

EGG AND CLUTCH SIZE IN RELATION TO BROOD REDUCTION
IN THE YELLOW-HEADED BLACKBIRD.

by

COLLEEN ANNE BARBER

A thesis
presented to the University of Manitoba
in fulfillment of the
thesis requirement for the degree of
MASTER OF SCIENCE
in
DEPARTMENT OF ZOOLOGY

Winnipeg, Manitoba
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COLLEEN ANNE BARBER

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
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MASTER OF SCIENCE

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Morning has broken, like the first morning,
Blackbird has spoken, like the first bird,
Praise for the singing, praise for the morning,
Praise for them springing, fresh from the world.

- Cat Stevens -

Whatever you can do, or dream you can,
Begin it.
Boldness has genius, power and magic in it.
Begin it now.

- Goethe -

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ABSTRACT

Brood reduction in relation to egg size and clutch size in the Yellow-headed Blackbird (Xanthocephalus xanthocephalus) was studied at Crescent Pond, Delta Marsh, Manitoba during the 1988 and 1989 breeding seasons. Clutch size ranged from 2 to 5 eggs with 3- (35.6%) and 4-egg clutches (57.9%) being the most common. Egg length and breadth, measured on the day of laying, were used to calculate egg size (cm^3). For each clutch size, eggs were significantly larger in 1988 than in 1989. Egg size varied inversely with clutch size in 1988, but not in 1989. In 1989, eggs in four-egg clutches became significantly smaller as laying progressed, while in 1988, egg size did not vary significantly with laying order in any of the clutch sizes. Despite the absence of a decreasing egg-size strategy in 1988, brood reduction continued to occur (67% of nests underwent brood reduction with 30.1% of nestlings dying). Females did not consistently produce smaller terminal eggs to facilitate brood reduction. Instead, energetic constraints on egg size were likely present in 1989, with females producing terminal eggs that were as large as possible within constraints set by the food supply and/or their own physiological condition.

Clutches were enlarged or reduced experimentally by one egg to test the individual optimization hypothesis (IOH), which states that a female lays a clutch of a size that is optimal to her ability to rear nestlings. Predictions that enlarged or reduced broods would be less productive or have lowered offspring growth rates/fledging masses were not supported in 32 of 35 instances, hence the IOH was rejected for this population. Productivity was similar for the modal clutch size of four eggs (mean \pm SE = 2.31 \pm 0.19 fledglings/nest) and the clutch size of three eggs (mean \pm SE = 2.58 \pm 0.20 fledglings/nest). The insurance-egg hypothesis, which states that an "extra" egg is laid as insurance against hatching failure or accidental death of other eggs or young, was invoked as a plausible alternative explanation for the maintenance of a modal clutch size of four eggs in the Yellow-headed Blackbird. The finding that a 0.316 probability existed that the fourth egg would hatch when at least one of the first three eggs would not suggests a relatively high potential insurance value for fourth-laid eggs in this species.

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GENERAL INTRODUCTION

Lack (1954) developed the brood reduction hypothesis, which states that individual, altricial female birds commonly lay more eggs than they are likely able to rear to fledging. Hatching asynchrony within broods was then assumed to set up competitive asymmetries among nestlings that would facilitate the elimination of the later-hatched nestlings in the event of a food shortage. Brood reduction was thought to allow parents to facultatively balance brood size with the available food supply, maximizing their reproductive success in an environment with fluctuating amounts of resources.

Hatching asynchrony is commonly considered to be the main manipulation (sensu Alexander 1974) employed by parents to enhance brood reduction (Ricklefs 1965, O'Connor 1978, but see Clark and Wilson 1981). Another parental manipulation considered to facilitate brood reduction in some species is laying smaller terminal eggs (O'Connor 1978, 1979, Slagsvold et al. 1984). Nestlings from smaller eggs die quickly unless food is abundant (O'Connor 1979). For species that adopt such a brood-reduction strategy, egg size should decline with laying order (Slagsvold et al. 1984). Yellow-headed Blackbirds (Xanthocephalus xanthocephalus) have one of the highest frequencies of

brood reduction (Young 1963, Richter 1984) and are thus ideal subjects to examine factors promoting brood reduction. Chapter one of this study examines whether or not Yellow-headed Blackbirds conformed to the brood-reducing strategy of a decreasing egg size with laying order over a two-year period.

According to Lack's (1954) original brood reduction hypothesis, the production of more young than can usually be reared is still adaptive because it increases productivity in years when resources, especially food, are abundant. In poor resource years, females that lay larger clutches would be subject to excessive brood reduction, while those laying fewer eggs would not be able to achieve this maximum reproductive potential even in good resource years. When considered over the long term, Lack suggested that the most productive clutch size for a species or a population should be the most common. More recently, Perrins and Moss (1975) advanced an alternative hypothesis, which Nur (1986) termed as the individual optimization hypothesis, and which is hereafter referred to as the IOH. The IOH states that females adapt their clutch size according to their individual ability to raise young (Perrins and Moss 1975). These individually optimum clutch sizes permit each female to maximize her own reproductive output. Females that lay larger clutches, are expected to

have greater reproductive output than do those laying smaller clutches (Nur 1986), and contrary to Lack (1954), the most productive clutch size need not be the most common. Females that lay more or fewer eggs than this individual optimum would be subject to a lower reproductive output. In Chapter II, I examine these hypotheses by comparing the reproductive output of Yellow-headed Blackbird females in natural and manipulated clutches of different sizes. All results in this chapter were obtained in 1988 due to extensive predation in 1989 (172 of 178 nests were depredated).

Chapter I

EGG-SIZE VARIATION IN THE YELLOW-HEADED BLACKBIRD

INTRODUCTION

Egg size in birds is an important measure of parental reproductive effort because it is strongly correlated with nestling survival (Parsons 1970, Schifferli 1973). As a result, variation in egg size may lead to differential survival of offspring. Considerable intraspecific variation exists within both precocial (e.g. Ankney and Bisset 1976, Rohwer 1986) and altricial species (e.g. Murphy 1983, Jarvinen and Vaisanen 1983, 1984, Jarvinen and Ylimaunu 1986). The pattern of this intraspecific egg-size variation varies in different populations (Jarvinen and Vaisanen 1983, Pietiainen et al. 1986) and years (Andersson 1976b, Schreiber et al. 1979, Pietiainen et al. 1986).

Clutch size is sometimes a correlate of egg-size. In altricial species, egg size may increase with clutch size (Ojanen et al. 1978), decrease with clutch size (Bancroft 1984, Briskie and Sealy 1990) or remain constant irrespective of clutch size (Richter 1984, Rofstad and

Sandvik 1985).

At least two hypotheses have been advanced to explain reductions in egg size with increasing clutch size. The incubation-capability hypothesis proposes that parents are limited in the volume of eggs they can effectively incubate (Andersson 1976a, Hills 1980; but see Baltz and Thompson 1988), hence hatchability of eggs would be lower in larger clutches unless smaller eggs were produced. Lack (1967, 1968) proposed the egg-production hypothesis, which predicts an inverse relationship between egg size and clutch size due to constraints on the female's ability to produce eggs. If parents had a fixed level of resources to commit to reproduction (Smith and Fretwell 1974), a trade-off would occur between egg size and clutch size.

Aside from varying with clutch size, egg size may also vary within a clutch. It may decrease with laying order (Richter 1984, Rofstad and Sandvik 1985), increase with laying order (Howe 1976, Weatherhead 1985, Briskie and Sealy 1990) or remain the same (Walkinshaw 1966, Holcomb 1972 in Briskie and Sealy 1990).

Several hypotheses have been proposed to explain the causes and adaptive value of intraclutch egg-size variation. Parsons (1972, 1976), for example, proposed

that a smaller terminal egg permits more rapid embryonic development, which promotes hatching synchrony. This would offset costs often associated with asynchronous hatching. The insurance-egg hypothesis, on the other hand, proposes that the terminal egg survives only when previously laid eggs do not hatch (Dorward 1962) or if other nestlings die early (Graves et al. 1984, Cash and Evans 1986). Where the probability of brood reduction is very high, the reproductive value (RV) of the terminal egg is derived mainly from its insurance value, which acts as a "replacement unit of parental fitness" and is typically well below the RV of its older siblings (Mock and Parker 1986). A small terminal egg has been interpreted as an adaptive response by parents to the lower RV of this egg (Quinn and Morris 1986). The apparent relationship between RV and the magnitude of brood reduction suggests that small terminal eggs would be especially favored when the probability of brood reduction is high. This trend should, however, be offset by the high insurance value of terminal eggs.

Reduced food availability or energetic constraints on the female may also limit the size of the terminal egg (Pierotti and Bellrose 1986). If food is scarce or female condition poor, then the cost per gram of egg would be expected to increase (Evans 1990), and a female should

reduce her clutch volume either by laying a smaller terminal egg or by producing clutches with smaller eggs. As found by Pierotti and Bellrose (1986), Western Gulls (Larus occidentalis) produced larger terminal eggs than usual in years when food was abundant, which suggests that food availability and energetic constraints are important.

The final hypothesis that I will examine, which is the focus of this chapter, is the brood reduction hypothesis. Females of certain altricial, avian species commonly lay more eggs than they are likely able to rear to fledging (Lack 1954). Brood reduction is thought to be facilitated through asynchronous hatching (Lack 1954, 1968, Ricklefs 1965, O'Connor 1978, Hahn 1981) and by laying a smaller terminal egg (O'Connor 1978, 1979, Slagsvod et al. 1984). Both mechanisms place the last-hatched nestling at a competitive disadvantage relative to its older siblings, which allows its early death should food be limited, while still permitting its survival should food be abundant. Should food be limited, the early death of the youngest nestling would increase the resources available to its siblings. This strategy enables parents to maintain their reproductive success at a maximum level in an environment with fluctuating amounts of resources. Whether or not decreasing egg size with laying order actually promotes brood reduction is controversial, and remains unresolved

(Slagsvold et al. 1984, Jarvinen and Ylimaunu 1986).

