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RED-WINGED BLACKBIRD STUDIES:

I. PREDATION ON RED-WINGED BLACKBIRD EGGS AND NESTLINGS

II. CLUTCH SIZE ADAPTATIONS OF RED-WINGED BLACKBIRDS

by

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PREDATION ON RED-WINGED BLACKBIRD EGGS AND NESTLINGS

Frank S. Shipley

The contents of Red-winged Blackbird (Agelaius phoeniceus) nests are subject to extensive and highly variable losses. Normally, most redwing eggs fail to produce young that are able to leave the nest. Most researchers have found 60 to 100 percent of the losses to be due to predation on nest contents, where the entire brood or clutch is lost at once. Some 0- 5 percent of the losses appear to be related to starvation of nestlings or nestling competition. The remainder of the losses (0- 40 percent) result from a variety of causes including egg infertility, nest desertion, and nest tipping due to growth of the supporting vegetation. In this study, predatory losses of redwing nestlings and eggs are related to water depth at nest sites, habitat type, progression of season, and number of young in the nest.

Goddard and Board (1967) observed increasing nesting success with increasing water depth at nest sites. For nests built over water 0 to 10 cm deep, nesting success was 23.2 percent; for water depth over 20 cm, success was 43.5 percent. Francis (1971) found no significant difference in nesting success for redwings nesting over different water depths, but believes (pers. comm.) that deep water may deter mammalian predators from preying on nest contents.

Robertson (1972) found an inverse relationship between the percent of redwing nests preyed on and water depth at nest sites, indicating a deterring effect of water depth on predators. Marsh nests were found to be more successful than upland nests in Robertson's extensive study: successful marsh nests fledged more young than successful upland nests and more nests were successful in marsh habitat than in upland. 30.2 percent of marsh nests were preyed upon, compared to 45 percent of upland nests. Francis (1971) and Case and Hewitt (1963) likewise found nesting success to be generally lower in upland than in marsh habitat.

Seasonal peaks in nest predation were observed by Robertson (1973). He attributed the peaks to predator response to nesting density. Peaks in predation were often preceeded by corresponding peaks in nesting activity. The predators in some cases preyed on nests in a positive density dependent manner while in others were apparently "swamped" by high redwing nesting densities, resulting in individual nests having a decreased probability of being preyed upon.

Methods and Study Areas

Six study areas were chosen for the investigation, all within 20 km of Manhattan, Kansas. Two upland sites (designated A and B) had similar topography and vegetation and were within the boundaries of Konza Prairie Research Natural Area, south of Manhattan. Each consisted of a draw con-

taining a small stream and the surrounding lowland. Vegetation was of the tall grass prairie type, largely treeless. Redwings nested in scattered brushy growth, primarily buckbrush (<u>Symphoricarpos</u> <u>orbiculata</u>) and willow (Salix spp.). Except for one 4 m diameter pool in area A, there was no standing water and no cattails (<u>Typha</u> <u>latifolia</u>).

Study area C, north of Manhattan, was also designated "upland". It was similar to A and B, but contained many young trees and was bordered by farmland.

Areas D, E, and F were designated "marsh". D and E, on the edges of an old oxbow of the Kansas River, contained large unbroken stands of cattails and standing water from 0 to 80 cm in depth. In 1974, area D dried up as the season progressed: water completely disappeared by early July in all but one corner of the area. Area F, a cattail marsh, was within Tuttle Creek State Park, below the dam at Tuttle Creek Reservoir north of Manhattan.

Data were taken in areas A, B, C, D, and E during the nesting season of 1974, and in D, E, and F, (the marsh areas) in 1975. Red-winged Blackbird nests were located and marked with small flags placed about 10 m distant from the nest site. Water depth at the nest site at the time of discovery and contents of the nest were noted, and nests were visited on alternate days until the clutch or brood had either been destroyed by a predator or the young had fledged. Of 254 nests observed, the history of 194 is known from the egg stage to fledging or de-

struction by a predator, and were used in the study.

Brood sizes were in some cases experimentally manipulated by removing nestlings from one nest and adding them to another. Nestlings were moved as soon after hatching as possible (usually the same day) and broods were augmented only by nestlings of the same age in days. Thus "augmented" broods had more young in the brood than there were eggs in the original clutch, and "depleted" broods had less. "Natural" broods had the same number in the brood as were present in the original clutch, including several nests to which nestlings were added at hatching but in which natural brood reductions occured early in the nestling period.

When a nest was encountered which had been preyed upon since the last visit, observations were made on contents of the nest, condition of the nest, condition of the supporting vegetation, and on tracks when they were present. Measures of predation pressure were calculated after Mayfield (1961) as

$$\frac{\text{Number of nests preyed on}}{\text{Number of nest-days exposure}}$$

in order to account for the effects of finding nests in which eggs had been present for varying lengths of time.

Results

Based on signs left by the predators of redwing nest contents, predation was found to fall into three categories and was thereafter classified by type. "Type 1" was

characterized by the eggs or nestlings being gone with the nest left intact, and was thought to be the result of avian predation, particularly by the Common Grackle (<u>Quiscalus</u> <u>quiscula</u>) and occasional predation by snakes, particularly the water snake (<u>Natrix</u> <u>sipedon</u>).

"Type 2" predation was characterized by the nest and supporting vegetation being ripped down, with the eggs or nestlings gone. It was thought to be due primarily to racoons (<u>Procyon</u> <u>lotor</u>), skunks (<u>Mephitis</u> <u>mephitis</u>), and possibly mink (<u>Mustela</u> <u>vison</u>). Type 2 was the most distinctive type of predation found; its signs overlapped least with the signs of predation by other species.

In "Type 3" predation, the nest was intact, the eggs destroyed, and the eggshells left in the nest. Type 3 was observable only before hatching and was thought to result primarily from small mammal predation. Type 3 probably contained an avian component as well and is thus not entirely distinct from type 1. Type 3 was the least frequently observed type of predation. In no case was predation of any type observed actually taking place.

Predation and Water Depth

Total predation on marsh redwing nests was inversely related to water depth at the nest site (fig. 1). Predation pressure in the shallowest (0- 20 cm) depth range was .053 nests lost per nest-day exposure, while predation pressure in the deepest (30- 40 cm) depth range was .014.

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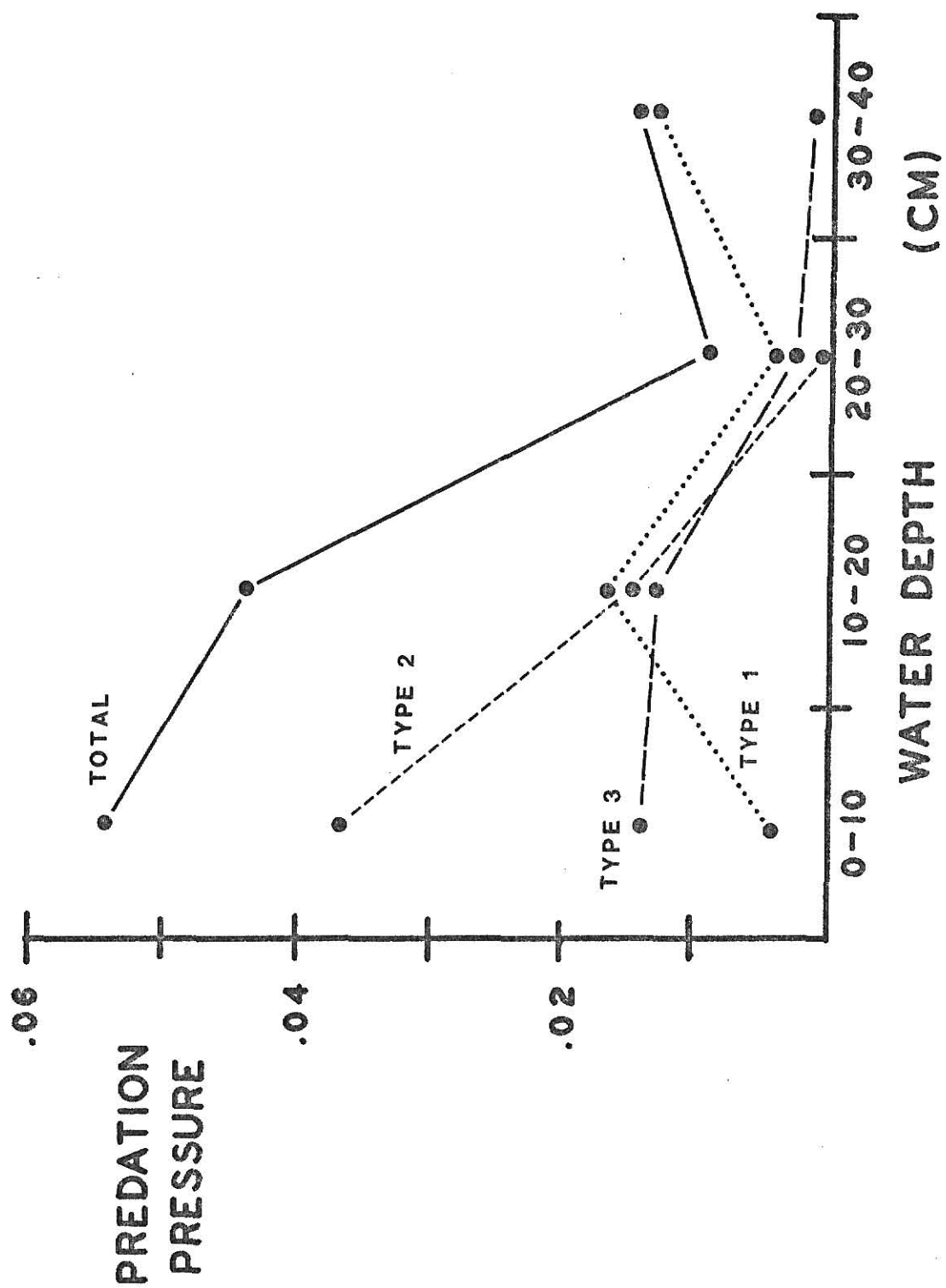THIS IS AS RECEIVED FROM CUSTOMER.

FIG. 1

Fig. 1. Predation on the contents of marsh Red-winged
Blackbird nests, as a function of water depth at the nest
site.

These findings agree with those of Robertson (1972), who
also found a negative correlation between percent nests
preyed on and water depth, and Goddard and Board (1967)
who found nesting success to increase with increasing water
depth at nest sites.

The effect of water depth varied for the three ob-
served types of predation. Type 2 predation, thought to
be mammalian, was the most intense of the three types,
and steeply decreased with increasing water depth. For
depths beyond about 20 cm, there were no recorded instances
of predation by large mammals. Since type 2 is the most
intense component of total predation, water depth effects
on type 2 are largely responsible for the overall observed
dependence of predation on water depth.

Type 3 predation, thought to result primarily from
small mammals, was also inversely related to water depth
but was less intense, on the average, than type 2. Type 3
predation pressure was only about a third as intense as
type 2 in water 0- 10 cm in depth, but closely corresponded
to type 2 values in deeper water. The fact that small mammal
predation slightly exceeds large mammal predation in deep
water probably results from the inclusion of some nests
preyed on by birds in predations designated as type 3,
since birds and small mammals left quite similar signs
in nests where eggs were preyed on. Type 1 predation,
thought to be avian, was variable and not apparently in-
fluenced by water depth.

