. Nestlings that disappeared were assumed to have died of starvation if earlier they had been less vigorous, smaller, and lighter than their nest-mates.

RESULTS

Breeding season, clutch size, and hatching success.—Nesting activity peaked in mid-May and continued through June into early July. The size of completed redwing clutches ranged from 1 to 5 eggs, with 3- and 4-egg clutches equally common. The mean clutch size was 3.4 eggs in 72 completed clutches. Of 145 eggs that survived the incubation period, 130 (90%) hatched.

Nest success.—There were no significant differences among experimental, control, and natural nests in the number of nests that had at least one young survive to leave the nest (chi-squared test, $\chi^2 = 0.1$, $df = 2$, $P > 0.05$) (Table 1). There were no

TABLE 2. Losses of Red-winged Blackbird nestlings in relation to nest category.

	Natural	Control	Experimental
Number of nests	15	10	17
Number of young hatched	39	26	88
Number (%) of young taken by predators	12 (30.8)	10 (38.5)	27(30.7)
Number (%) of young abandoned	3(0.1)	2(0.1)	8(0.1)
Number (%) of young starved	3(0.1)	0(0.0)	18(20.5)

significant differences among the three categories of nests in the number of complete broods lost to predators ($\chi^2 = 1.5$, $df = 2$, $P > 0.05$) or to abandonment ($\chi^2 = 0.6$, $df = 2$, $P > 0.05$).

Nestling success.—There were large but not significant differences among the three groups of nests in the number of young that successfully left the nest ($\chi^2 = 3.0$, $df = 2$, $P > 0.05$). There were no significant differences in the number of nestlings lost to predators and abandonment from nests in the three groups ($\chi^2 = 0.4$, $df = 2$, $P > 0.05$), but there were significantly more young lost to starvation in experimental nests than in natural and control nests ($\chi^2 = 9.2$, $df = 2$, $P < 0.05$) (Table 2). Of 21 nestlings that starved, 14 (67%) disappeared on the 5th or 6th days of the nestling period. Nine of these 21 nestlings were from the last egg laid in the clutch, but there was no significant difference between the number of last-hatched and earlier-hatched young that died of starvation ($\chi^2 = 0.9$, $df = 1$, $P > 0.05$). Although sample size is small, there is no evidence that young added to experimental nests were more likely to starve than those that hatched in the nest ($\chi^2 = 1.8$, $df = 1$, $P > 0.05$).

Number of young produced.—There was no significant difference between the mean number of young produced in successful natural and control nests (Wilcoxon $T = 39$, $n_1 = 6$, $n_2 = 8$, $P > 0.05$). Despite greater starvation, successful experimental nests produced more young than pooled natural and control nests ($T = 66$, $n_1 = 9$, $n_2 = 14$, $P < 0.05$) (Table 2).

Feeding trips in relation to brood size.—Females at experimental nests made significantly more feeding trips/h on the 3rd ($T = 64$, $n_1 = 9$, $n_2 = 12$, $P < 0.05$) and 6th ($T = 24$, $n_1 = 6$, $n_2 = 6$, $P < 0.05$) days of the nestling period than did females at pooled natural and control nests (Table 3).

The number of feeding trips·nestling⁻¹·h⁻¹ to experimental nests did not differ significantly from that to the pooled natural and control nests on the 3rd day ($T = 81$, $n_1 = 9$, $n_2 = 12$, $P > 0.05$). On the 6th day, however, the number of trips·nestling⁻¹·h⁻¹ to experimental nests was significantly less than to the pooled natural and control nests ($T = 24$, $n_1 = 6$, $n_2 = 6$, $P < 0.05$) (Table 3).

Growth of body parts.—There were no significant differences among the three

TABLE 3. Number of female Red-winged Blackbird feeding trips on the 3rd and 6th days of the nestling period in relation to nest category.

	Mean number trips·nest ⁻¹ ·h ⁻¹		Mean number trips·young ⁻¹ ·h ⁻¹	
	Day 3	Day 6	Day 3	Day 6
Natural and control	7.1	7.8	2.1	3.2
Experimental	10.2 ^a	10.2 ^a	1.8	2.1 ^a

^a Indicates experimental means that are significantly different ($P < 0.05$) from natural and control means; see text.