Yellow-headed Blackbirds (Xanthocephalus xanthocephalus) have a high frequency of brood reduction. For example, Young (1963) reported a loss of 23.2% of Yellow-headed Blackbird nestlings to brood reduction while Richter (1984) observed a loss of 52.1%. Willson (1966) attributed starvation as the main cause of nestling mortality in this species and found that it was invariably the last-hatched nestling that died. If reduced size of terminal eggs is in fact an adaptation to facilitate brood reduction, it should be clearly and consistently present in Yellow-headed Blackbirds. The objective of this chapter was to test this prediction, along with the alternative hypotheses and interpretations outlined above, in the Yellow-headed Blackbird.

METHODS

This study was conducted during the springs and summers of 1988 and 1989 near Delta, in southwestern Manitoba (99° 19'W, 50° 7'N). Crescent Pond is a small pond of 8.6 ha, with a maximum depth of 1.35 m. It is located adjacent to a dune-ridge forest which separates Delta Marsh from Lake Manitoba (for further description of study site see Hooper and Robinson 1976).

Yellow-headed Blackbirds built their nests among the cattail (Typha sp.), the dominant vegetation surrounding Crescent Pond. Fewer than 2% of the nests were constructed among reeds (Phragmites sp.) that surrounded the outermost border of Crescent Pond.

I began daily searches for nests in mid-May, within one day of laying onset. When a nest was fully constructed, it was marked with flagging tape tied to cattail within 2 m of the nest. An additional small, numbered tag was placed immediately below the nest.

Yellow-headed Blackbirds lay one egg per day (Roberts 1909, Fautin 1941a). When found, each egg was numbered on the broad end with a waterproof felt marker, according to its laying sequence, i.e. 1 = first-laid egg,

etc. A few nests were discovered after two or more eggs had already been laid. Eggs already in the nest were numbered randomly and all subsequent eggs were numbered as they were laid. Once all eggs in a clutch had been laid, I checked the nest daily to record predation and hatch dates. I defined clutch size as the number of eggs laid by each female in her nest. Clutches were considered complete when clutch size did not increase for two days. Active nests refer to those nests in which at least one Yellow-headed Blackbird egg was laid.

Hatchability (egg viability) of unpredated eggs was calculated for each year by dividing the number of eggs that hatched across all clutch sizes by the total number of eggs laid in that year. Mean incubation period was calculated as the mean time from and including the day of laying until the day of hatching for each egg in a clutch (Willson 1966). The mean hatching spread was calculated by averaging the number of days between hatching of first and last nestlings in nests of each clutch size. Both incubation period and hatching spread were calculated only in 1988 due to high predation rates on eggs in 1989.

Eggs were measured on the day of laying. Randomly numbered eggs from clutches that were initiated prior to being found were not measured. Maximum egg length (L) and

breadth (B) were measured to the nearest 0.05 mm with dial calipers. Egg volume (V) was calculated using the equation:

$$V = 0.51 \times L \times B^2 \quad (\text{Hoyt 1979}).$$

All statistical analyses were performed with the aid of BMDP-P3V (1985). Analyses of variance on egg sizes used a nested design with unequal replications due to missing eggs within nests and unequal sample sizes for the different clutch sizes. A two-tailed Student t-test was used to test for mean clutch size differences between years. A Cochran test was used to determine whether egg viability varied with laying order. Chi-square tests were performed on egg hatchability both between years and among clutch sizes. Two- and five-egg clutches were included in the results for comparative purposes, but were usually not included in the analysis because they occurred infrequently. Results were considered significant if the p-values were less than 0.05.

RESULTS

A total of 144 active Yellow-headed Blackbird nests was found in 1988 and 218 in 1989. The first eggs were laid on 14 May 1988 and 19 May 1989. Laying was spread over 24 and 30 days in 1988 and 1989, respectively. In both years, most laying occurred between 20 and 24 May (Fig. 1). Mean \pm SE incubation period in 1988 was 12.8 ± 0.15 days for the clutch size (CS) of 3 eggs ($n=10$ nests), 13.1 ± 0.20 days for CS=4 ($n=6$), and 12.6 ± 0.24 days for CS=5 ($n=4$). Incubation period did not differ significantly ($F=1.45$, $p=0.26$, $df=2$) among clutch sizes. The overall mean incubation period was 12.9 ± 0.11 days. All eggs hatched according to their laying sequence. However, some first- and second-laid eggs hatched in a short time span prior to my visit, making hatching order indiscernible. Mean hatching spread in 1988 increased significantly with clutch size ($F=18.30$, $p=0.0001$) and was 1.5 ± 0.22 days for CS=3 ($n=13$ nests), 2.5 ± 0.27 days for CS=4 ($n=10$), and 4.0 ± 0.00 ($n=4$) days for CS=5.

Hatchability of unpredated eggs was 86.2% ($n=334$ eggs) in 1988 and 91.6% in 1989 ($n=107$ eggs). Hatchability did not differ significantly between years ($\chi^2 = 1.67$, $df = 1$, $p > 0.05$) or among clutch sizes (1988: $\chi^2 = 0.27$, $df=2$, $p > 0.05$; 1989: $\chi^2 = 0.47$, $df = 2$, $p > 0.05$) (Fig. 2).

Figure 1. Number of known clutch initiations in May and June of 1988 and 1989.

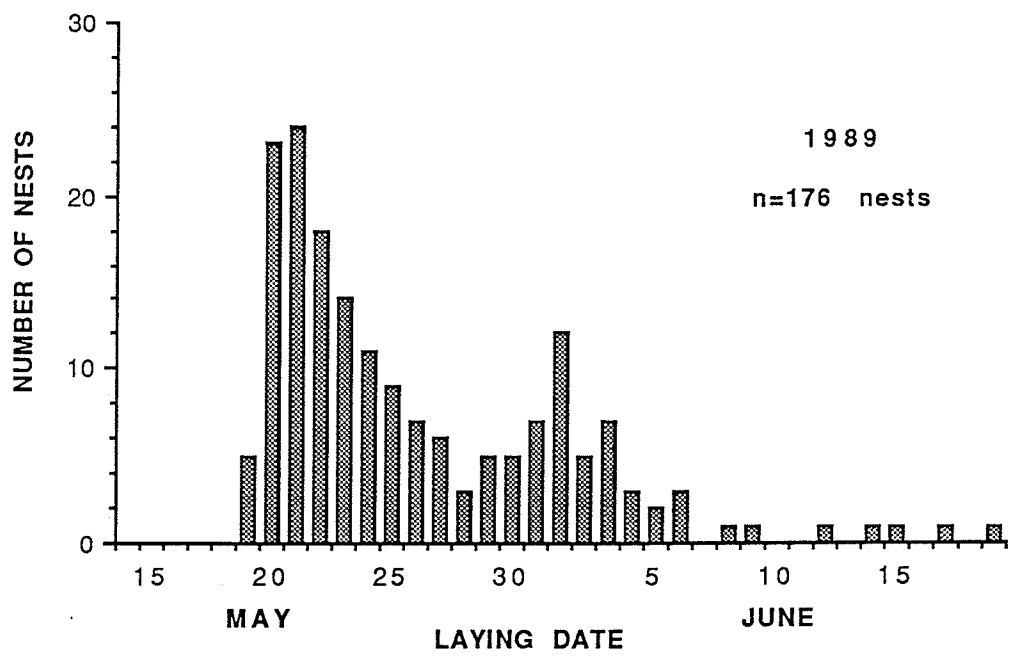
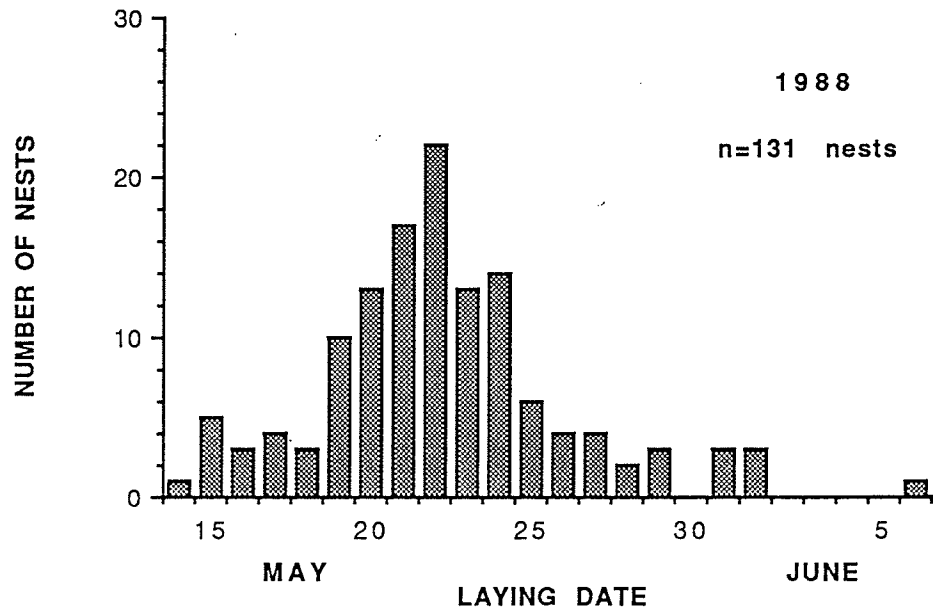
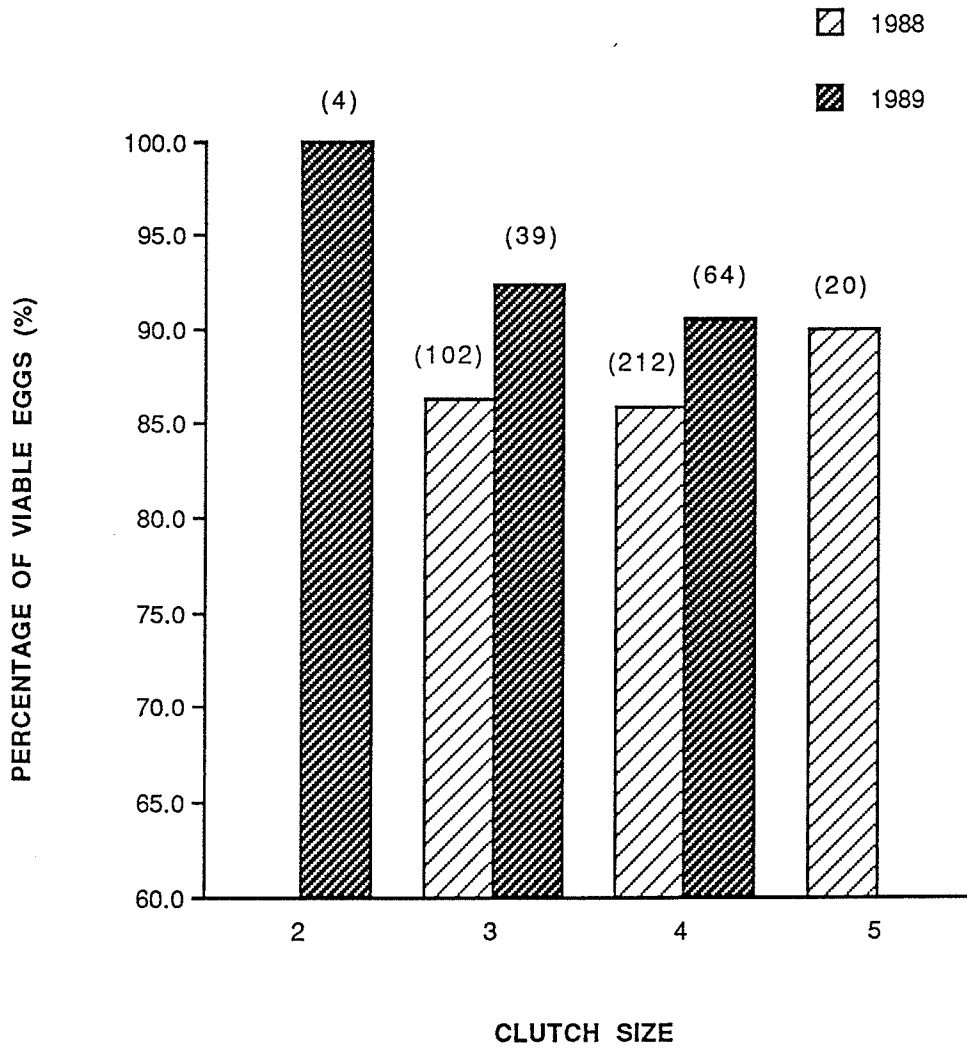