Marsh area D dried up rapidly during the latter part of the 1974 nesting season. Large expanses of redwing nesting habitat, previously with water present in depth up to 60 cm became completely dry by early July. Mammalian predation increased markedly at this time. During the five day interval beginning July 5, when no water was present, mammalian predation had risen to .33, or equivalently, a third of all nests destroyed per day. This exceptional condition, however, was represented by only 3 nest-days of exposure and one nest preyed on, since nesting activity was nearly ended.

Predation in Marsh and Upland Habitat

Predation differences cannot be meaningfully related to habitat per se, without considering the variables included in the term "habitat". Thus consideration of water depth, nesting density, and other potentially important factors should be made, and only then extended to include habitat differences in predation.

Nesting redwings are generally more successful in marsh than in upland. Robertson (1972; 1973), Francis (1971) and Case and Hewitt (1963) all found higher fledging success in marsh than in upland. My data (table 1) show insignificantly higher predation rates in the marsh (.043) than in the upland (.039). Even when the major effects of water disappearing in marsh area D are accounted for by considering only predation before the area completely dried,

TABLE 1

PREDATION PRESSURE[1] ON RED-WINGED BLACKBIRD NESTLINGS AND EGGS IN MARSH AND UPLAND HABITAT

	Marsh	Upland
No. of nests	161	33
No. of nests preyed on	83	15
Percent of nests preyed on	51.6	45.5
Total predation pressure	0.043	0.039
Type 1 predation pressure	0.009	0.018
Type 2 predation pressure	0.022	0.016
Type 3 predation pressure	0.011	0.005

[1] Predation pressure = $\dfrac{\text{No. of nests preyed on}}{\text{No. of nest-days exposure}}$

there is no significant difference between total marsh
and upland predation pressure, or between marsh and up-
land predation of any of the three types, using X^2 analysis
at the .05 confidence level.

Predation and Season

Using the data from 1974 when both marsh and upland
sites were studied, predation pressure was plotted for
five-day intervals over season (fig. 2). Predation in the
marsh peaked between the 15th and 20th of June, then
declined until early July, with a second lesser peak
during the first 5 days of July. Predation in the upland
peaked about 10 days later than in the marsh, but with
about the same intensity. Upland predation thereafter
declined continuously until the end of nesting in early July.

Predation and Brood Size

Variation in water depth, season, and predator species
identity, unless they are accounted for, tend to obscure
effects of brood size on predation rate. To eliminate
those effects, only nests in water less than 20 cm deep,
which were relatively "available" to all predators, were
considered. Data from the entire season were lumped to-
gether to reduce the effect of seasonal changes in the
influence of brood size on predation, and predations of the
different types were considered separately to account for
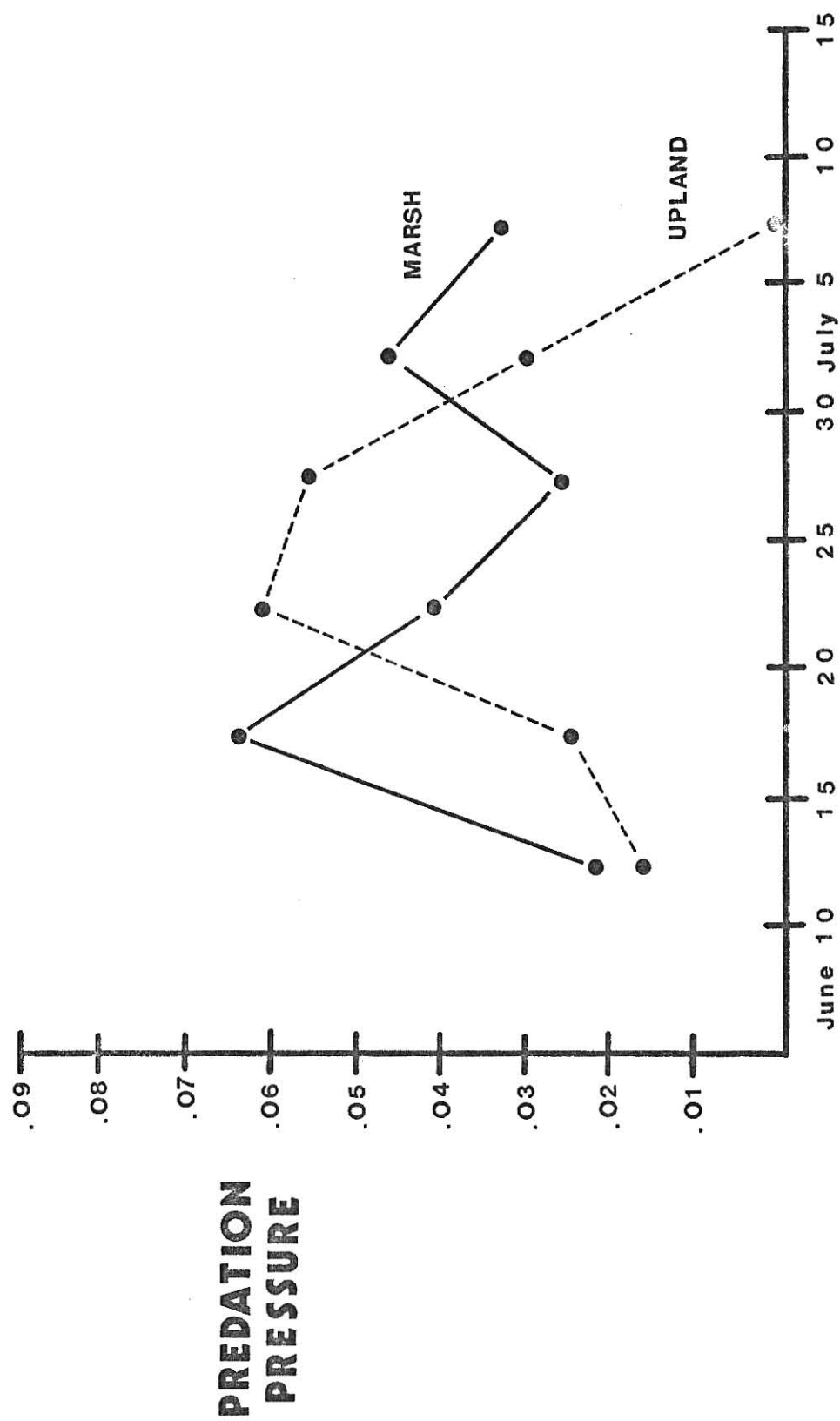different predator species types.

FIG. 2

Fig. 2. Total predation pressure for 1974 nests averaged
over five-day intervals, as a function of time.

Figure 3 relates after-hatch predation pressure of types 1 and 2 to the number of nestlings present in the brood. Data are lumped together for augmented, depleted, and natural broods. Type 3 predation, thought to result mainly from small mammals, is not included since it was recognizable only prior to hatching. Type 2 predation pressure, thought to be caused primarily by racoons, was for all brood size categories more intense than type 1, and increased with increasing brood size. The most pronounced increase in type 2 predation rate, nearly a doubling in magnitude, occured over the brood size increment from 4, the usual natural brood size, to 5, which in all cases were artifically augmented broods. Thus the actual number of nestlings present in the brood may have been less important in influencing the probability of young being preyed on than artificial manipulation of the number present. This is further emphasized by considering predation pressures on augmented, natural, and depleted nests (table 2). Augmented nests were subject to a type 2 predation pressure of .041, compared to .021 for broods of natural size and .024 for depleted broods.

Type 1 predation pressure, thought to be largely avian, was essentially constant over all brood size categories, and was influenced oppositely by brood size manipulation in comparison to mammalian predation: predation pressure values for natural and depleted nests were approximately double the values for augmented nests.

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FIG. 3

PREDATION PRESSURE

BROOD SIZE

TYPE 1

TYPE 2

-15-
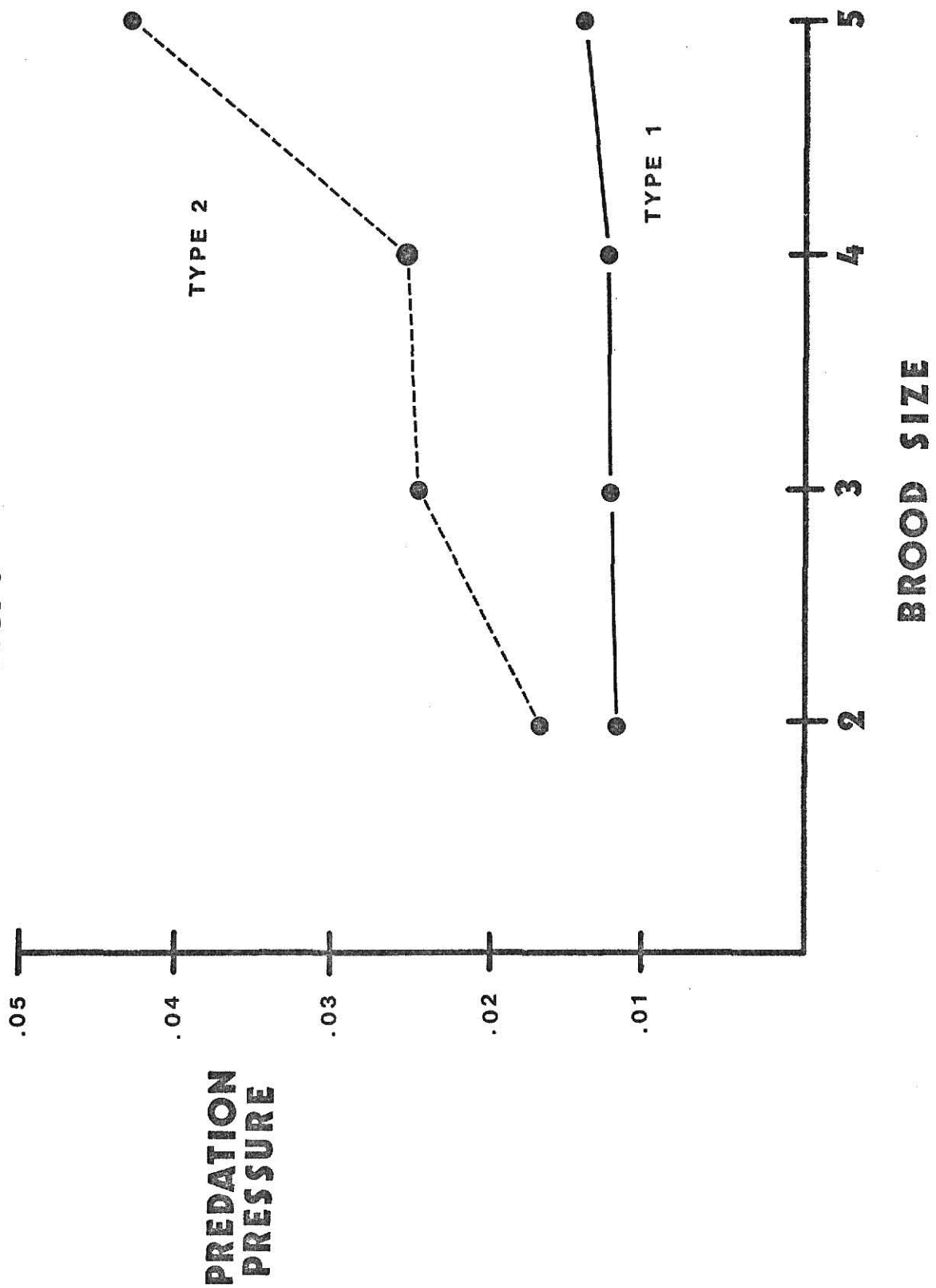
Fig. 3. Predation pressure on Red-winged Blackbird nestlings as a function of brood size, for nests built over water less than 20 cm deep. Data are for natural and manipulated broods.