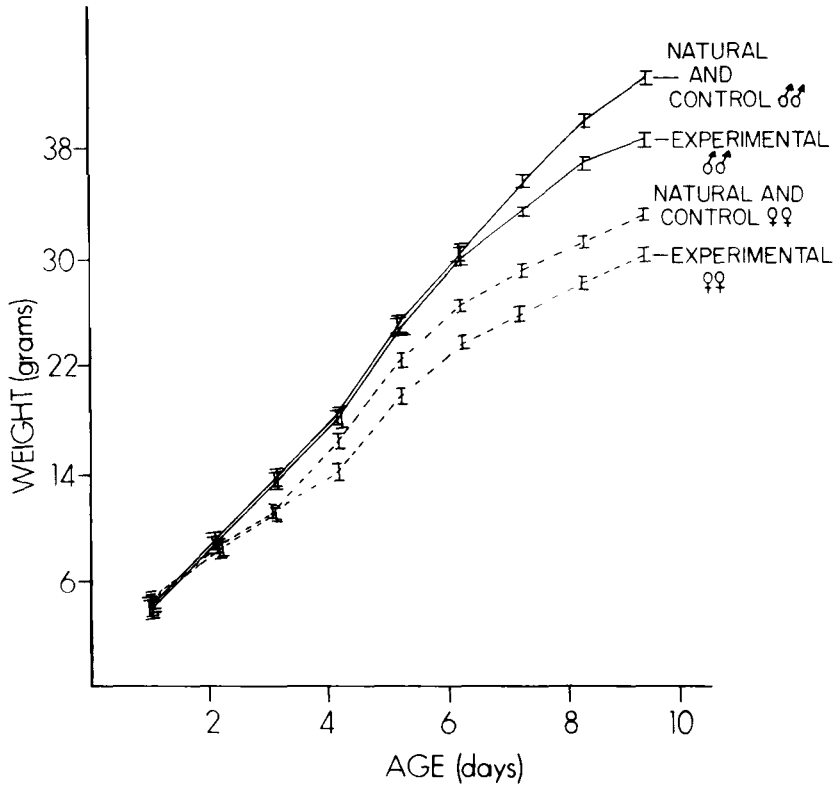


Fig. 1. Weight of male and female Red-winged Blackbirds in relation to nest category; natural and control nestlings pooled. Daily mean weights and 95% confidence intervals of the means are presented.

groups of nests for either sex during any day of the nestling period in the lengths and rates of growth of the bill, body, eighth primary, tarsus, or wing of nestlings (see Cronmiller 1978).

Weight.—Figure 1 summarizes the daily mean weights of males and females in the three groups from day 1 to day 9. Only young that survived to leave the nest are included.

There was no significant difference in the weights of male or female nestlings on any day in natural and control nests. Male nestlings in experimental nests were significantly lighter than those in pooled natural and control nests by day 7. Females

TABLE 4. Growth rate^a of Red-winged Blackbird nestlings in relation to nest category.

	Natural			Control			Experimental		
	<i>a</i>	<i>K</i>	<i>Ka/4</i>	<i>a</i>	<i>K</i>	<i>Ka/4</i>	<i>a</i>	<i>K</i>	<i>Ka/4</i>
Male weight	40.8	0.548	5.6	40.5	0.541	5.5	37.4	0.533	4.9
Female weight	32.0	0.516	4.1	32.2	0.516	4.1	30.0	0.464	3.5

^a *K* is the growth constant representing overall growth rate in g/day derived from the fitted logistic equation. *Ka/4* represents the maximum instantaneous growth rate of the young in g/day, which occurs at the inflection point of the fitted logistic curve, and *a* is the asymptote in g (Ricklefs 1967).

in experimental nests were significantly lighter than female nestlings in pooled natural and control nests by day 4 (Fig. 1).

Rate of weight gain.—The mean rate of weight gain, K , and the mean maximum weight attained at the inflection point were similar for natural and control nestlings. The rate of weight gain in both male and female nestlings in experimental nests was lower than that of male and female nestlings in natural and control broods (Table 4). Thus, nestlings in enlarged broods had not gained as much weight at the point of inflection as nestlings in natural and control broods (Fig. 1).

Survival of young after leaving the nest.—Fifteen of 35 (43%) young from experimental nests, 10 of 21 (48%) from natural nests, and 6 of 14 (43%) from control nests were found in the field within 3 days after they left their nests; none of these differences is statistically significant ($\chi^2 = 0.13$, $df = 2$, $P > 0.05$). Only three young, all from natural nests, were seen in the field after they had been out of the nest for more than 3 weeks.