Figure 2. Hatchability of unpredated eggs for each clutch size found in 1988 and 1989. Number of eggs is in brackets.



Laying order had no significant effect on egg hatchability within three- or four-egg clutches in either year (Table 1).

Modal clutch size was four eggs in both years, with a range of two to five eggs; no five-egg clutches were present in 1989 (Fig. 3). Mean clutch size in 1988 was 3.7 ± 0.05 eggs/nest, significantly higher than the mean of 3.5 ± 0.05 eggs/nest in 1989 ($t = 3.27$, $df = 297$, $p = 0.001$).

Egg Dimensions

Egg volume differed significantly between years in clutches of three and four eggs combined ($F = 8.71$, $p = 0.0032$). Separately, eggs were significantly larger for each clutch size in 1988, but not in 1989 (Figs. 4 and 5). No significant interaction existed between year and clutch size for volume ($F=1.10$, $p=0.29$).

In 1988, the volume of eggs in four-egg clutches was significantly smaller than that in three-egg clutches ($p < 0.0001$). In 1989, eggs decreased in size as clutch size increased, but there were no significant differences in volume among clutch sizes of two, three, and four eggs ($F = 2.35$, $p = 0.096$).

Table 1. Percent hatchability of unpredated eggs in relation to laying order for clutches of three and four eggs. Number of nests is in brackets.

Year	Clutch Size	Laying Order				X ²	df	p
		1	2	3	4			
1988	3 (34)	90.32	96.77	80.65	--	4.75	2	NS
	4 (53)	81.63	89.80	93.88	85.71	4.00	3	NS
1989	3 (13)	92.31	92.31	92.31	--	0.00	2	NS
	4 (16)	93.75	87.50	87.50	93.75	0.86	3	NS

NS = Not significant ($p > 0.05$).

Figure 3. Frequency of clutch sizes present in 1988 and 1989. Number of nests is in brackets.

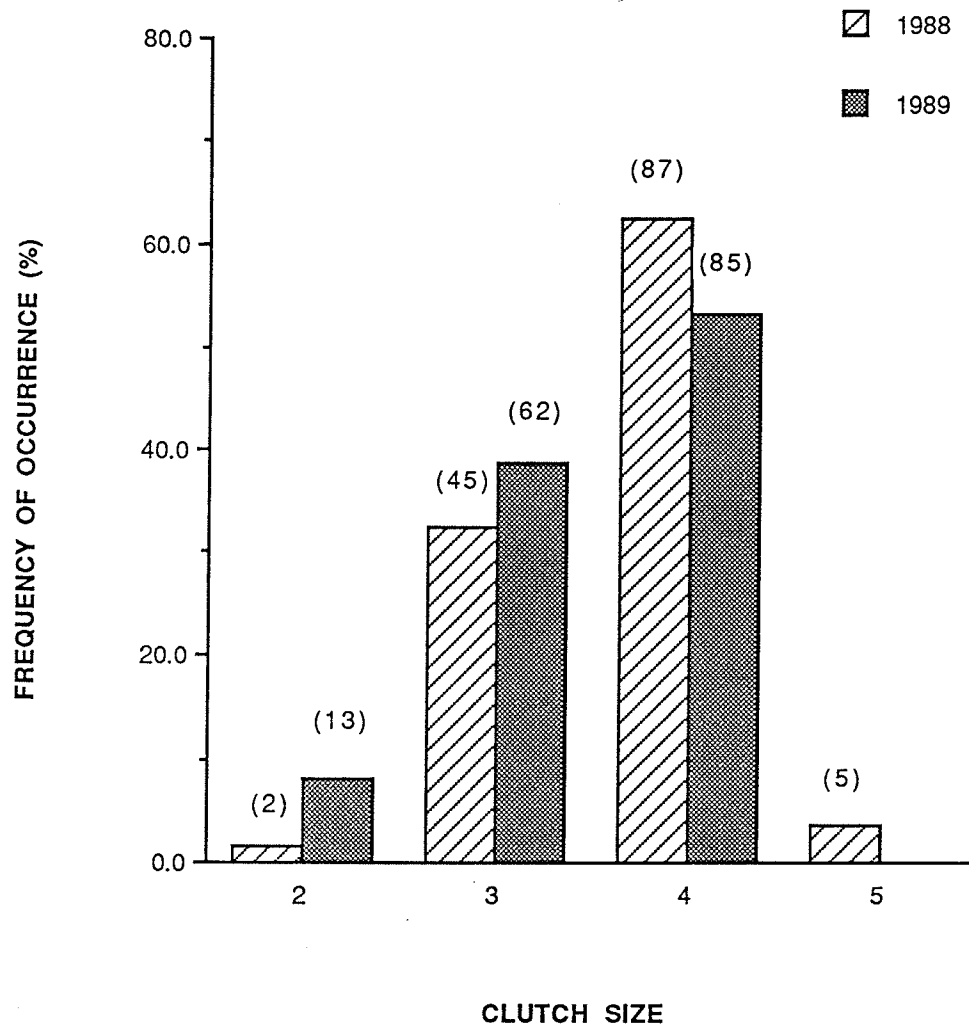


Figure 4. Mean \pm SE egg volume (cm^3) of three-egg clutches in 1988 and 1989 with respect to laying order. Number of eggs is in brackets.