	No. of nests	Predation Pressure	
		Type 1	Type 2
Augmented nests	26	0.010	0.041
Natural nests	15	0.021	0.021
Depleted nests	44	0.021	0.024

Table 2.   Predation pressure on Red-winged Blackbird nestlings in augmented, natural, and depleted broods, from nests built over water less than 20 cm deep.

Discussion

Water depth at nest sites, habitat type, date, and number of young present in the brood after hatching all affect predation on the contents of redwing nests. Ideally, multiple regression analysis would indicate the relative importance of the effects of each of these, as independent variables, on predation pressure. Several factors preclude such an analysis. First, the observed variables were not mutually exclusive, and may partially interact. For example, water depth may well be an aspect of habitat which accounts for part of the predation difference observed between marsh and upland nests. Thus, such variables as nest density, food availability, and water depth, all aspects of habitat, should be considered separately.

Second, predation pressure, as measured in this investigation, is essentially a population phenomenon determined by data from a number of nests rather than from individual nests. Thus for particular values of the independent variables, too few nests are available in any single study to produce valid predation pressure values. Ideally a large number of nests from separate nesting colonies should be studied for a number of years to produce the sample size needed for valid multivariate analysis of the determinants of predation.

This investigation has nonetheless discerned several patterns in predation on redwing nest contents. Water depth at nest sites was quite important in its effect on

predation pressure, and the effects were predator-specific. Mammalian predators were deterred increasingly with increasing water depth beneath nests while avian predators were not apparently influenced by the presence of water. Diminishing returns associated with deep-water foraging may correspond to the depth at which mammalian predators must begin to swim, and thus account for the sharp decrease in predation at a depth of approximately 25 cm. Further emphasizing the predator-deterring influence of water on mammals was the marked increase in mammalian predation when, in 1974 in marsh study area D, water receeded to expose previously inaccessable nests.

Francis, in a 1971 review of redwing literature, found no significant difference in nesting success for sites of varying water depth. The influence of water depth must certainly vary with mammalian predator species identity. Avian predation apparently occurs independently from water depth and non-predatory nest destruction, sometimes important in affecting losses, is not related to water depth. Thus in areas where birds are important predators and where non-predatory losses are high, water depth may be of little importance in its affect on overall nesting success. At other locations where mammalian predation is quite important, as in this study, the presence of deep water may be expected to result in high overall nesting success. While predation is normally the most important determinant of nesting success, it is not the only one.

Redwing nesting densities are normally higher in marsh than in upland habitat. Robertson (1973) has found nest densities that differ by as much as an order of magnitude. Thus, in marsh areas with relatively shallow water, predators should be more efficient than upland-searching predators in finding nests. Further, by temporarily specializing on marsh redwing nest contents as they become seasonally dense, predators could maximize their prey discovery rate. This density dependent predation mechanism has been termed "switching" by Murdoch (1969). Such an ability in predators would further be enhanced if they are able to form a search image, or key on the activity of the females caring for their hatchlings.

My data may reflect such density dependent switching, particularly where dense nests become available to mammals by decreasing water depth. In some cases, signs left at nests preyed upon by racoons indicated a systematic searching pattern, resulting in nearly complete destruction of the redwing nesting in the area. Seasonal fluctuations in predation may also be responses to fluctuations in redwing nest density or nesting activity, as Robertson (1973) has proposed. Case and Hewitt (1963) found the marsh nesting peak to precede the nesting peak in the upland by a week to 10 days. In this study, the peak in marsh predation also preceded the upland peak by about 10 days, and was possibly a result of predators responding to high density or activity as they occured in each habitat. Similarly,

the secondary marsh predation peak may have been a predator response to a secondary nest density peak resulting from the renesting of birds which had their initial attempts curtailed by predation. Predation peaks in both habitats occured a week or more after actual peak nesting activity. Such a temporal lag between maximum prey density and the peak in predation rate is often an attribute of predator-prey interaction, and is consistent with density dependence. Whether predators actually switched their prey consumption from other kinds of prey to redwing nestlings and eggs can only be determined by considering the composition and density of alternate foods available to the predator (Holling 1959). The predator experiences not just a temporal peak in potentially exploitable redwing nests, but a series of often overlapping peaks in other potentially exploitable prey.

My observations do not support Robertson's (1972; 1973) hypothesis that nesting synchrony and the tendency toward nesting coloniality in marsh sites result in high enough nesting density to satiate predators and thus reduce the probability of predation on each nest in the population. Rather, all of my study areas resemble those of Robertson's where predation exhibited positive density dependence. Since my observations were not aimed at determining the relative density dependence of predation, however, I have no nest density data and may have been dealing with relatively low nesting densities in comparison to other areas.

More work clearly needs to be undertaken, perhaps in manipulation of nest density.

Water depth and nest density probably constitute important variables in most "habitat" differences in predation on redwing nest contents. The frequently observed pattern of higher predation in upland than in marsh sites should thus normally be explainable in these terms. The presence of water in marsh habitats may also influence the density of nests, by allowing higher nesting densities without corresponding high predation rates. Further, benefits which accrue from the "mobbing" of potential nest predators, a behavioral consequence of the density itself rather than a habitat factor, may make dense nesting even more reproductively advantageous.

The avian and mammalian components of total predation both varied with the number of nestlings present in nests. Mammalian predation pressure and brood size were positively correlated. Predation pressure on nests containing 5 nestlings was more than double the value for nests containing 2 nestlings. This trend possibly exists apart from artificial brood size manipulation, although adding a single nestling to natural broods nearly doubles the mammalian predation rate. Removing a nestling has little effect on predation by mammals.

If clutch size is adapted to the limits of the female's feeding ability (Lack 1954), adding a nestling could result in a disruptive change in the feeding activity

of the female. Brood activity might also be increased, and in the presence of predators keying on activity at the nest, augmented nests should be subject to increased predation rates. Diurnal predation increases due to brood augmentation would result from predators keying on the female's feeding activity, while both nocturnal and diurnal predation should be affected by brood activity. Since nocturnal predation constituted most of the mammalian predation in this study, predators may have been keying on nocturnal brood activity. There is presently little evidence to indicate why avian predation was decreased by augmenting broods.

Summary

Predation pressure on the eggs and nestlings of Red-winged Blackbirds (<u>Agelaius</u> <u>phoeniceus</u>) was related to water depth at nest sites, habitat type, progression of season, and number of young in the nest. On the basis of signs left by predators, predations were classified into three types, thought to correspond to avian, large mammal (primarily racoon), and small mammal predators. Mammalian predation varied inversely with water depth at nest sites, particularly for large mammalian predators, the most important predator type. Avian predation varied independently from water depth. Total predation on nest contents was not significantly different between marsh and upland situations, although there were differences in the seasonal distribution of predation. Marsh predation was bimodal over season, with a primary intensity peak early in nesting followed by a secondary peak late in the season. Upland predation was unimodal over season and was most intense about 10 days after the primary marsh predation peak. This may result from density dependent responses of mammalian predators and synchrony in redwing nesting and renesting. Mammalian predation was positively correlated with brood size, where some broods were of artificially manipulated size. This pattern may exist apart from manipulation, but augmenting broods approximately doubled mammalian predation pressure and halved avian predation pressure on nestlings, compared

to natural and depleted broods. These results are discussed with particular emphasis on the effects of water depth at nest sites and the possible influences of search imagery and brood size on density-dependent mammalian predation.

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CLUTCH SIZE ADAPTATIONS OF RED-WINGED BLACKBIRDS

Frank S. Shipley

Under the influence of natural selection, organisms
tend to evolve reproductive strategies which maximize their
genetic contributions to the future. The family size which
represents the maximal transmission of a parent organism's
genes to future generations is one characteristic which is
now well recognized as being under such selective pressure.
In considering such selection among birds, Lack (1954) pro-
posed that the clutch sizes of nidicolous species are
adapted to maximize the number of surviving offspring and are
limited by the parent birds' maximal ability to provision
their hatchlings. This idea, now empirically validated for
a number of situations (Lack et al, 1957; Perrins, 1965;
Royoma, 1966; Ricklefs, 1968 and others) explains a number
of broad patterns of variation in mean clutch size, includ-
ing intra-specific differences related to latitude and many
inter-specific differences.

The number of eggs laid by individual females of many
species frequently deviates from the long term mean clutch
size of the corresponding population. The magnitude of this
deviation can vary over the course of a breeding season and
between individuals at a particular time. The clutches within
populations of red-winged blackbirds (Agelaius phoeniceus)

in temperate regions, for example, are often larger early in the season, and may vary from 2 to 6, although 4 is by far the most common over broad parts of the species' range. This kind of variation in clutch size is often greater than one would expect if clutch size is selected only to suit average environmental and parental conditions which determine the amount of food available to young.

There are 3 potential sources of clutch size variation which could explain these observations:

1) Random variation imposed by accident or circumstance. Mutation, for example, always exerts a baseline level of genetic variation. Also, pathological or nutritional influences on laying females may in some cases influence clutch size.

2) Genotypic variation maintained by natural selection as an adaptively balanced polymorphism. This could occur under conditions of varying food availability if clutch size is entirely specified by the genotype of the laying female. The clutch size of the central European swift (Apus apus) appears to be so selected (Lack, 1954). Since the availability of aerial insects which are fed to young swifts varies between years, swift productivity is maximized in bad years by birds which lay relatively few eggs, because the larger broods of other pairs are selected against by their starvation in the nest. In good years, the pairs with larger broods are more productive and are favored by natural selection; consequently clutch size is maintained

by temporally balanced selection as a dimorphism of clutches of 2 and of 3 eggs.

3) Adaptive phenotypic variation. Environments (and hence food availibilities) may change rather quickly; hence an individual with a genetically specified clutch size would be at a disadvantage under many sets of conditions (Skutch, 1967). A mechanism by which clutch or brood size is determined phenotypically (behaviorly, for example) as an adaptive response to environmental conditions, would be selected for. Such a mechanism could involve A) reduction of clutches or broods subsequent to laying. Brood reduction in the curve-billed thrasher (Ricklefs, 1965) and cannibalism among siblings in some broods of Swiss barn owls (Tyto alba, Schifferli, 1949) are examples of this kind of adaptation. Or B) adaptive phenotypic variation in the number of eggs originally laid could occur. For example, Swanberg (1951) showed that the European nutcracker (Nucifraga caryocatactes) in Sweden adapted its clutch size to the quantity of hazlenuts available for storage in the autumn prior to breeding. When Swanberg artificially supplied nuts to wild nutcrackers during the winter, these individuals laid 4 eggs, even in years when the nut crop was poor and neighboring nutcrackers laid only 3.

Thus there is probably no general solution to the problem of why so much individual variation in clutch size exists. However, there are some conditions which apply to broad

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categories of birds. On the basis of some of these conditions, I have developed a graphical model which assumes that facultative adjustment of clutch size occurs among nesting female red-winged blackbirds, as in 3(B) above. According to the model, female redwings respond to labile conditions which affect their ability to nourish young by adaptively varying the number of eggs they lay. The predictions of the model were tested with data gathered from nesting redwings.

Conditions for Adaptive Adjustment of Clutch Size

For a number of species (Klomp, 1970) the proportion of nestlings surviving to maturity depends upon their weight at some critical period during their development. Perrins (1965) for example, found the survival of great tit (Parus major) nestlings as measured by recovery of banded individuals, to be well correlated with their weight immediately before the fledge. Similar results were obtained by Lack (1947) for starlings (Sternus vulgarus).