DISCUSSION AND CONCLUSIONS

Interpretation of brood-enlargement experiments.—Any consideration of the results of brood-enlargement experiments must address the caveats of Hussell (1972) and Perrins and Moss (1975). Hussell (1972: 353) suggested that clutch size and feeding ability are coadapted to the average food supply in the environment, and Perrins and Moss (1975) pointed out that enlarged broods may be less productive than normal broods simply because some parents are unprepared to cope with an increased number of nestlings. In defense of brood-enlargement experiments, Askenmo (1977) argued that an adapted limitation to foraging abilities seemed unrealistic and would require a genetic linkage between clutch size and foraging ability. We agree and think that in any case such problems were minimized in our experiment for the following reasons: first, females laying three eggs were not less successful raising their enlarged broods than females laying four eggs; second, enlarged broods were within the range of variation found in the population; and, third, females did respond to enlarged broods by increasing their feeding rates. Thus, redwings evidenced no inability to respond to enlarged broods, as might be expected of a long-lived species that is regularly exposed to unpredictable fluctuations in its food supply.

Lack (1966: 273) criticized the definitiveness of several enlargement experiments on the grounds that feeding conditions were unusually favorable and were not the conditions under which natural selection had operated to produce the observed clutch sizes. In our case, there is no reason to suspect that the redwings experienced conditions unlike those under which they evolved; on the contrary, marsh was probably the original habitat of the species.

Number of young produced.—There were no significant differences among the numbers of experimental, natural, and control nests that successfully produced at least one young nor in the proportion of nestlings to leave the nest. Successful experimental nests in which two additional young were placed did produce more young, however, than did natural and control nests (Table 1).

There were no differences between control and natural nests in the daily mean weights, asymptotic weights, and growth rates of nestlings. Therefore, handling and switching among nests did not affect the growth of nestlings. But male and female nestlings in experimentally enlarged broods gained weight more slowly and left the

nest at lower weights than nestlings in natural and control broods (Fig. 1). Lack (1966: 38–42), Ricklefs (1969), and von Haartman (1971: 420–424) suggested that the weight at nest-leaving directly influences the survival of young during the following months. Perrins (1965) found that weight at nest-leaving and recapture rates, and, therefore, presumably survival rates (cf. Dhondt 1979), were positively correlated in Great Tits (*Parus major*), which led Perrins (1965: 642–643) to suggest that losses of lighter young were probably caused by insufficient energy reserves for use during periods of food shortage. The potential importance of energy reserves to fledglings is enhanced by Smith's (1978) report that fledgling, rather than nestling, Song Sparrows (*Melospiza melodia*) may put the greatest strain on the ability of parents to feed their offspring.

It is not unreasonable to assume that light young from our experimentally enlarged broods may have had a significantly lower survival rate than the heavier young from broods of normal size. If so, the modal clutch sizes of three and four eggs may have produced more future breeders than did the enlarged broods. Only in the unlikely event that smaller clutches (one or two eggs) produced more young that survived to breed would the most frequent clutch size not produce more future breeders. The results, then, are probably consistent with Lack's hypothesis that the modal clutch size should produce the maximum number of young likely to survive to breed in future years.

Selective pressures on clutch size.—In Lack's (1968: 165) words, clutch size “. . . has been evolved through natural selection to correspond with that brood-size from which, on average, most surviving young are produced, the limit normally being set by the amount of food that the parents can collect for their nestlings.” Hussell (1972: 353) pointed out that this has been construed as a statement that the limit of clutch size is determined simply by the food supply in the environment, when, in fact, “. . . the hypothesis can be interpreted to mean that clutch sizes and feeding abilities have both evolved by natural selection and are coadapted to the prevailing conditions.” Considering this distinction, we conclude that our results are consistent with the view that the food supply and the redwing's ability to exploit it determine clutch size.

If nest predators or effects on adult survival have been important selective forces on clutch size (e.g. Skutch 1949, Charnov and Krebs 1974, Perrins and Moss 1975), redwing clutches should average less than that set by the food-limited maximum, and females should be able to raise enlarged broods successfully. But in this experiment, females were apparently unable to feed their young adequately when broods were increased by two nestlings, suggesting that the modal clutch size and brood size was at or near the food-limited maximum. Limitations imposed by only a single season's data and our lack of knowledge of the redwing's food supply during the study, however, preclude definitive conclusions concerning the role of these potential selective forces. Ricklefs (1977: 212) and Perrins (1977) presented arguments suggesting that predation effects on clutch size were likely not to have been great in many nidicolous species. Although our enlarged broods did not suffer significantly greater losses to predators, sample size was inadequate to detect any small, but potentially important, differences.

In conclusion, we point out that although our results are consistent with Lack's hypothesis, short-term experiments cannot hope to identify and estimate the importance of all the selective forces potentially operating on so important a component of reproductive effort as clutch size. What is needed are long-term brood-manipu-

lation experiments concerned with not only food availability and the impact of nest predators but also with the relationship between brood size and adult and juvenile survival.

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