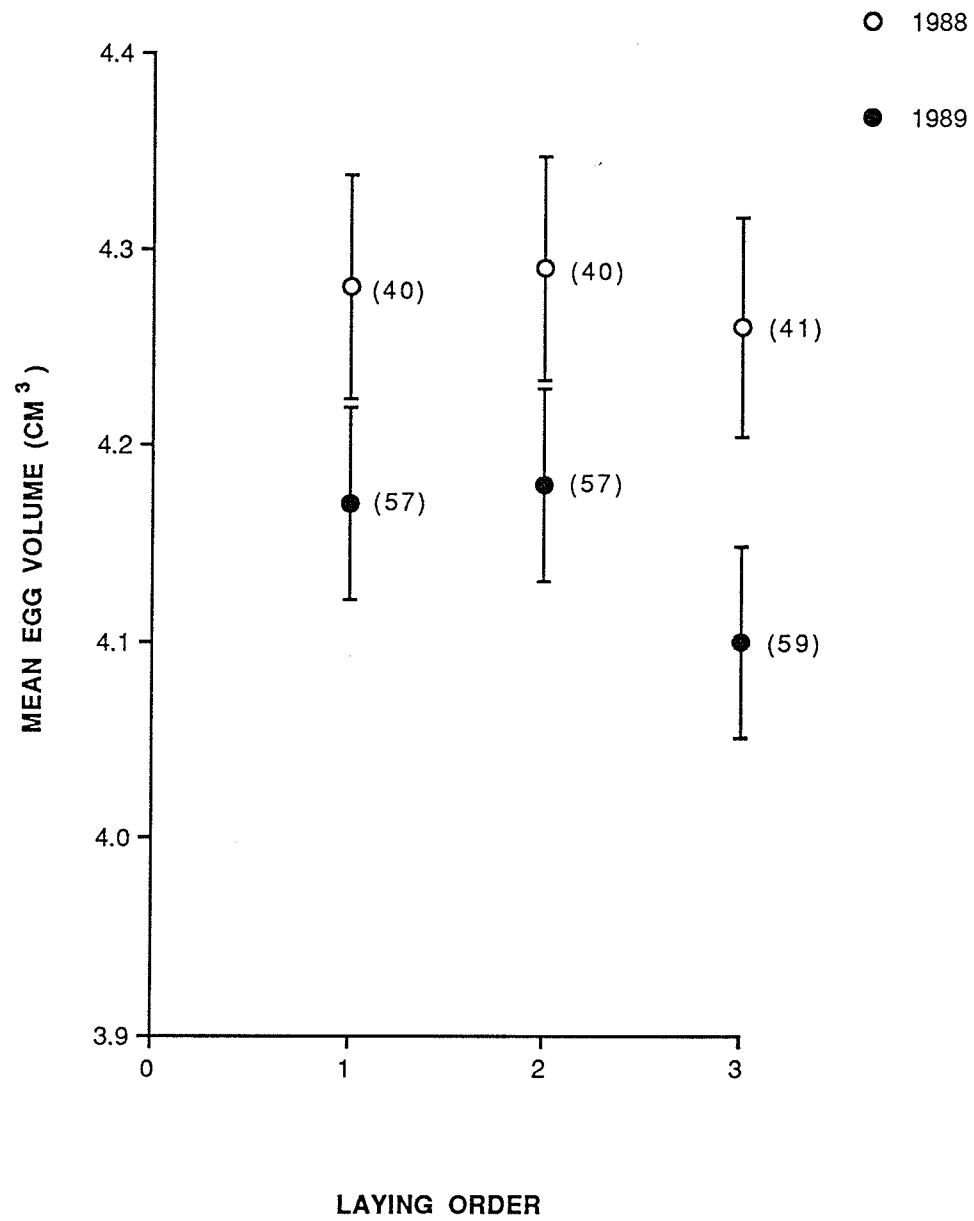
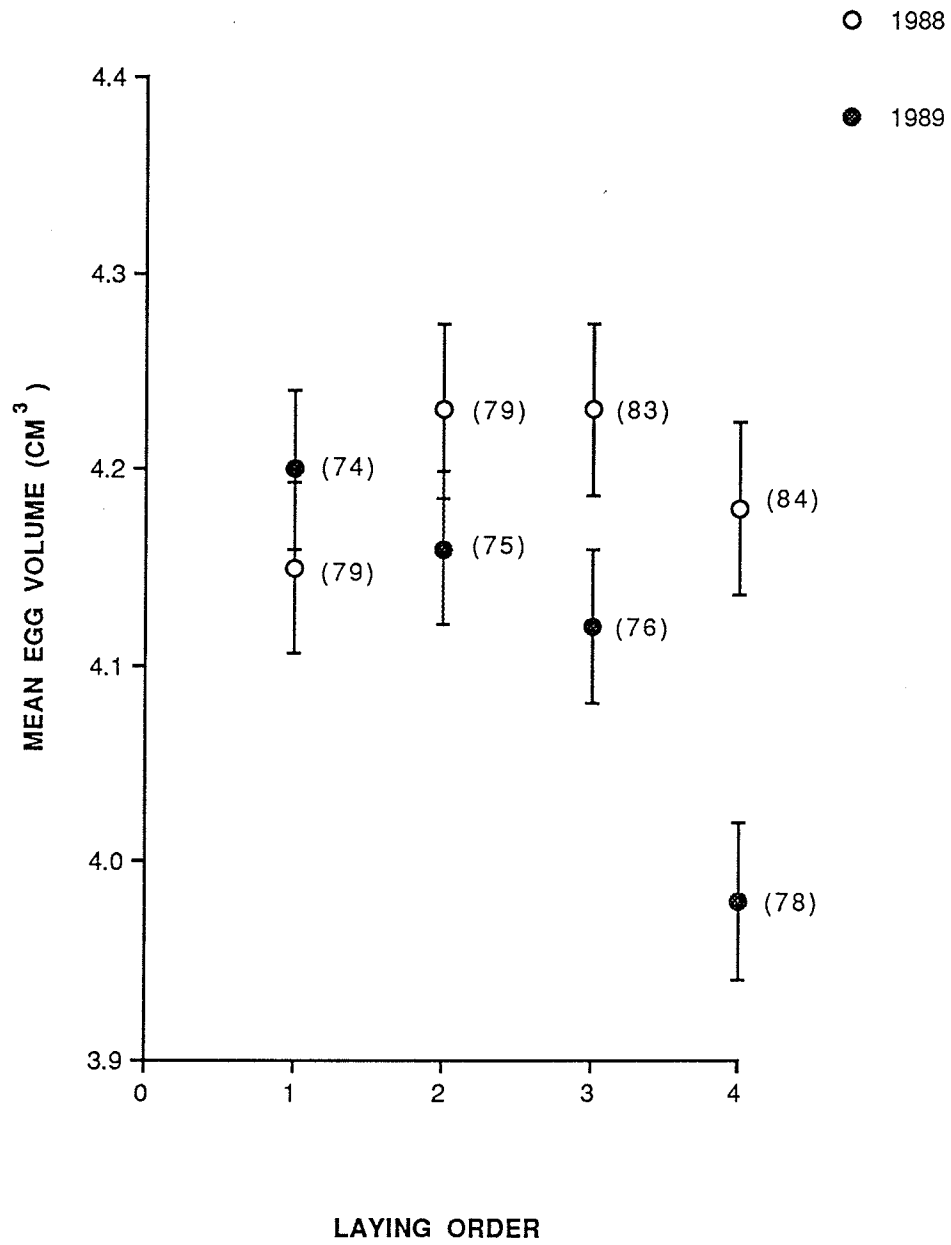


Figure 5. Mean \pm SE egg volume (cm^3) of four-egg clutches in 1988 and 1989 with respect to laying order. Number of eggs is in brackets.



Egg volumes within four-egg clutches in 1989 differed significantly ($F=15.50$, $p < 0.0001$) with laying order (Fig. 5); the terminal egg was significantly smaller than the first- ($p < 0.0001$), second- ($p < 0.0001$), and third-laid eggs ($p < 0.0001$). The third-laid egg also had a smaller volume than did the first-laid egg ($p = 0.018$). The third- and fourth-laid eggs from four-egg clutches were significantly smaller in volume in 1989 than in 1988 ($t = 1.99$, $df=157$, $p = 0.047$; $t = 3.41$, $df = 160$, $p = 0.0006$, respectively) (Fig. 5). No significant differences in volume occurred with laying order for clutches of three eggs in 1989 ($F = 2.43$, $p = 0.091$) (Fig. 4) or for either three- ($F = 0.16$, $p = 0.85$) or four-egg clutches ($F = 2.53$, $p = 0.057$) in 1988.

DISCUSSION

Egg size in Yellow-headed Blackbirds varied inversely with clutch size in 1988, but not in 1989. Due to this inconsistent relationship between egg and clutch size over the two years, Lack's egg-production hypothesis (1967, 1968), proposed for waterfowl, which predicts a trade-off between egg size and clutch size due to a female's limited ability to produce eggs, is rejected.

Similarly, the incubation capability hypothesis (Andersson 1976a, Hills 1980) must also be rejected. Egg size did not consistently decrease with clutch size nor did any differences in egg viability exist with respect to clutch size or laying order.

In 1989, four-egg clutches conformed to the brood-reduction strategy in that eggs were significantly smaller as laying progressed (Fig. 5). However, in 1988, there was no significant change in egg size with laying order in any clutch size. The possibility that the first-laid eggs in 1988 clutches were unusually small such that egg size could not decrease further without decreasing viability was dismissed, because the first- and second-laid eggs from four-egg clutches did not differ significantly in size between 1988 and 1989 (Fig. 5).

Brood reduction nevertheless occurred in 1988, despite the absence of decreasing egg size; all broods with four eggs and one-third of those with three eggs were reduced (Chapter II). Since there would appear to be no constraints inhibiting females from decreasing the size of terminal eggs if it were advantageous to do so, I conclude that decreasing egg size is not an adaptive parental manipulation to facilitate brood reduction in this species. For the same reason, the hypothesis that a smaller terminal egg is adaptive because it hatches sooner and is thus more synchronous with the rest of the clutch than a larger egg would be (Parsons 1972, 1976) was also rejected since this strategy presumably could have been, but was not, present in both years.

The alternative interpretation that egg size may depend on food availability or on female condition immediately prior to, or when laying (Jarvinen and Vaisanen 1983, 1984, Pietiainen et al. 1986), appears to be in closer accord with the data. In 1988, females put more energy into each egg in three-egg clutches than in four-egg clutches. This effect was absent in 1989 due to the smaller egg volumes within three-egg clutches in that year. This result suggests that there may have been energetic constraints on egg size in three-egg clutches in 1989. Mean egg volume within four-egg clutches was also

significantly less in 1989 than in 1988 (Fig. 5). In addition, the last two eggs within four-egg clutches in 1989 decreased significantly in size. This decreased input in eggs, especially in latter-laid eggs in 1989, suggests also that energetic constraints existed on egg size that year. This conclusion is further supported by the occurrence of a significantly smaller mean clutch size in 1989.