The weight of nestlings before their independence is is turn a function of the size of the brood from which they fledge. Due to limitations on the abilities of parents to provision the young with food, individuals from large broods in many species each fledge weighing less, on the average, than do individuals from smaller broods (see Klomp, 1970, for a summary). In investigations where brood size has been artificially increased, the weight descrepency between individuals from augmented broods and natural broods is often

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even more pronounced. Such is the case for redwings (Robert-
son, 1973). Also owing to the limited ability of parents to
procure food, post-fledge conditions of food availability
for young will depend upon brood size, for species in which
the young continue to be fed by the parents subsequent to
fledging (Lack, 1966).

When the above conditions obtain, the number of young
from a brood which survive to independence will increase as
brood size increases until a critical brood size is reached.
Each additional nestling in broods larger than this critical
number will result in a net decrease in the productivity of
the nesting attempt due to starvation-related mortality.
This general unimodal relationship between brood size and pro-
duction of surviving young was postulated by Lack (1947)
and has subsequently been verified by Lack (1948b) for Swiss
starlings and by Lack (1950), Lack, Gibb, and Owen (1957),
Perrins (1965), and Perrins and Moss (1975) for titmice of the
genus Parus.

The effect of natural selection is to increase the fre-
quency of genotypes in a population which, over the parents'
breeding lifespan, corresponds to the brood size most pro-
ductive of surviving young. Under conditions of varying food
availability, however, the size of the most productive
brood would vary. Hence selection would favor either gen-
etic polymorphism or genotypes which provide for adaptive
phenotypic modification of clutch size. If the modification
of clutch size is perfectly adaptive, these parents would

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have higher fitness than parents in a polymorphic sit-
uation, since the most productive clutch size would be laid
by each female under most environmental conditions rather
than under just some. And, if the amount of food which
individual parents are able to provide to the young varies
apart from environmental conditions, as for example if food
gathering ability increases with age, adaptive adjustment of
the number of eggs laid by the female would confer further
increases in fitness. Thus facultative clutch size deter-
mination would evolve by maximizing the number of surviving
young produced, within wide limits of food availibility
determined by the natures of the environment and individual.

The Model

Let S= the proportion of nestlings surviving to maturity from a given brood and let FW= the weight of each nestling at fledging. Because of starvation-related mortality following fledging, S will be an increasing function of FW (fig. 1). The slope of the function becomes progressively shallower because weight differences at low values of FW produce disproportionately higher differences in the probability of survival than do weight differences at high values of FW, at which most young survive regardless of slight weight differences.

For each young the value of FW can be influenced by three variables: the amount of food available in the environment; the ability of the female parent to gather food for the young (in redwings, normally only the female participates in provisioning young); and the number of young present in the brood (B). Under similar environmental conditions, as for females nesting in the same habitat, FW will be determined by the female parent's ability to feed young and the number of young present in the nest. Fig. 2a represents how FW varies as an inverse function of B for the young of females with differing abilities to provision young. The weight of young from these differing females converges with decreasing B to a common value determined by physiological limitations on nestling growth rate (Ricklefs, 1967). The curves become relatively shallower
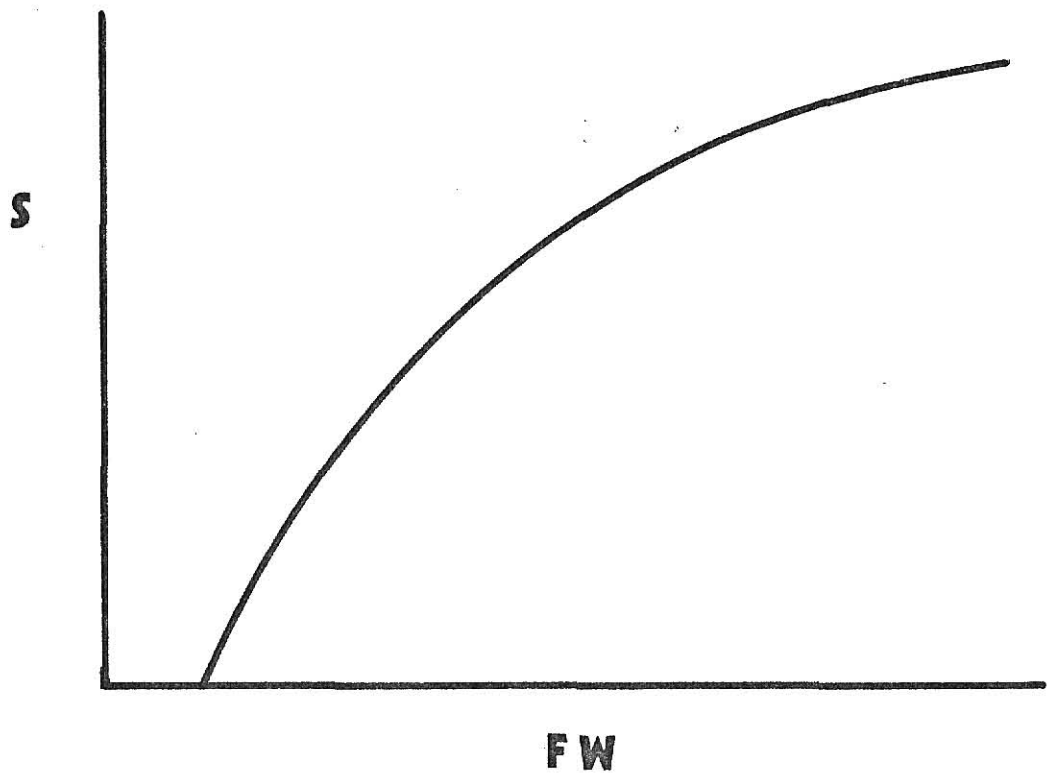
FIG. 1

S

FW

Fig. 1. Theoretical relationship between S (the proportion of nestlings surviving to maturity from a given brood) and FW (the weight of each nestling at fledging). S is an increasing function of FW with decreasing slope because of the effects of body weight on starvation-related mortality following fledging.

in slope for young from females of progressively higher
feeding ability, because increasing the brood size by an
equal increment for females of low and high ability re-
presents proportionally higher increases in feeding demands
on females of low ability than on females of high ability.

Under the conditions of fig. 1 and fig. 2a, the pro-
ductivity of each breeding attempt (P) for females of dif-
fering feeding abilities will vary with B as shown in fig.
2b, where P is defined as the number of surviving young
produced by the nesting attempt: $P = B (S)$. The graphically
derived productivity functions produce modes which differ
for females of differing feeding abilities. These produc-
tivity maxima correspond to differing values of B, repre-
sented on the abscissa in fig. 2b by the respective $\hat{B}$. For
females selected to maximize the productivity of each
breeding attempt, these $\hat{B}$ correspond to the most adaptive
number of eggs to lay, for the respective females.

Measurable Variables

For nesting redwing females, several kinds of data are
suggested by the variables of the model:

Clutch Size (C). The number of eggs laid by each fe-
male in a single nesting attempt (C) is easily determined
by nest observation.

Brood Size (B). The number of young present in the
nest between hatching and fledging (B) may also be determined
by observation. In some nests, B will differ from C due to

FIG. 2
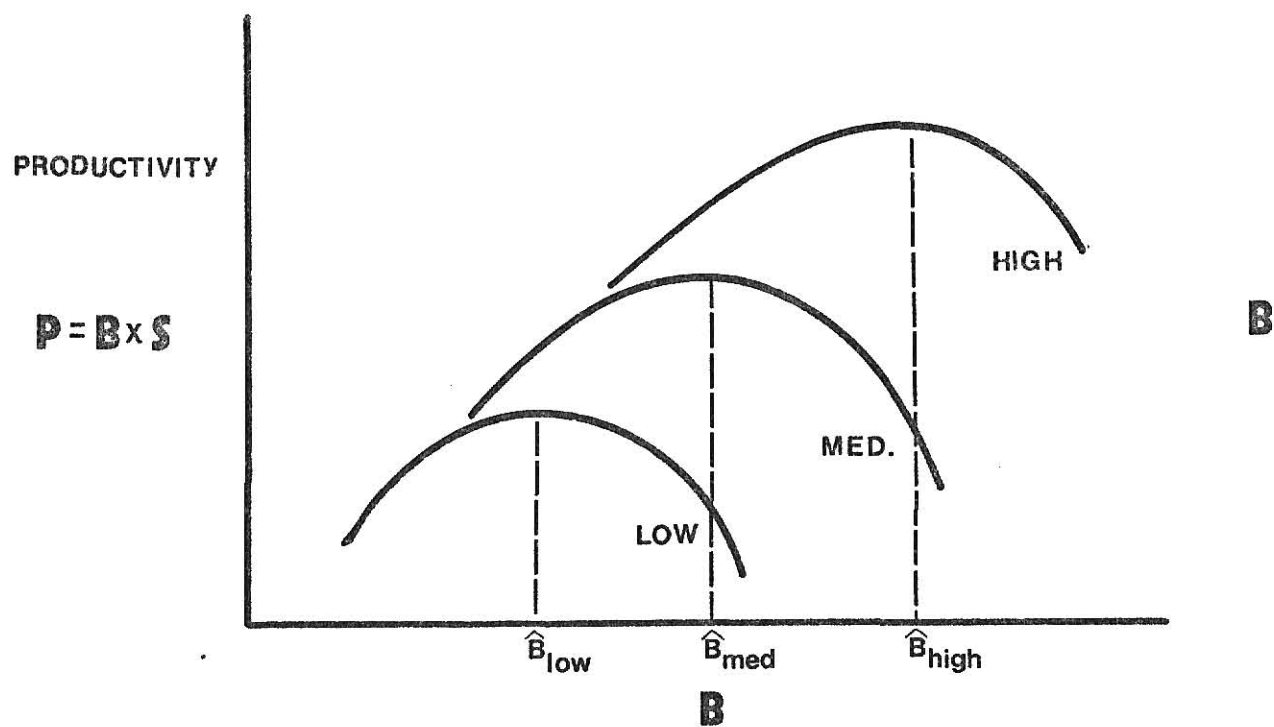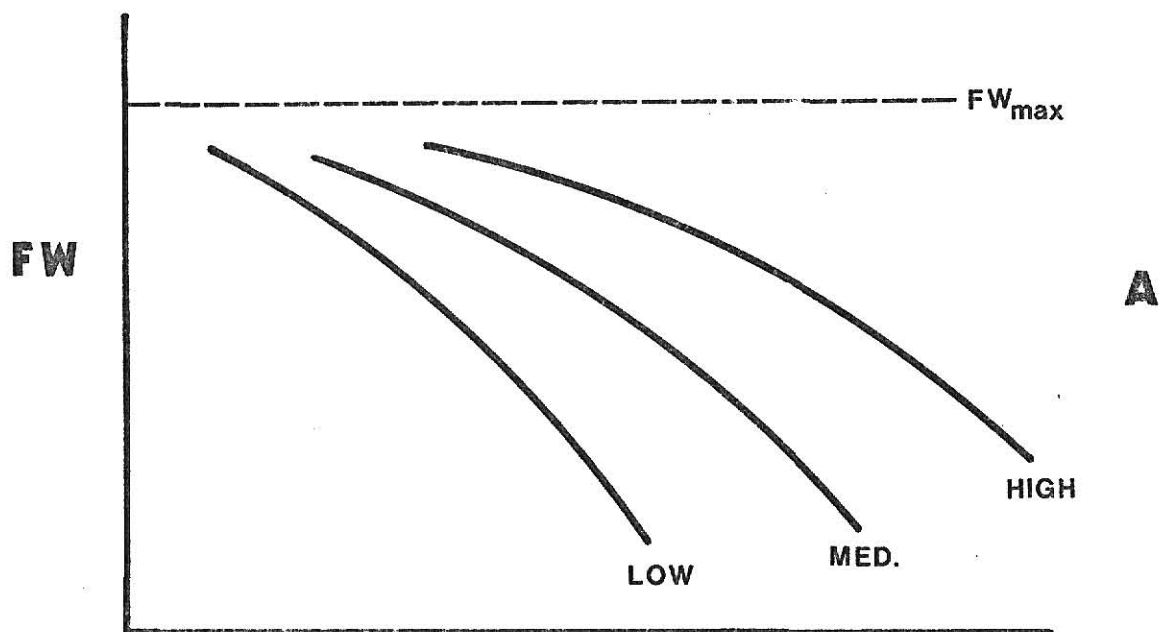
Fig. 2. A. For a given breeding attempt, FW (the weight of
a nestling at fledging) theoretically depends upon B (brood
size) and the ability of the female parent to provision young
(shown as low, med., and high). It is assumed that environ-
mental availability of food is the same for all females. At
low B, FW is limited by physiological limitations on nestling
growth rate (producing FW_{max}).