Some passerine females began laying earlier and laid larger eggs when provided with extra food (Kallander 1974, Ewald and Rohwer 1982) while Magpies (Pica pica) also laid larger clutches (Hogstedt 1981a). Further evidence of the importance of food availability is shown in Jarvinen and Vaisanen's (1984) study where they classified years into "good" and "bad" breeding seasons with respect to ambient temperature and female's physiological condition. In these "good" years, female Pied Flycatchers laid earlier, had a larger mean clutch size, and their clutches contained larger eggs than they did in the "bad" years. Similar egg differences (earlier laying, larger mean clutch size and larger eggs in 1988 than 1989) were observed on my study site (Table 2). All point to the conclusion that energetic constraints on egg production were present in 1989.

Table 2. A comparison of breeding parameters in 1988 and 1989.

<u>Parameter</u>	<u>Between-year comparisons</u>
Initiation of the first clutch	Earlier in 1988 (May 14 vs May 19)
Mean clutch size	Larger in 1988 * (3.7 ± 0.05 vs 3.5 ± 0.05)
Mean egg volume	Larger in 1988 * (4.34 ± 0.041 vs 4.16 ± 0.034)
Two-egg clutches	Fewer in 1988 (n=2 vs n=13)
Five-egg clutches	Only in 1988 (n=5 vs n=0)

* $p < 0.05$.

The dependence of egg and clutch size on food availability/female condition has also been documented in non-passerine species. Pietiainen et al. (1986) observed that Ural Owls (Strix uralensis) adjusted their egg and clutch size according to the quality of the breeding season. In years where food was abundant, the eggs from four-egg clutches were of similar size while in poorer years, the last two eggs were significantly smaller than the first two eggs. Mean clutch size was also significantly greater in good years than in poorer years. Reid (1987) observed that Glaucous-winged Gulls (L. glaucescens) increased the size of their terminal egg when food was increased experimentally. When feeding on superior food supplies, Herring Gulls (L. argentatus) laid larger clutches and larger eggs (Pierotti and Annett 1987).

In this study, only one female fledged more than three young (Chapter II), while Richter (1984) found that only 11.8% of females fledged four young. Females that laid four- or five-egg clutches, in effect, adopted a severe form of the facultative brood-reducing strategy since brood reduction usually occurred, and was concentrated on the youngest nestlings. Those laying two- or three-egg clutches, in contrast, adopted a less extreme facultative brood-reducing strategy because they sometimes did and sometimes did not experience brood reduction. As a result

of a high frequency of brood reduction in four- or five-egg clutches, terminal eggs in these clutches were of greatly reduced RV. Females laying larger clutches would therefore be expected to bias egg size against terminal eggs having relatively low RV (Mock and Parker 1986). This effect should be most pronounced when females are faced with low levels of resources or poor physiological condition and a corresponding increase in investment cost per gram of egg and a decrease in optimum levels of parental input to eggs (Evans 1990). This was evidently the case for Yellow-headed Blackbirds in 1989. Nestlings that survived from terminal eggs of large clutches did so primarily as insurance young - i.e. when an older sibling died. Insurance young may also survive when a previously laid egg fails to hatch. However, unhatched eggs were not a factor in this study since they were replaced with newly hatched nestlings to maintain the initial brood size (Chapter II). Hatchability in both years averaged 88.91%. Fautin (1941a) observed a hatchability of 91% in Yellow-headed Blackbirds. In the present study, the survival of fourth- or fifth-laid nestlings as insurance offspring occurred in 6.3% of four- and five-egg clutches (Chapter II). In the event that the terminal nestling does replace a sibling, it should be advantageous for the terminal egg to be at least as large as earlier eggs so it could more easily overcome the initial disadvantages set by an asynchronous hatching

pattern. Hence, larger terminal eggs could be favored in clutches of four or five eggs despite their somewhat lower RV. Where significant insurance values are present, it should be adaptive for females to produce larger terminal eggs whenever good female condition or abundant food combine to lower investment costs, as appears to have occurred for four-egg clutches in 1988.

In two- and three-egg clutches, all young had a greater chance of surviving (Chapter II). Consequently, females should presumably distribute their energy more equally among the eggs. When egg investment costs are high, females laying smaller clutches should be more likely to reduce the size of all their eggs rather than to reduce only that of the terminal egg. This is in effect what Yellow-headed Blackbirds did in 1989.

The most parsimonious conclusion from this study is that female Yellow-headed Blackbirds did not actively control egg size as an adaptation to enhance brood reduction, but instead produced terminal eggs that were as large as possible within constraints set by the food supply or other local resources, and finally, by their own physiological condition.

Chapter II

CLUTCH-SIZE MANIPULATIONS IN THE YELLOW-HEADED BLACKBIRD: A TEST OF THE INDIVIDUAL OPTIMIZATION HYPOTHESIS

INTRODUCTION

Lack (1954) hypothesized that the most productive clutch size in a population would also be the most common. By contrast, in a study of the Yellow-headed Blackbird (Xanthocephalus xanthocephalus), Richter (1984) reported that progressively larger clutch sizes produced more offspring than did the most common clutch size. This has also been observed in several other passerine species (e.g. Bryant 1975, Perrins and Moss 1975, De Steven 1980, Askenmo 1982, Haydock and Ligon 1986, Briskie and Sealy 1989), which suggests the existence of many different optimum clutch sizes within a species (Hogstedt 1980, Nur 1987), rather than just the one.

This intraspecific variation in clutch-size is the essence of the 'individual optimization' hypothesis (Nur 1986), which assumes that individual females adapt their clutch sizes according to their ability to raise young (Perrins and Moss 1975). The individual optimization

hypothesis (IOH) accounts for clutch-size variability by proposing that females have different optima. Accordingly, each female is hypothesized to lay a clutch size that is best suited to her ability to rear nestlings (Schifferli 1978, Richter 1984, Power et al. 1989) under prevailing conditions of her physiology (Drent and Daan 1980) or territory quality (Hogstedt 1980). The different optima would permit individual differences in maximizing reproductive output (Hogstedt 1980). Thus, the young in larger broods would not be disadvantaged (Perrins and Moss 1975) nor would parents of large broods necessarily be more likely to die than those raising smaller broods (De Steven 1980, Hogstedt 1981b), as proposed by Charnov and Krebs (1974).

Despite frequent post-hoc appeals of the IOH in explaining results, little conclusive evidence exists to support it (Nur 1987). Hogstedt's (1980) work on the Magpie (Pica pica) is the only study that supported the critical predictions of this hypothesis. Nur (1986), through his study on Blue Tits (Parus caeruleus), rejected the hypothesis. Further studies are needed to test the IOH by manipulating clutch size (Nur 1987), and, as Andersson (1978) suggested, by carrying out these manipulations relative to the original brood size. The primary objective of the investigation reported in this chapter was to test

experimentally the IOH in Yellow-headed Blackbirds, a species that lays clutches of two to five eggs (Willson 1966, Richter 1984, Chapter I).

If individual clutch sizes reflect parental abilities, and if the clutch size produced by each female is optimal for her, then females that lay a clutch of 'x' eggs should have greater reproductive fitness than with a clutch of 'x+1' or 'x-1' eggs (Nur 1986). Fitness is best assessed by the reproductive contribution of offspring to the next generation (Nur 1987), commonly estimated by nestling quality, as measured by nestling growth rates and/or fledging masses (Perrins 1965, Ricklefs and Peters 1979), and nestling survival. In an experimental context, a clutch of the original size (control clutch) should do better with respect to nestling survival or quality than would an experimental clutch of the same original size to which one egg was either added (enlarged) or removed (reduced). I tested these predictions by comparing control four-egg clutches (C4) with clutches of four increased to five (4->5) and four reduced to three (4->3) eggs, and with C3 clutches against 3->4 and 3->2 eggs. In each case, I estimated female fitness by measuring nestling survival until fledging and both fledging masses and growth rates of surviving young.

Since my experimental manipulations involved increasing or decreasing clutch size, predictions about offspring growth rates or mass are subject to possible effects of the trade-off between offspring quantity and quality commonly suggested by life history-theory (Williams 1966, Smith and Fretwell 1974, Stearns 1976). Of particular relevance here, and in direct contrast to predictions of the IOH, life-history considerations suggest that nestling growth rates and/or fledgling masses (nestling quality) should be greater in an experimentally reduced group than in its corresponding control group, since the female now has one less nestling to feed. This alternative prediction was therefore also examined for reduced broods.

An assumption of the IOH is females that lay larger clutches are more capable of rearing young (greater fitness) than those that lay smaller clutches (Nur 1986). Thus, clutch size and nestling survival/quality are expected to be positively related. I examined this prediction for C3 and C4 clutches. To examine further the assumption that females that lay larger clutches are more fit, I also tested the prediction that young produced in the 4->3 group would do better in growth rate, fledging mass and productivity than the C3 group, and that C4 clutches would do better, with respect to the above

parameters, than clutches of 3->4.

If one sex is more costly to rear than the other, nestling sex ratio may confound the testing of the IOH. Yellow-headed Blackbirds, the subjects of this study, are markedly sexually dimorphic, with adult males being much larger than females (body weight ratio of female/male is 0.62) (Mewaldt, unpub. in Dunning 1984). Sexual dimorphism is also present at the nestling stage (Willson 1966, Patterson and Emlen 1980), which indicates that males could be more costly to raise than females (Fisher 1930). If a female whose clutch has been experimentally enlarged is physiologically stressed, she might produce more offspring of the less costly sex (Trivers and Willard 1973) as opposed to producing fewer nestlings. To control for this possibility, I assessed nestling sex ratios for:

- 1) control, 2) experimentally enlarged, and
- 3) experimentally reduced broods.

METHODS

Field work was carried out during the spring and summer of 1988 at Crescent Pond, near Delta, Manitoba (see Chapter I). During late incubation, experimental and control clutches were randomly selected within each of the most common natural clutch sizes of three and four eggs. After depredated and abandoned nests were removed from the experimental design, final sample sizes consisted of 19 enlarged, 31 reduced, and 25 control clutches. Clutches were enlarged by adding one egg to clutches of three and four eggs to create clutches of four and five eggs respectively. Clutches from which an egg was removed were reduced to either two or three eggs. To maintain approximately normal within-clutch hatching asynchrony in experimental nests, first- or last-laid eggs were taken from donor nests and used to extend the hatching period of recipient nests by approximately one day. Eggs from C3 and C4 clutches were handled on the day of laying, then monitored daily along with the experimental nests.

Eggs that failed to hatch were replaced with newly hatched nestlings in both the experimental and control groups to maintain the required initial brood size. To determine if egg transfers affected egg viability, the hatchability of transferred eggs was compared to that of

control eggs. This was achieved by adding the number of eggs hatched in clutches within each of the experimental and control groups and dividing by the total number of eggs in each group. Nestlings that died were not replaced.

Nestlings were individually marked on the day of hatching with blue and black fingernail polish applied to their toes (J. Blank, *in litt.*, Feb. 1988). The polish was reapplied every second day. When more than one newly hatched nestling appeared in the nest, hatching order was estimated by wetness of feathers and relative size of the nestlings. Nestlings were weighed at least once every two days with a pesola spring scale (50 ± 0.1 g and 100 ± 0.25 g), and the time was recorded. Timing of measurements was randomized among the different groups and usually occurred between 0800 and 1700. Nests were monitored until all nestlings either fledged or died. The sex of each nestling was determined by its mass on my last visit prior to its fledging (Patterson and Emlen 1980). By this time, two distinct weight classes are present, one for males and one for females (Willson 1966, Patterson and Emlen 1980). This method of size-based classification has been shown to be very reliable (Richter 1983). Nestlings that died were not sexed.

Growth rates (mean mass gained per day) were

determined by randomly taking the mass of one nestling per nest of each sex at seven or eight days of age, subtracting the mean hatchling mass of a known sample (n=11) of newly hatched birds, then dividing by the age of the bird (seven or eight days). ANOVAs performed on the data for each sex between day seven and eight birds indicated there were no significant differences between the growth rates on these two days and that no interaction existed between days and treatments, so data for both days were pooled. It should be emphasized that fledging mass and growth rate were determined on different days of the nestling period. Fledging mass was the last measured mass of a nestling prior to its leaving the nest and could have been measured anywhere from day 9 to day 12 posthatch, while growth rate was standardized over the first seven or eight days posthatch.

Hatching date was unclear in certain cases since some nestlings hatched either soon after a visit or prior to a visit on the following day. Thus, I used the following method to assign these birds a hatching date: mean hatching mass and mean mass gained per hour was first calculated for the sample of 8 nestlings of known hatching time that had also been measured the following day. Negligible growth was assumed between 2200 and 0500. To determine hatch time of the other nestlings, mean hatching mass was subtracted

from the first recorded mass of the nestling, giving the mass gained by the nestling since hatch. This mass gain was divided by the mean mass gained per hour, which gave the number of hours since the nestling's hatch, and allowed me to backdate to the time of hatch. If the predicted time of hatch fell between 2200 and 0500, the hatch was assigned to the previous day.

If a nestling was missing upon a daily nest check, it was assumed to have fledged if it had spent nine or more days in the nest. This time approaches the usual 10 or 11 days for fledging in this species, and falls within the range of nine to twelve days (Fautin 1941b, Willson 1966). If 8 days or younger, it was assumed to have starved. Dead nestlings were sometimes found in the nest, but usually they disappeared. Nests were assumed to have been preyed upon when all nestlings were missing between successive daily visits (they typically fledge asynchronously). Abandoned nests and those in which young were depredated were not included in this analysis.

Due to the sexual dimorphism in Yellow-headed Blackbirds, results for growth rate and fledging mass were analysed separately for males and females. Two-tailed t-tests were performed on both the growth rate and fledging mass data to determine if sexual differences were in fact

significant. The growth rates and fledging masses of males and females, along with combined male and female results for nestling productivity were then each analysed separately using the GLM and LSD procedures in SAS (1985), for the a-priori predictions summarized in Table 3.

Chi-square tests were performed on egg hatchability data to detect differences in hatching success between control and experimental clutches. In addition, chi-square tests were performed on the number of male and female fledglings within each of the control, enlarged and reduced clutches to determine if sex-ratio deviated from unity. Finally, these tests were also performed on the proportion of males to females fledging within the predicted comparisons. Results were considered significant if p-values were less than 0.05.

Table 3. Predictions of the IOH where "a > b" means group "a" has greater productivity and/or growth rates or fledging masses than group "b".

<u>Direct Predictions</u>	<u>Ancillary Predictions</u> ¹
C4 > 4->5	C4 > C3
C4 > 4->3 ²	4->3 > C3
C3 > 3->4	C4 > 3->4
C3 > 3->2 ²	

¹Predictions derived from the assumption that females laying larger clutches have a greater ability to rear young.

²Alternate predictions for growth rates/fledging masses are: C4 < 4->3, C3 < 3->2, based on presumed trade-off between offspring quantity and quality as suggested by life-history theory.

RESULTS

Sixty-seven per cent (50/75) of all experimental and control nests suffered brood reduction in 1988 (excluding nests preyed upon or abandoned) with 30.1% of the nestlings dying. Of these, most nests (90.0%) exhibited the typical pattern of brood reduction with the last-hatched nestling dying first, followed, when two were lost, by the penultimate nestling. Last-hatched nestlings survived in 6.3% of four- and five-egg clutches, replacing earlier-hatched nestlings that had died. The age at which nestlings succumbed did not differ significantly among any of the groups ($F=1.72$, $df=5,44$, $p=0.15$) (Fig. 6). The hatching success of transferred eggs in 1988 was 84.2% ($n=19$ nests), similar to that of control eggs (88.5%; $n=26$ nests) ($\chi^2 = 0.17$, $df=1$, $p > 0.5$). Evidently, adding or removing an egg from a clutch had no effect on its viability. Newly hatched nestlings had a mean \pm SE mass of 3.0 ± 0.11 g ($n = 11$; range = 2.5 to 3.5 g) and a mean \pm SE growth rate of 0.115 ± 0.01 g/hr ($n=8$) for the first day (exclusive of 2200 to 0500h) following hatch.

Nestling productivity (Fig. 7) was significantly greater in the C3 clutches than in the 3->2 clutches (Table 4), as predicted by the IOH. All other productivity predictions (Table 4) had non-significant results.

Figure 6. Mean \pm SE age of mortality (days) within controls and experimental clutches in 1988. Number of nests exhibiting brood reduction is in brackets.

Figure 7. Nestling productivity \pm SE (number of fledglings/nest) within control and experimental clutches. Sample size of nests is in brackets.

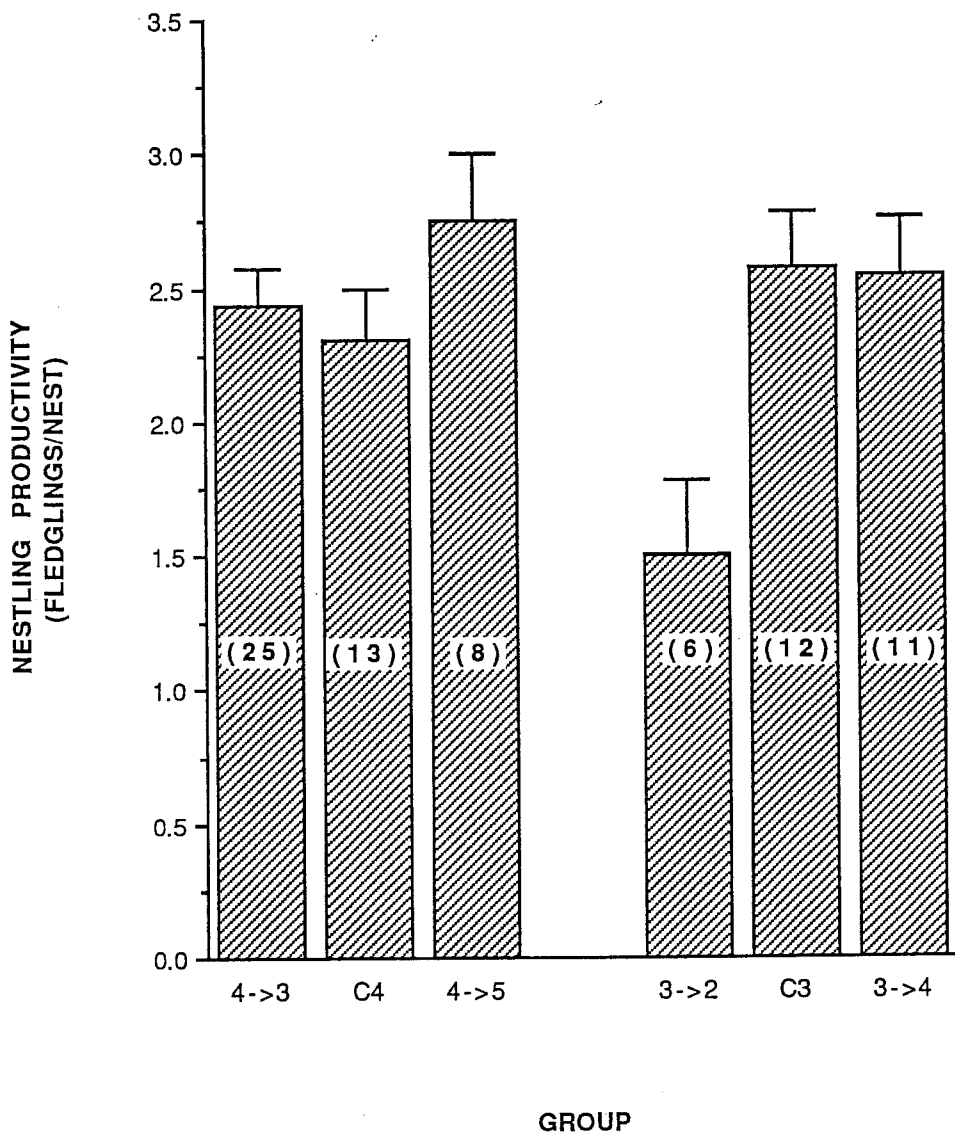


Table 4. Summary of statistical comparisons for nestling productivity, growth rates and fledging masses among the predicted comparisons of the individual optimization hypothesis.