B. Productivity (P) is graphically derived from figures 1 and
2A, producing unimodal functions over B which differ for fe-
males of differing ability to provision young. If natural
selection favors maximum productivity for each breeding attempt,
the most adaptive B is given for the females of differing abil-
ity by the respective B, corresponding to maxima in the
functions.

natural reductions in the number of young present, for example when one or more young in a marsh nest fall out and drown. Further, B may be experimentally manipulated by removing nestlings or by augmenting the brood with young from other females.

Pre-fledge Weight (PFW). The weight of each young on the eighth day following the mean date of hatching of the young in the brood (PFW) may be used to approximate FW. FW can only be approximated in this way because approaching young in a redwing nest after approximately one day prior to their normal date of fledging results in a high probability of premature fledging being caused by the observer. Nestlings normally fledge about 11 days after hatching.

Number of Young Fledged. The number of young which fledge from each brood may be determined by visiting nests, inferring mortality from the absence of young prior to the expected date of fledging.

Post-fledge Growth Rate. Young redwings can often be located and captured within 20 m of the nest, for up to 3 days following fledging. Their weight at the time of capture, constitutes the mean post-fledge growth rate during this period.

Post-fledge Survivorship (S). The proportion of fledged young which survive to maturity (S) is notoriously difficult to determine. For redwings, an index, based upon differential rates of sighting and recapture of marked birds corresponding to differing PFW categories can be used

in making comparisons between post-fledge survivorship of
the members of these categories.

Predictions

1) B and the Number of Young Fledged per Nest. The
model does not account for mortality prior to fledging.
If the assumption is valid that such mortality is unim-
portant in selecting for females which lay the most pro-
ductive C, then the number of young fledged from a brood
should always be increased by depletion. Manipulation of
B could alter the proportion of young fledging from broods,
but should not depress the number of young fledged to a
value lower than the numbers fledged at lower values of
B.

2) PFW and S. According to fig. 1, S depends upon
the weight of nestlings at the time of fledging. This as-
sumption can be tested by marking nestlings on the basis
of PFW and comparing post-fledge sighting and recapture
frequencies to the frequencies to be expected in the ab-
sence of differential mortality among weight categories.
Also, if such differential mortality after fledging re-
sults from inadequate nutrition, then post-fledge growth
rates should vary with B or with PFW or both.

3) Brood Size Manipulation and PFW. According to
fig. 2a, adding nestlings to broods should decrease PFW
while subtracting nestlings should increase PFW by decreas-
ing magnitude   for successively larger brood reductions

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as PFW approaches an asymptote set by the physiological limits to growth rate. This should occur regardless of the female's ability to feed young, and can be tested by manipulating B at hatching and determing PFW for differing values of (B-C).

4) C, B, and PFW. If females lay differing numbers of eggs according to their differing abilities to feed young as predicted by the model, then the functions in fig. 2 A corresponding to females of low, medium and high ability should lay clutches which are small, medium and large, respectively. Then, females with differing C which, by virtue of artificial manipulation of the number of young present in their nests have the same B, should subsequently produce young of differing PFW. For example, a clutch of 4 augmented to produce a brood of 5 should produce young of lower PFW than broods of 5 from clutches of 5.

Methods and Study Areas

Data were gathered from 254 red-winged blackbird broods from 6 areas during the breeding seasons of 1974 and 1975. Owing to predation on nest contents (more than 50 percent of all nests were preyed on), desertion by female parents, tipping of the nests due to disproportionate growth rates among plants supporting the nest, and nest destruction resulting from storms, 93 of the 254 original nests comprised the data base for most aspects of the investigation. Nests which were found which contained young of unknown hatching date were not considered, since it was required that the age of nestlings be known.

Six study areas were utilized, all within 20 km of Manhattan Kansas. In 1974, 3 upland sites and 2 marsh sites were used. Two of the upland sites were in the Konza Prairie Research Natural Area, south of Manhattan, and each consisted of a draw containing an intermittent stream. Both areas were within undisturbed tall grass prairie communities, with redwings nesting primarily in buckbrush (Symphoricarpos orbiculata) and willow (Salix spp.). Except for one 4 m diameter pool in one area, there was no standing water, and very few cattails (Typhus latifolia) were present.

The third upland area used in 1974 was an old field surrounded by cropland. A small intermittent stream flowed through the site, and many young trees were present and were

used for nesting by redwings.

The two marsh sites used in 1974 were separate parts
of an oxbow marsh created by a past change in the course
in the Kansas River, west of Manhattan. Water depth varied
from 0 to 80 cm, with deeper water being free from emergent
vegetation and shallow water areas dominated by extensive
stands of cattails. The shallowest of the marsh sites be-
came completely dry during the summer due to below average
rainfall and above average temperature.

In 1975, only marsh-nesting redwings were studied.
Both study areas in the oxbow marsh were used, but another
area was chosen for most work. It consisted of a cattail
marsh north of Manhattan in Tuttle Creek State Park, and
is here called the "Beaver Dam Area". Redwings nested in
extensive stands of cattails over water 40-60 cm deep.

The number of eggs in the clutch were recorded upon
the discovery of each nest. The date of hatching for each
nestling was determined by subsequent visits to the nest on
alternate days. During hatching most broods were experimen-
tally augmented or depleted by removing one or more nestlings
from one nest and placing them in another. Each nest be-
longed to a "manipulation category" given by the value
(B-C) for the nest. (B-C) values ranged from -3 to +3,
with manipulations involving 0, 1 or 2 individuals being
the most frequent. Nestlings which were moved were usually
moved the same day they hatched, and never more than two
days after hatching. Such nestlings were placed only in

nests where there were nestlings of the same age in days. there were no known desertions by the female caused by observer activity.

In 1974 the nestlings in each brood were individually marked as they hatched by clipping one claw with a finger-nail clipper. The nests were then visited on alternate days until the young had either fledged or succumbed to predation or nest destruction. At each visit weight and tarsus length was recorded for each individual.

In 1975, the average hatching date for each brood was determined by averaging the hatching dates of the nestlings. As in 1974, broods were experimentally augmented and depleted during hatching to provide nests with varying B. Each nest in 1975 was not visited again until the eighth day after the average date of hatch of its nestlings. At this time PFW were determined using a Pesola 100g spring scale, and pre-fledge tarsi lengths were determined by measurment.

On the basis of dimorphism in PFW and tarsi lengths, nestlings were sexed in the field. There was sufficient PFW and tarsus length difference between the sexes on day 8 to make the distinction reliable. Sexing by this technique closely corresponded to subjective determination of sex on the basis of appearance and behavior: males appear larger, less coordinated, and less active than females.

In the Beaver Dam Area in 1975, each nestling was banded on day 8 during the gathering of pre-fledge data.

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In banding, 2 PFW categories were distinguished: nestlings which weighed more than the mean weight of all 1974 birds of the same sex and age were banded on the right leg and termed "heavyweight"; nestlings which weighed less than the mean weight of all 1974 birds of the same sex and age were banded on the left leg and termed "lightweight". The Beaver Dam Area was chosen for this part of the investigation because of its isolation from other marsh habitat into which fledglings could disperse, its relatively small size which allowed banding of essentially all nestlings, and its relatively deep water, which reduced the incidence of mammalian predation on nest contents.

Because fledgling survival in some species may be related to the date of hatch as well as to brood size or prefledge nutritional condition (Perrins 1965, Fretwell 1969, Nisbet and Drury 1972, Perrins and Moss 1975, Parsons et al 1976), data were taken only from nestlings hatched during the peak of breeding activity, insofar as was possible. Eggs were layed in the Beaver Dam Area from approximately 1 May to 10 July, but all banded nestlings were hatched from 4 June to 1 July, with most hatching near the middle of this period.

Nests containing banded individuals were visited several times during and after fledging. On such visits, if the brood had not yet fledged, the nest was not closely approached. If the brood had fledged, an area of approximately 20 m diameter surrounding the nest was searched for fledg-

lings. Fledglings could often be found and the leg carrying the band determined for up to a week after fledging. Fledglings could sometimes be caught by hand, weighed, and their band number ascertained for up to three days following fledging.

Following fledging, young redwings tended to stay in the marsh for at least 2 weeks. Daily binocular observations of birds in the marsh at large were conducted to identify banded individuals. Sightings of these banded fledged young, in which the leg carrying the band could be identified, were counted to make a comparison with the expected sighting frequency based upon equal survival of the lightweight and heavyweight fledglings. Observations were not counted which were believed to duplicate previous sightings (i.e. a banded fledgling being fed in the same location by apparently the same female on two or more consecutive days would be counted as one observation). Otherwise, sightings are assumed to represent a random sampling of the banded fledglings alive in the marsh.

In order to account for sexual size dimorphism in the weight of nestlings and fledglings in correlating their PFW with pre-fledge conditions and post-fledge survivorship, the PFW of each individual is given as a percentage of the mean day 8 weight of all nestlings of the same sex from "natural" nests (i.e. where C = B). For example, a male and a female nestling, each with a PFW of 94 percent are defined as similarly underweight, though the actual weight of these two

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would differ by some 10 g at fledging due to sexual di-
morphism.

Results

Brood Size and Number of Young Fledged per Nest

In fig. 3, each point plots the mean number of young
fledged per nest for broods of the same B belonging to the
same manipulation category. The mean number of young fledged
per nest increased with B, shown by the regression line. In
spite of decreased PFW of nestlings from augmented broods
(described below), mortality due to starvation was insuf-
ficient to depress fledging success at high values of B.
Thus, over all manipulation categories and for resulting
broods of all sizes, the proportion of the brood which fe-
males were able to raise to successful fledging remained
approximately constant at a value denoted by the slope of
the regression line. These data do not imply, however, that
production of surviving young increased with B. Productiv-
ity of a nest is defined for this investigation as P = B(S),
where S = the proportion of the brood which survives to
maturity.

A substantial part of the variation in mean number
of young fledged per nest is explained by the manipulation
category to which nests belong. In general, broods which
were experimentally reduced to a given B fledged more young
than did broods which were augmented to that size. Thus in
fig. 3, points which represent brood depletions fall above
points representing brood augmentations, where there were
depleted and augmented broods of the same size.