<u>Predictions</u>	<u>p-values for:</u>				
	<u>Product- ivity</u>	<u>Growth</u>		<u>Mass</u>	
		<u>Female</u>	<u>Male</u>	<u>Female</u>	<u>Male</u>
C4 > 4->5	0.08	0.38	0.40	0.13	0.13
C4 > 4->3	0.29	0.14	0.40	0.0002 [^]	0.31
C3 > 3->4	0.45	0.34	0.50	0.24	0.39
C3 > 3->2	0.001*	0.18	0.30	0.17	0.02*
C4 > C3	0.16	0.47	0.29	0.20	0.39
4->3 > C3	0.28	0.13	0.35	0.004*	0.19
C4 > 3->4	0.11	0.41	0.30	0.36	0.29

* = Significant differences ($p < 0.05$)

[^] = Significant differences, but in the direction opposite to the prediction of the IOH.

For female mass in the C4 > 4->3 comparison, the result agrees with the alternative prediction derived from life-history theory.

No significant differences were found in either male or female growth rates between any of the predicted treatments (Table 4, Fig. 8). Most differences in fledging mass within females and males were also not significant (Table 4). However, males from the C3 group fledged at significantly higher masses than did those from the 3->2 group (Table 4, Fig. 9), and females from the 4->3 group were significantly heavier at fledging than were those from the C3 group, both as predicted. However, the 4->3 females were also heavier than those from the C4 group.

Overall, 115 female and 66 male nestlings were produced. This ratio is significantly biased towards females ($X^2 = 13.27$, $df=1$, $p < 0.005$). The sex ratio of males to females was 0.56 for the control clutches (63.9% of nestlings were female), 0.52 for the enlarged clutches (66% female) and 0.63 for the reduced clutches (61.4% female). Significantly more females than males fledged from control clutches ($X^2 = 4.74$, $df=1$, $p < 0.05$), and from enlarged clutches ($X^2 = 5.12$, $df=1$, $p < 0.025$), while results approached significance in reduced clutches ($X^2 = 3.66$, $df=1$, $p = 0.06$). There were no significant differences in the proportion of females to males that fledged between any of the predicted comparisons listed in Table 4.

Figure 8. Mean \pm SE nestling growth rates (grams/day) for a) females and b) males within control and experimental clutches. Sample size of nests is in brackets (it is lower than that of Fig. 7 because females and males were not present in all nests).

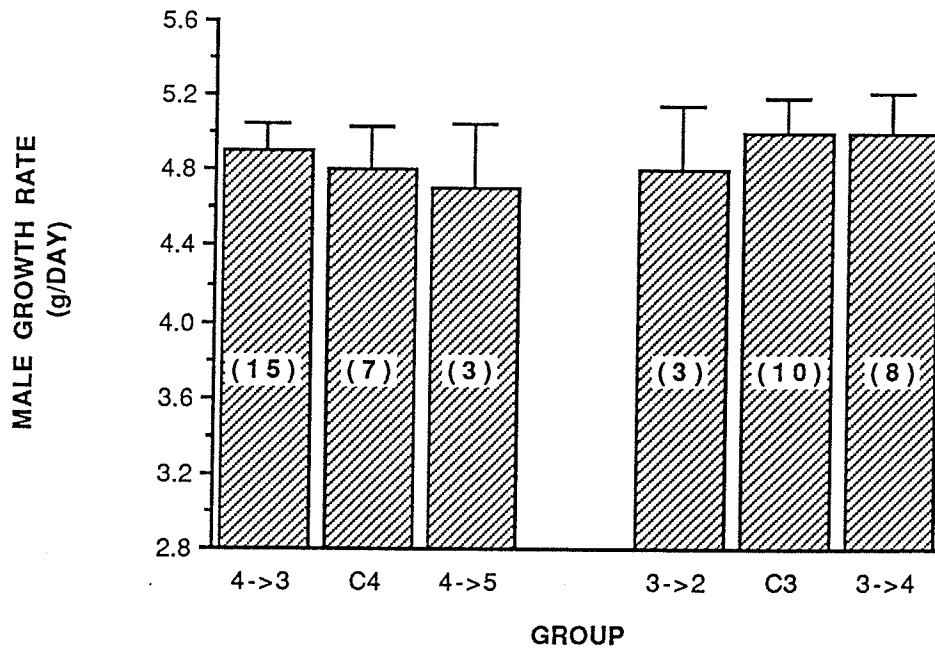
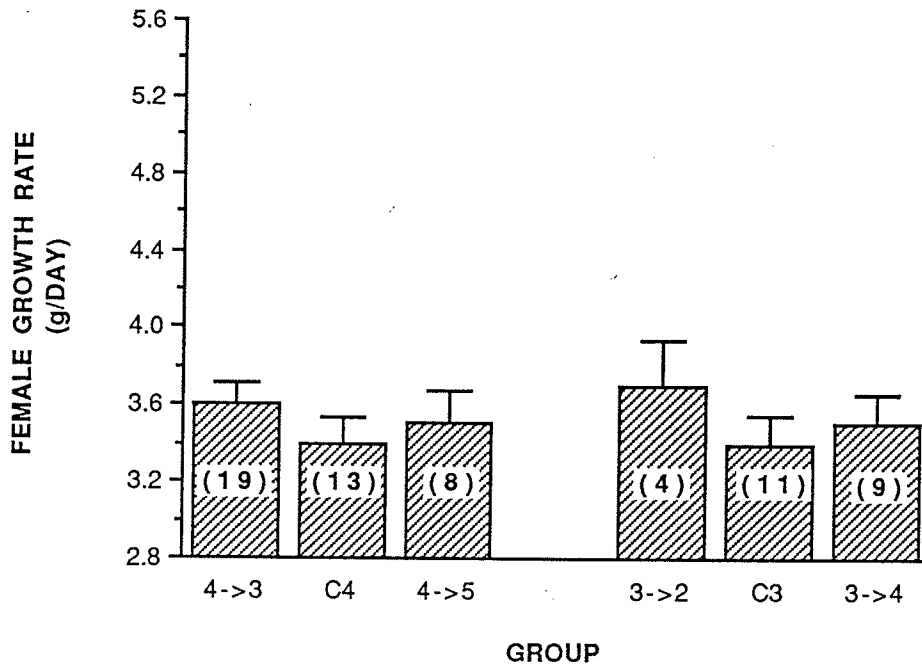
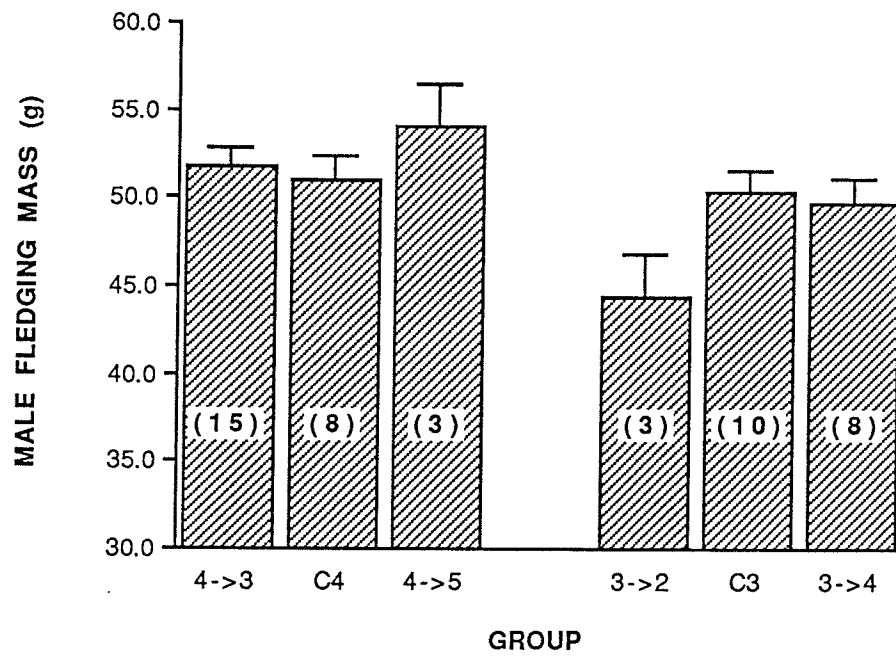
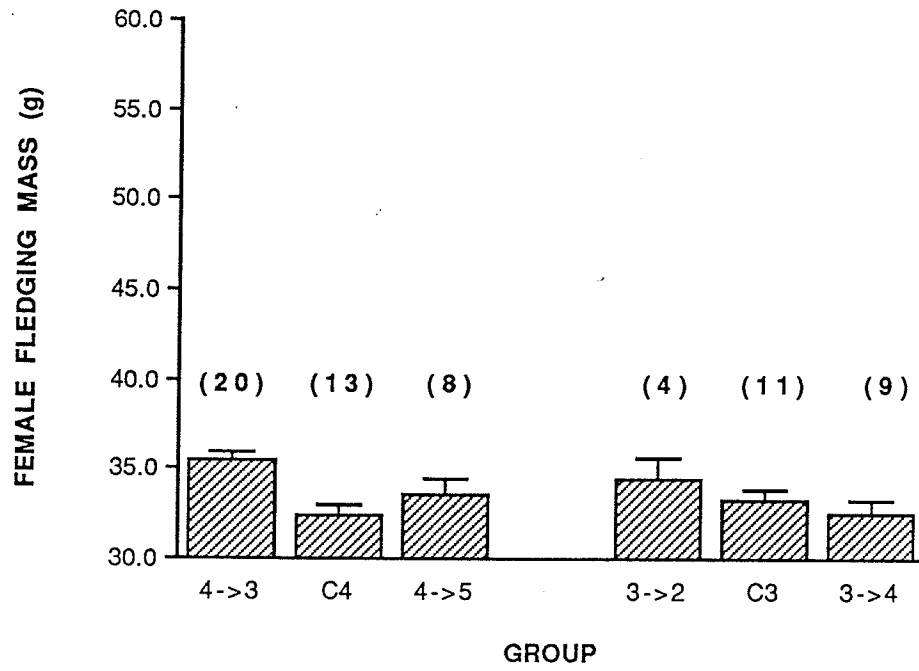