FIG. 3

YOUNG FLEDGED PER NEST

B
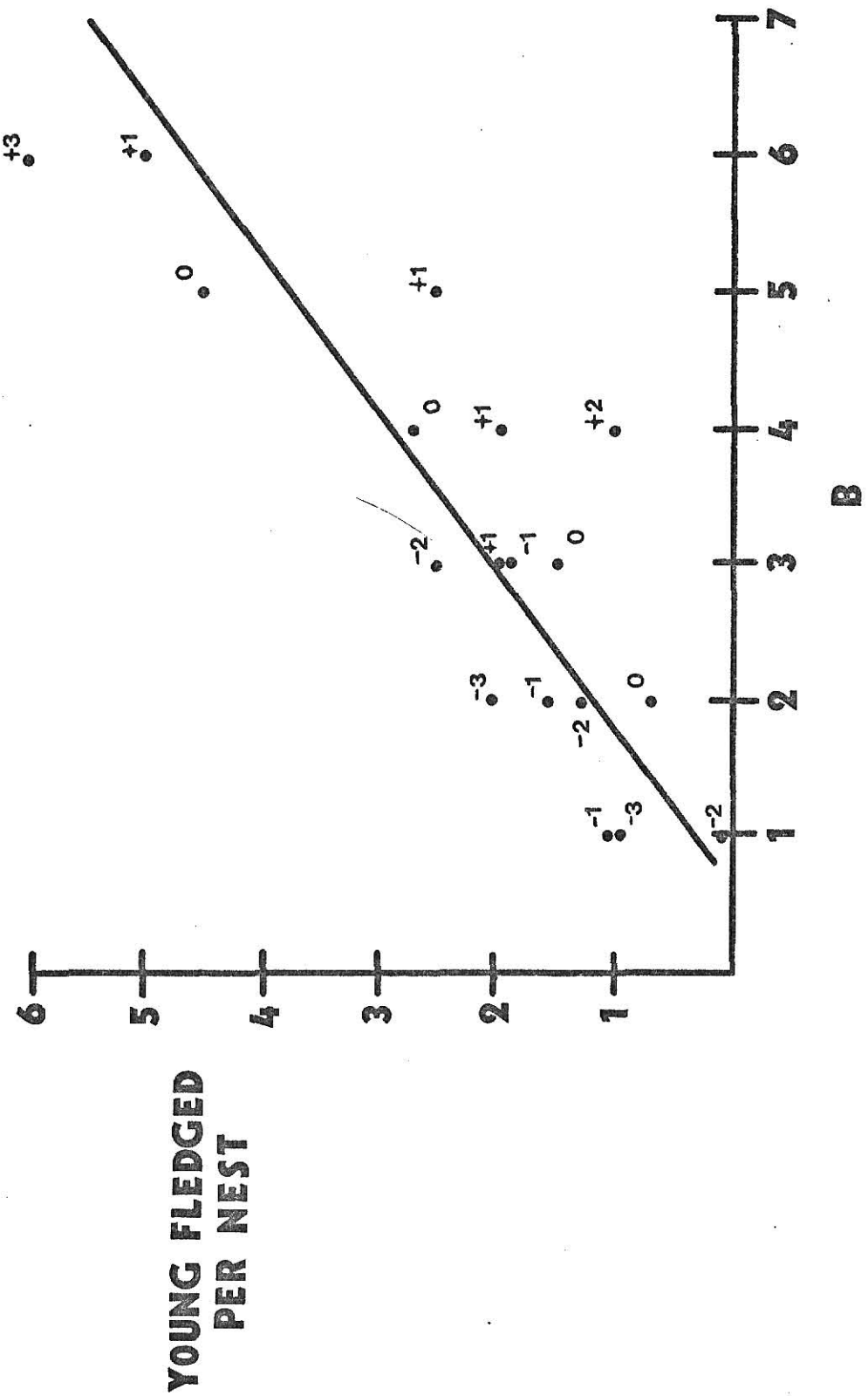
Fig. 3. Number of young fledged per nest is given as a function of brood size (B), for all nests in which young hatched. Each point represents the mean value of nests of the same manipulation category. The manipulation category is given by the figure associated with each point; negative values represent broods which were experimentally depleted at hatching and positive values represent broods of originally smaller clutch size which have been experimentally augmented at hatching. 0 denotes broods which were equal in size to the original number of eggs laid. The linear regression line is plotted.

Nestling Pre-fledge Weight and Survival

The relative frequencies of post-fledge sightings
were different for lightweight and heavyweight nestlings
(table 1). Taking into account the difference between these
two PFW categories in numbers of young fledged, heavyweights
were represented more frequently in post-fledge sightings
than were lightweights, by a factor of about 2.7. Using X^2
contingency analysis and assuming randomization in the sight-
ings of all banded fledglings in the marsh, the frequency
of sighting was found to be dependent on the PFW category
(for all $\alpha \geq .025$).

The relative frequencies of fledgling hand recaptures
differed similarly between lightweight and heavyweight in-
dividuals. However, owing to the small number of fledglings
recaptured, X^2 analysis was unable to show any dependence
of recapture frequency on PFW category (at the $\alpha = .05$
level).

Based on a comparison of the nestlings' PFW and their
weight at the time of recapture, for nestlings which were
recaptured near the nest following fledging, mean total
weight changes and mean daily rates were calculated for
fledglings from augmented, natural, and depleted broods
(table 2). Fledglings from depleted broods had a mean daily
growth rate which was positive during this period, while
nestlings from natural and augmented broods had negative
mean daily growth rates. When the data for nestlings from
natural and augmented broods were lumped and compared to

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	Lightweight Nestlings	Heavyweight Nestlings
Total no. banded	47	71
Mean PFW	83.72	103.20
No. known deaths in nest	5	1
No. thought to fledge	37	69
No. post-fledge sightings	5	25
No. post-fledge recaptures	2	10

Table 1. Data related to post-fledge survival of lightweight and heavyweight nestlings banded in the Beaver Dam Area in 1975. See methods for an explanation of "lightweight" and "heavyweight" nestlings. Pre-fledge weight (PFW) is expressed as a percent of the sex-specific mean pre-fledge weight of all young from undisturbed nests, in order to account for sexual size dimorphism in the lumping of data from nestlings of both sexes. Sighting frequencies do not necessarily represent separate individuals.

	Brood Manipulation Category		
	Depleted	Natural	Augmented
Mean brood size	2.5	5	5
No. fledglings re-captured	6	2	4
Mean post-fledge weight change (g)	+0.50	-2.25	+1.50
Mean post-fledge weight change per day (g)	+0.32	-1.63	-1.19

Table 2. Post-fledge growth data for fledglings banded in the Beaver Dam Area in 1975, which were recaptured near the nest from which they fledged 1- 3 days subsequent to fledging.

depleted brood data, both the mean total weight change and mean daily weight change were found to be significantly greater for the young from depleted broods (for all $\alpha \geq .02$ using a 2-tailed t-test).

Brood Size Manipulation and Nestling Pre-fledge Weight

Nestling PFW was significantly affected by brood size manipulation during hatching (fig. 4). The mean PFW of nestlings from broods augmented by 1 or 2 individuals was about 90 percent of the mean PFW of nestlings from broods depleted by 1 or 2 nestlings. The difference in mean PFW between all augmented brood nestlings and all depleted brood nestlings was significant (for all $\alpha \geq .01$, using a 2-tailed t-test).

For brood augmentations of 1 nestling the mean PFW was reduced by about 7 percent; for augmentations of 2 nestlings, the mean PFW was reduced by about 27 percent, below the mean PFW of young from non-manipulated broods. For brood depletion, however, there was no significant difference in mean PFW between non-manipulated broods and the -1 or -2 manipulation categories. A one-way ACV on nestling PFW among the 0, +1, and +2 manipulation categories detected a significant difference among the mean PFW of these categories (for all $\alpha \geq .002$, using a 2-tailed test). A similar analysis on the 0, -1, and -2 manipulation categories could not detect a difference among mean PFW values for these categories (for $\alpha = .05$).
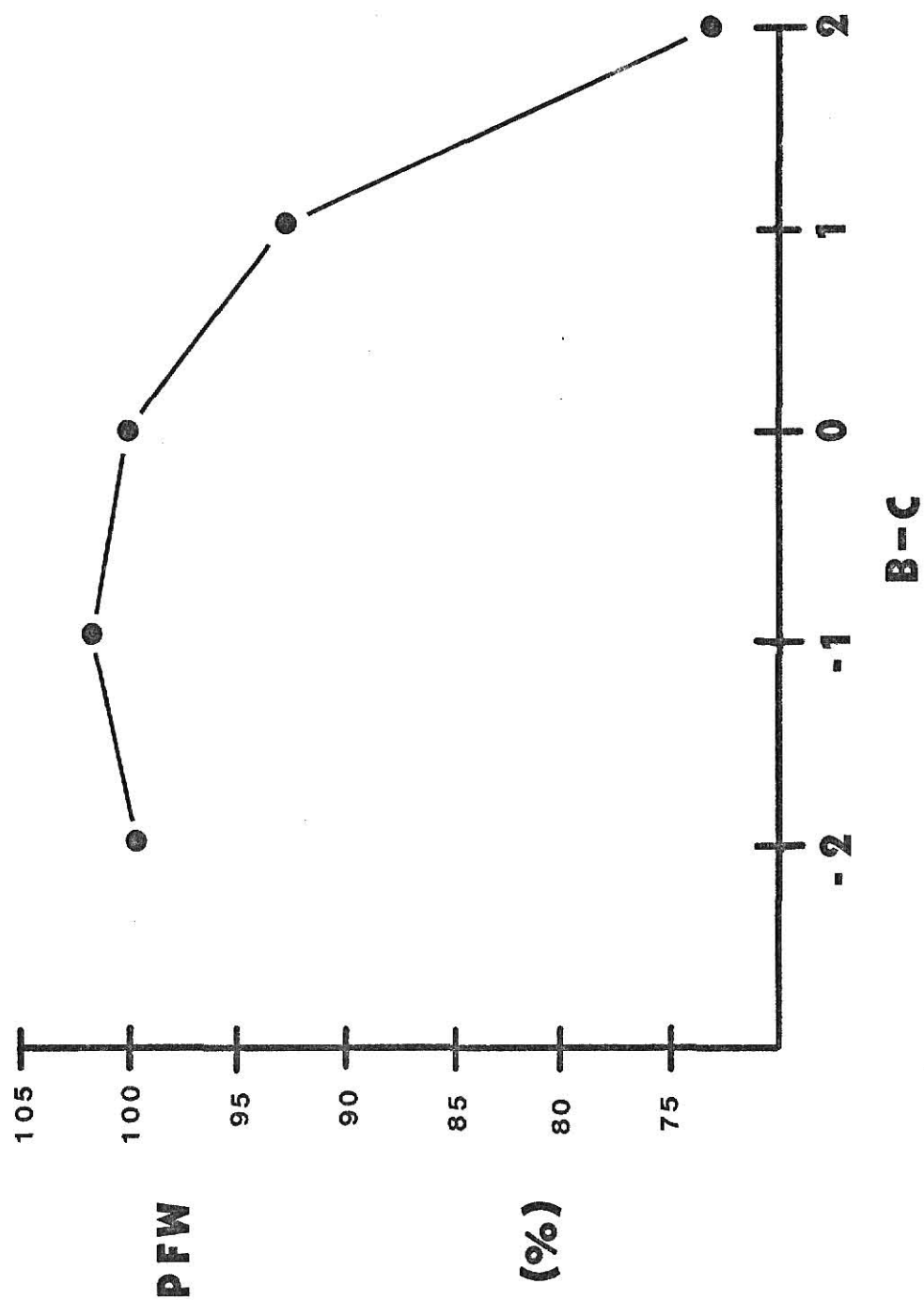
-55-

FIG. 4

Fig. 4. Pre-fledge weight (PFW) is plotted for young from broods of different manipulation categories. Brood size (B) minus clutch size (C) designates the manipulation category of the nests (number of nestlings added to or subtracted from the brood during hatching). Each point plots the mean PFW for all young belonging to the same manipulation category.

Clutch Size, Brood Size, and Nestling Pre-fledge Weight

Nestling PFW was found to vary as an inverse, curvilinear function of B, with substantial variation. Much of this variation was explained by differences in C (fig. 5). Each of the four functions is approximately level to the left of the point where C = B, due to the similarity in the mean PFW among all depletion categories. (See fig. 4). To the right of the point where C = B, each function declines, a result of successively lowered PFW for broods augmented by successively more individuals.

Due to the relative infrequency in nature of nests which contained clutches of 2 and of 5, and because the necessity of exact timing in exchanging nestlings between nests dictated which C:B combinations could be generated, some by points plotted in fig. 5 are represented by few nestlings. Points which are represented by 2 or fewer nestlings are plotted as a double circle in the figure.

FIG. 5

C=2 ......
C=3 ——
C=4 ———
C=5 -----

PFW

(%)

B

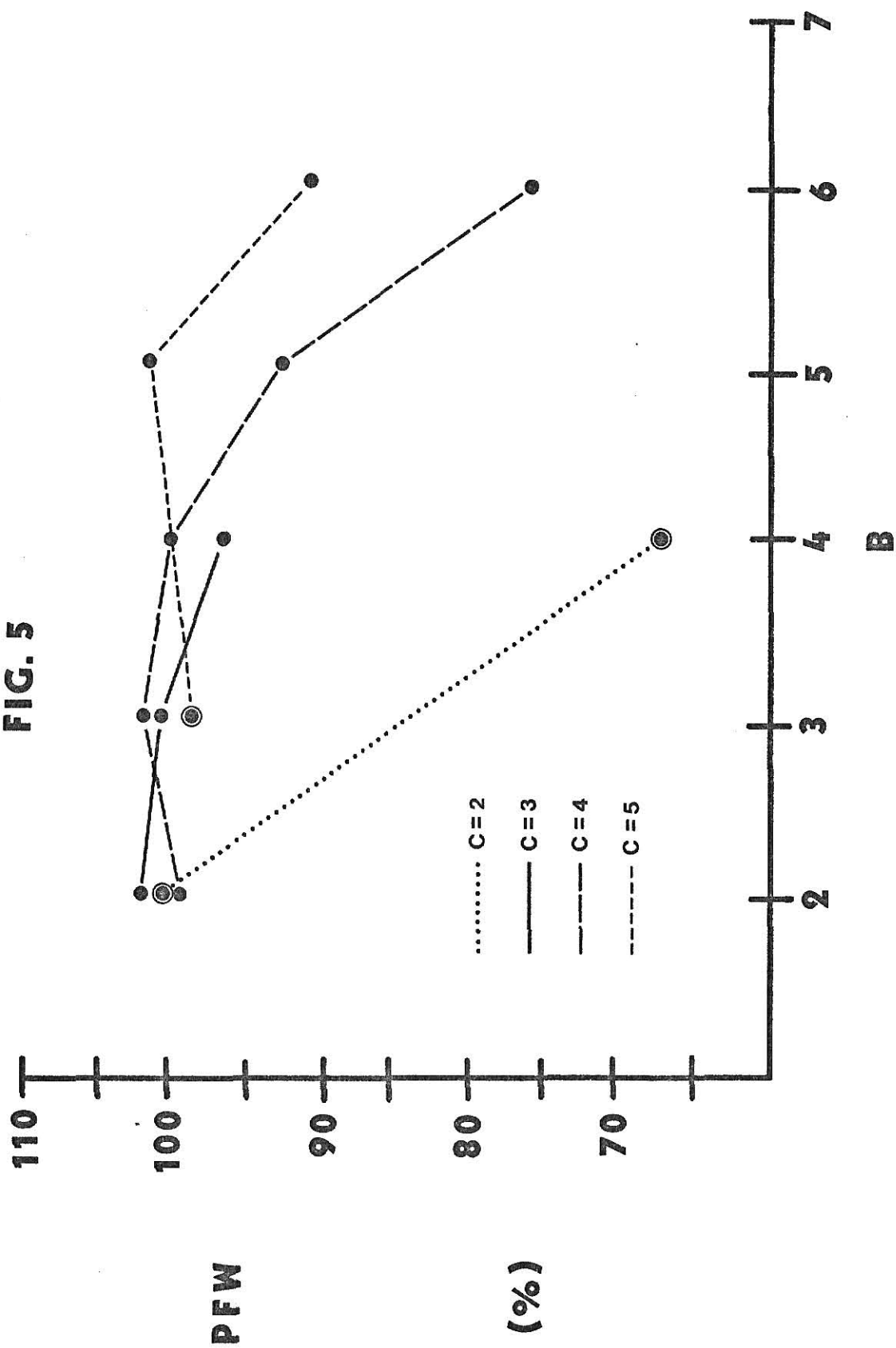Fig. 5. Relationship between clutch size (C), brood size (B), and nestling pre-fledge weight (PFW). C and B usually differ for each nest due to experimental augmentation and depletion of broods during hatching. Each point plots the mean PFW for all young of a particular C and B. Points plotted as double circles represent 2 or fewer young due to the rarity in nature of extremely large and small clutches.

Discussion

The existence of adaptive phenotypic variation in the clutch size of birds has previously been suggested. In a 7-year study of the collared flycatcher (Ficedula albicollis), Lohrl (1957) found the percentage of young successfully fledging from natural nests to increase with clutch size. Because clutch size decreased with season, he suggested that the birds were laying more eggs when conditions for raising young were more favorable.

Kluyver (1963) found that the productivity of female great tits, as measured by the recovery of banded females the next year, steadily increased with the number of young fledged. The number of young fledged in a season was quite variable between females, and according to Kluyver, phenotypically so. Klomp (1970) has interpreted this as evidence for the adaptive non-hereditary modification of clutch size.

Ward (1965) manipulated the clutch size in nests of the black-faced dioch (Quelea quelea) in Nigeria. In 3 artificially augmented broods of 4 individuals, 66 percent of the nestlings fledged, compared to 81 percent for 4 natural broods of 4. Although these results are inconclusive due to small sample sizes, they show the possibility of adaptive variation in this species.

Perrins (1965) found the clutches of great tits to be larger for older female parents than for yearlings.

Since the older birds also produced more surviving young per brood, Perrins proposed that natural selection must favor the laying of a small clutch among yearlings; by doing so females could maximize their production of surviving offspring over their breeding lifespan. This would constitute natural selection for adaptive phenotypic determination of clutch size.

Evidence from this investigation suggests that adaptive phenotypic modification of clutch size occurs among red-winged blackbirds. For females in the Beaver Dam Area with the same experimentally determined brood size, the mean number of young fledged was partly dependent on how many eggs were added or subtracted to form the brood; the larger the original clutch, the more young fledged, on the average (fig. 3). The reasons for this are not entirely clear. However, mortality in the nest (primarily starvation) is known to have occured in 5 cases for lightweight young and only once for heavyweights. Because the lightweight young were largely from augmented broods and the heavyweight young from depleted and natural broods (see fig. 4), such mortality would tend to explain differences in the proportion of young fledging for nests of different manipulation categories with broods of the same size. Natural brood reduction may also have occured more frequently in augmented nests than in depleted or natural nests. Such reductions were present, though they were infrequent and not carefully investigated in this study. For cases where broods were

naturally reduced in size, it is unknown whether the occur-
ence resulted from adaptive behavior by the female parent,
from accident (for example a nestling falling out of the
nest) or from predation, where the predator was unable to
eat an entire brood. In any case these factors were rela-
tively insignificant in showing ability differences be-
tween females; essentially all young fledged regardless of
experimental treatment.

Stronger evidence for the existence of adaptive clutch
size adjustment is evident in the test of prediction 4 of
the model, the results of which are given in fig. 5. Mean
PFW of nestlings was related inversely to the size of man-
ipulated broods, and increments of B over which declines
in PFW occured depended largely upon the original number
of eggs in the clutch. Two points are important. First,
there was no significant difference among mean PFW of nest-
lings from non-manipulated broods of different sizes, indi-
cating that females which had larger clutches procured
more food for their brood. These data agree with Robertson
(1973) who found no significant difference in growth rate
or mean fledging weight among redwing nestlings in natural
nests of various clutch size. Second, there were pronounced
differences in mean PFW for nestlings belonging to broods
of the same size but which were formed from clutches orig-
inally different in size, indicating that females with
small original clutches could not provision more young
than the number of eggs they laid, without reductions in

nestling weight.

On the basis of mortality prior to fledging, it would appear that clutch size is not constrained by limitations on the provisioning of young: large broods fledged more young on the average than did small broods, regardless of differences in PFW brought by manipulation. This is in agreement with Robertson (1973) who found the number of redwing young fledging per successful nest to be directly related to clutch size, for nests of natural and manipulated brood size. These conditions however, are assumed in the model (prediction 1) and point to the possibility of events after fledging as being of highest potential importance in selecting for an adaptive clutch size adjustment mechanism. If the PFW of young is important in influencing their chances for survival following fledging, females which lay clutches of differing size could be doing so adaptively on the basis of their ability to provision young.

The sighting frequency for fledglings was found to be dependent upon PFW category: heavyweight fledglings were sighted some 2.7 times more frequently than one would expect if sightings occured randomly on the basis of numbers fledged in each category. Undernourished fledglings could have dispersed from the marsh more readily upon fledging, but because redwing young depend upon parental feeding for up to several weeks after fledging, differential dispersal seems unlikely at least until fledglings become independent. There remains the possibility that lightweight fledglings

were less active or less able to climb to high perches in the vegetation, and thereby were less conspicuous, but there are no data available to evaluate this possibility.

These data on survival and nestling weight changes resulting from experimental brood size manipulation show the importance of brood size in its effect on offspring fitness, supporting the idea that natural clutches are adjusted individually by each female parent to assure that young are provisioned adequately for survival.

The post-fledge growth data, although scant, provide further information related to mortality of young. Nestlings from depleted broods gained weight at an average rate of about 1.3 percent per day during the period beginning at fledging, based on recaptures of 6 individuals. Fledglings from natural broods and those from augmented broods both lost weight at an average rate of about 4 percent for these two categories lumped. Surprisingly, young from natural broods had a greater average weight loss than did the young from augmented broods, but this could result from inadequate sample size. Also, the weight changes could result from brood size per se, since depleted broods averaged only half as large as augmented and natural broods.

Royoma (1966), Lack (1966), Perrins (1965), Klomp (1970) and others have stressed the potential importance of internal stored food reserves, in the form of fat, to fledging young birds. For redwings this appears to be quite important; the presence of stored reserves in nest-

lings may allow survival from fledging until nutritional
independence; the absence of these reserves could explain
the apparent mortality of lightweight young.

Post-fledge mortality may also have been influenced
by brood augmentation apart from the nutritional effects
caused on young prior to fledging. When redwings fledge,
they normally radiate from the nest in all directions for
up to approximately 20 m. Because they are scattered and
often quite hidden, the effort put forth by the female in
feeding them may at this time become limited such that she
cannot supply their needs as adequately as when they are
all together in the nest. Increased activity of the young
may further increase demands on the female. These influen-
ces may compound the nutritional effects on nestlings
caused prior to fledging and thus increase mortality of
young from inordinately large broods.