Figure 9. Mean \pm SE fledging masses (grams) for a) females and b) males within control and experimental clutches. Sample size of nests is in brackets.



DISCUSSION

Contrary to the positive relationship between clutch size and nestling survival predicted by the IOH, clutches of four eggs in Yellow-headed Blackbirds were not more productive than clutches of three eggs. Equal numbers of nestlings fledged from control clutches of three and four eggs, with no relationship being demonstrated between nestling survival and these clutch sizes. These results are also contrary to Lack's hypothesis (1954) that the most common clutch size (four eggs in Yellow-headed Blackbirds: Willson 1966, Richter 1984, Chapter I) should be the most productive. In contrast, both Willson (1966) and Richter (1984) found higher offspring production in larger clutch sizes of Yellow-headed Blackbirds. Clutches of 3->4 were also no more productive than C3 clutches (Table 4) as they should have been if Lack's hypothesis was to be supported.

According to the IOH, a female lays the number of eggs that maximizes the number of young she can fledge. Therefore, adding an extra egg to her clutch should curtail reproductive output, either through lowered productivity, or reduced growth rates and fledgling masses. No such effect was observed. According to the hypothesis, removal of an egg from a clutch should also result in a reduced reproductive output through lowered productivity,

presumably because the female is without the extra nestling that she supposedly could have raised to fledging. The 3->2 group had a lower productivity than did the C3 group (Table 4), consistent with the hypothesis, but the 4->3 group showed no such effect. Thus, in only one of the five main predictions did productivity data support the hypothesis. Inspection of Fig. 7 suggests that most females fledged from 2 to 2.5 young, thus reducing a clutch to two (3->2) evidently produced a sub-optimal clutch. Taken together, the results thus provide evidence for an advantage in having a minimum clutch size of about three, rather than for individual optimal clutch sizes.

Nestling quality, as measured by nestling growth rate and/or fledging mass, constitutes an alternative estimate of fitness, and thus an additional means to evaluate the IOH. Higher masses at fledging usually increase a fledgling's chances of survival (e.g. Murphy 1978, Howe 1979, Fiala 1981), and thus the fledgling is said to be of better quality. With respect to growth rates, no significant differences existed for any of the predicted comparisons. For fledging masses, males in the C3 group weighed significantly more than did those in the 3->2 group, and females in the 4->3 group were heavier than were those in the C3 group. Both of these results agree with the prediction of the hypothesis. By contrast, and in

opposition to the hypothesis, females fledged at significantly greater masses in the 4->3 group than did those in the C4 group, a result that favors the alternative prediction based on the trade-off between quality versus quantity of offspring, as developed in life-history theory (Williams 1966, Smith and Fretwell 1974). As summarized in Table 5, the evidence against the IOH obtained in this study clearly outweighs the few instances of support.

One possible confounding variable of these data is that females under physiological stress (i.e. with enlarged clutches) may not have reduced the number of offspring they produced, but instead adjusted the nestling sex ratio to favour the less costly sex. Female Yellow-headed Blackbirds are smaller than males near the end of the nestling period and as adults (Willson 1966, Patterson and Emlen 1980, Richter 1983). In some species (Red-winged Blackbirds, Agelaius phoeniceus, Fiala and Congdon 1983; Rooks, Corvus frugilegus, Slagsvold et al. 1986; and Great-tailed Grackles, Quiscalus mexicanus, Teather and Weatherhead 1988), females have lower energy demands than males, due to their smaller size. In the present study, presumed males grew faster and fledged at significantly larger masses than did their female siblings (Figs. 8-9). Female Yellow-headed Blackbird nestlings are thus presumably less costly to raise.

Table 5. A summary of results as compared to the predictions of the individual optimization hypothesis (IOH).

	The IOH predicts:		Results:			
			<u>+ve</u> ¹	<u>-ve</u> ²	<u>NS</u>	<u>Total</u>
1. Higher productivity in controls than in enlarged ³ or reduced clutches.			1	0	3	4
2. Higher productivity with increased clutch size in controls.			0	0	1	1
3. Greater productivity in a) C4 than 3->4, and b) 4->3 than C3.			0	0	2	2
4. Lower nestling growth rates in reduced ⁴ or enlarged clutches than in controls.	F:	0	0	0	4	4
	M:	0	0	0	4	4
5. Faster growth rates in a) C4 than in either C3 or 3->4, b) 4->3 than C3.	F:	0	0	0	3	3
	M:	0	0	0	3	3
6. Lower fledging masses in enlarged clutches than in controls.	F:	0	0	0	2	2
	M:	0	0	0	2	2
7. Lower fledging masses in reduced clutches than in controls ⁴ .	F:	0	1	1	1	2
	M:	1	0	1	1	2
8. Greater fledging masses in a) C4 than in C3 or 3->4, and b) 4->3 than C3.	F:	1	0	0	2	3
	M:	0	0	0	3	3
			3	1	31	35

¹+ve = supports the IOH ($p < 0.05$)

²-ve = contrary to the IOH ($p < 0.05$)

NS = $p > 0.05$

³Each enlarged and reduced group is compared to its corresponding control group (i.e. $x+1$, $x-1$ vs C_x).

⁴The opposite effect (greater growth rate or fledging mass in reduced clutches) is predicted from life-history theory.

The sex ratio of fledglings in 1988 strongly favoured females at the Crescent Pond colony. Despite the preponderance of females, the proportion of males to females did not differ significantly between any of the predicted comparisons found in Table 4. Thus adult females in groups for which productivity was predicted to be lower did not produce more females than did adult females in groups with higher predicted productivity. Thus, females raising experimental clutches did not compensate by producing more females than males, and significant support for the IOH remains wanting.

After rejecting the IOH for Yellow-headed Blackbirds, the question still remains as to why large clutch-size variation exists within this species, and in particular, why females most often lay clutches of more than three eggs if they can raise as many fledglings by hatching only three young. Crawford (1977) observed that yearling Yellow-headed Blackbirds lay smaller clutches than older females, although he found much overlap existed in the distribution of clutch sizes between the two age groups. This may account for some clutch size variation, but leaves open the question of why adult females would lay larger (≥ 4 eggs) clutches.

Annual variations in breeding conditions may also exist that favour different clutch sizes in different years (van

Noordwijk et al. 1980). This 'fluctuating selection pressures' hypothesis assumes that there is a best clutch size for any given year, but that it varies from year to year (Nur 1987). Accordingly, smaller clutches would do best in years when female condition was poor, or food was not plentiful enough to raise the larger clutches. In better food years, larger clutches would fledge more young. In the present study, all but the two-egg clutches fledged, on average, more than two nestlings. No significant differences in productivity existed between the C3 and C4 clutches, indicating that there was no single 'best' clutch size, provided at least three eggs were laid.

The apparent 'waste' associated with laying a fourth egg may be functional when evaluated in light of the insurance-egg hypothesis (Dorward 1962). According to this hypothesis, an extra egg is laid as a 'replacement unit of parental fitness' (Mock and Parker 1986) to insure against the possibility of an egg failing to hatch or the early death of an older sibling (Dorward 1962, Cash and Evans 1986). Forbes (in press) examines this hypothesis from a theoretical perspective and concludes that the insurance-egg hypothesis provides an explanation for larger clutch sizes. In this study, last-hatched nestlings survived in 6.3% of four- and five-egg clutches. They survived only in those clutches in which an earlier-hatched nestling had died. Only

one female actually fledged four nestlings (interestingly, they were all female), and no female fledged five young. Thus, a last-hatched nestling normally survived in these larger clutches only if a previously hatched nestling died, thereby securing its position as an insurance offspring.

The potential benefits of laying an insurance egg may be significantly higher than the small percentage of 6.3%, because as part of the experimental design, I replaced eggs that failed to hatch. For four-egg clutches, 85.8% (Chapter I) of eggs laid hatched. Given that hatchability was not affected by laying order (Chapter I), the probability of at least one of the first three eggs not hatching while the fourth did hatch would be 0.316. This represents a sizable insurance payoff for laying a fourth egg. The insurance-egg hypothesis is thus a plausible explanation for the maintenance of a modal clutch size of four eggs in Yellow-headed Blackbirds.

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