Whether mortality is selectively imposed upon nestlings
from different brood sizes during any period other than
immediately following the fledge remains to be demonstrated.
There are currently no data available on post-dispersal
mortality rates for redwings, and such mortality, if it
exists, may well bear no relation to conditions during the
breeding season. Perrins and Moss (1975) have stated that
differential mortality of great tits does not extend be-
yond three months after fledging. Similarly, Nisbet and
Drury (1972) found mortality in herring gulls (Larus arg-
entatus) to be related to pre-fledge conditions only for

several months following the breeding season. Also, if post-dispersal mortality is an agent selective on the basis of brood size, it may well constitute further selection against nestlings from large broods.

Starvation-related mortality of young prior to nutritional independence is thus likely to be the most important source of selection against parents which only poorly assess their ability to care for young and produce young too numerous to be nutritionally fit for survival. However, there are other parental fitness loses deriving from brood size-dependent mortality which are potentially important in determining the optimum brood size but which are not inherent in the model presented here because they are not related to the nutritional condition of nestlings. For example Fretwell (1969) has pointed out a mechanism by which dominance hierarchies may influence the parental fitness to be gained by a given breeding effort. If late-reared young have a reduced survival or reproductive potential because of subdominance to older young, then the parents of these late-reared young have a lower fitness than if they had bred earlier. In the extreme, when all young from a breeding attempt are certain to die as a result of interaction with more dominant individuals following the breeding season, the parents' most adaptive clutch size is zero. Fretwell offers this as an explanation for non-breeding. And if young within broods set up dominance hierarchies where dominant young receive more food than subordinates,

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this idea can explain reduced clutch size.

A second source of fledgling mortality which is potentially important in determining the most adaptive clutch size is predation. If predation is dependent on brood size because predators are able to locate larger broods more often than smaller ones (Perrins 1965, Shipley in prep.) or because they are able to key on the feeding activity of parents, as Skutch has proposed (1967), then the size of the most productive clutch could be reduced. If, for example, extremely high brood size-dependent predation rates occur where food is abundantly available to parents seeking to provision their young, then the most adaptive clutch size could be lower than the size which is most adaptive in the absence of predation. Whether these effects could be important for redwings was not apparent in this investigation, because deep water in the Beaver Dam Area reduced mammalian predation rates to near zero. However, because redwing clutches found in upland habitats can be smaller than those in marshes, (Robertson 1973) predation may be an important factor.

The model, then, is not valid when mortality of young is related to brood size but not to nutritional state. The extent to which such mortality occurs is unknown; only recently have dominance hierarchies been extensively considered in their effect upon population size. Predation of the sort described above has largely and perhaps unjustly been discounted, in favor of Lack's (1954) theory of clutch size.

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According to prediction (3) of the model, depleted broods should fledge young of an increased PFW. The results are somewhat surprising in that this clearly did not occur (fig. 4). There was no significant difference among the 0, -1, and -2 manipulation categories in mean PFW, based on an analysis of variance, while PFW for young from augmented broods was strongly and inversely correlated with the number of young added. From these results, clutch size appears to be adjusted to fledge young of a particular weight limited from above.

The factors which set this limit are not apparent, but potentially, this pattern could result from nestling growth rates approaching a physiological limit. Ricklefs (1967) has pointed out that selective pressure exerted by predation should tend to shorten the vulnerable nestling period. If such selection is strong enough, the period in the nest could be limited by the physiological limits to growth. It is unknown whether these young grew at the maximum rate possible - experimental gorging could determine whether this is true. Also, nestling behavior may mediate their consumption of food: begging may cease at the level of nutrition which is required for maximal growth. Thus while the potential amount of food available to each young from a brood reduced by 2 was more than the potential amount available to each young in a brood reduced by 1, nestling consumption of food could have been the same because in both cases young were assimilating a maximal amount.

There are some problems in interpreting the extent to which the model proposed here is valid. It assumes that the most adaptive clutch size is the one which is most productive of surviving offspring in any particular breeding attempt (fig. 2b). This is not likely to be a valid assumption under all circumstances.

Charnov and Krebs (1974) have produced a model which assumes that adult mortality increases with clutch size. When this condition is met over clutch size increments beginning below the most productive clutch size, the most adaptive clutch size is predicted to be below the most productive. There is little direct evidence that adult mortality is related to brood size, although brood size dependent predation could increase the probability of predation on a brooding parent. However, actual clutches smaller than the size most productive of surviving offspring are known in species for which enough data exist (Ward 1973, Perrins and Moss 1975) as the Charnov-Krebs model predicts.

Smith and Fretwell (1974), in dealing with the trade-off between the number and energetic expense of young have assumed that at any point in an organism's life history there is an optimum percentage of available energy that should be diverted to reproduction. Their fitness set analysis model predicts an optimum energy expenditure per offspring, which under most circumstances does not maximize the fitness of each offspring. Because reproductive energy expenditure is a constant, the optimum clutch size is also

specified by this prediction. The clutch size of redwings, if the assumptions of this model are met, could be smaller than the size which is most productive of surviving offspring, in order for the fitness of the female parent to be maximal. The Smith-Fretwell model further predicts that fitness is greater for females laying a number of eggs one fewer than the optimal clutch size than it is for females laying one more than the optimal number. Therefore, when adjustment of clutch size to correspond to nutritional resources and parental ability to procure resources is imperfect, the determination of clutch size by the parent should be conservative, tending to reduce the sizes of actual clutches even further below the size which is most productive.

Thus in applying the model, an assessment must be made as to how aspects of breeding other than the productivity of each attempt influence parental fitness. Even for redwings the idea that the most productive clutch is the most adaptive remains untested. Only an index to nestling survival was calculated here because of the difficulty of procuring complete survivorship data; the productivity of clutches varying in size is unknown. Productivity of surviving offspring, however, remains the most important determinant of fitness. Whatever factors cause clutch size to depart from the most productive size presumably act in a similar fashion among parents of differing ability to provision young. The identity of these factors and the extent to which

they operate in determining actual clutch sizes were beyond the scope of this investigation, but would be quite important in investigating the relationship between productivity and fitness.

Red-winged blackbirds may in fact be somewhat special in their ability to facultatively adjust clutch size. They are territorial but their territories do not necessarily function as a defendable food supply. Males and females forage both on and off the territory, making possible the simplifying assumption that the amount of food available to all females in a population at a given time is similar. Differences in the amount of food available to young are thus primarily a function of differences in the foraging abilities of the female parents. Any clutch size adjustment mechanism evolving will therefore be based on these ability differences.

In comparison, for species which maintain a territory as a defensible source of nutrition, the food available to young is a function of parental ability and of the size of the territory. Any clutch adjustment mechanism evolving under these circumstances need not be as perfectly adapted to parental ability; clutch size and territory size could intercompensate. This may explain why weights of fledging young vary between natural broods of differing size in many species. For a number of species (klomp 1970), the young from large natural broods each receive less food than young from small natural broods and thereafter fledge weighing

less. For great tits, such weight differences in some seasons (Perrins 1965) result in enough mortality of large-brood individuals to make large broods less productive than smaller broods. If clutch size adjustment exists here, it is imperfect.

What determines parental ability and how do parents assess their ability in relation to the quantity of food available? There is some evidence that age may be important in determining ability because younger birds have been observed to lay smaller clutches (Perrins, 1966; Coulson and White summarized in Lack 1966), but the mechanism by which the clutch is adjusted to adaptively account for variation in parental ability to feed offspring remains unknown.

Summary

In the context of more general aspects of clutch size
hypothesized by Lack (1954), a model was developed which
accounts for individual variation in the number of eggs laid
by female red-winged blackbirds (Agelaius phoeniceus). The
model assumes adaptive phenotypic variation in clutch size to
exist as a response to the plasticity of conditions affecting
the ability of female parents to nourish young. Artificial
manipulation of brood size and the monitering of nestling
weight and survival prior to, during, and immediately after
fledging were undertaken to test the model. In agreement
with the model, artificially manipulated broods of the same
size formed from original clutches of differing size fledged
young of differing weights, but pre-fledge weights of nest-
lings from natural broods of differing size were the same.
The pre-fledge weights of nestlings from augmented broods
were less than pre-fledge weights of young from natural broods,
but there was no difference between young from natural and
depleted broods. Brood size may therefore be adapted to
fledge young of a particular upper-limited weight. The num-
ber of young fledged per nest varied directly with brood
size, but post-fledge survivorship was strongly dependent
upon pre-fledge weight, with mortality imposed selectively
on lightweight young by starvation-related death following
fledging. These results tend to confirm the idea that red-
wing family size is facultatively adapted to the feeding
abilities of individual females, and mediated by the abun-

dance of food. The model may be generally applicable without modification only for species resembling redwings in their pattern of resource use.

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RED-WINGED BLACKBIRD STUDIES:

I. PREDATION ON RED-WINGED BLACKBIRD EGGS AND NESTLINGS

II. CLUTCH SIZE ADAPTATIONS OF RED-WINGED BLACKBIRDS

by

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AN ABSTRACT OF A MASTER'S THESIS

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I. Predation pressure on the eggs and nestlings of red-winged blackbirds (Agelaius phoeniceus) was related to water depth at nest sites, habitat type, progression of season, and number of young in the nest. On the basis of signs left by predators, predations were classified into three types, thought to correspond to avian, large mammal (primarily racoon), and small mammal predators. Mammalian predation varied inversely with water depth at nest sites, particularly for large mammalian predators, the most important predator type. Avian predation varied independently from water depth. Total predation on nest contents was not significantly different between marsh and upland situations, although there were differences in the seasonal distribution of predation. Marsh predation was bimodal over season, with a primary peak late in the season. Upland predation was unimodal over season and was most intense about 10 days after the primary marsh predation peak. This may result from density dependent responses of mammalian predators and synchrony in redwing nesting and renesting. Mammalian predation was positively correlated with brood size, where some broods were of artificially manipulated size. This pattern may exist apart from manipulation, but augmenting broods approximately doubled mammalian predation pressure and halved avian predation pressure on nestlings, compared to natural and depleted broods. These results are discussed with particular emphasis on the effects of water depth at nest sites and the possible influences of search imagery and brood size on density dependent mammalian predation.

II. In the context of more general aspects of clutch size hypothesized by Lack (1954), a model is developed which accounts for individual variation in the number of eggs laid by female red-winged blackbirds (Agelaius phoeniceus). The model assumes adaptive phenotypic variation in clutch size to exist as a response to the plasticity of conditions affecting the ability of female parents to nourish young. Artificial manipulation of brood size and the monitoring of nestling weight and survival prior to, during, and immediately after fledging were undertaken to test the model. In agreement with the model, artificially manipulated broods of the same size formed from original clutches of differing size fledged young of differing weights, but pre-fledge weights of nestlings from natural broods of differing size were the same. The pre-fledge weights of nestlings from augmented broods were less than pre-fledge weights of young from natural broods, but there was no difference between young from natural and depleted broods. Brood size may therefore be adapted to fledge young of a particular upper limited weight. The number of young fledged per nest varied directly with brood size, but post-fledge survivorship was strongly dependent upon pre-fledge weight, with mortality imposed selectively

on lightweight young by starvation-related death following fledging. These results tend to confirm the idea that red-wing family size is facultatively adapted to the feeding abilities of individual females, and mediated by the abundance of food. The model may be generally applicable without modification only for species resembling redwings in their pattern of resource use.