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# CLUTCH-SIZE MANIPULATIONS IN THE YELLOW-HEADED BLACKBIRD: A TEST OF THE INDIVIDUAL OPTIMIZATION HYPOTHESIS[1]

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*Abstract.* To test the critical short-term predictions of the individual optimization hypothesis (IOH), Yellow-headed Blackbird (*Xanthocephalus xanthocephalus*) clutches of three and four eggs were experimentally enlarged or reduced by one egg, and broods were monitored until fledging. Predictions that control clutches would a) have greater fledging success than experimental clutches, and b) produce heavier or bigger offspring than enlarged broods were generally not supported. Within control clutches, the number of nestlings that fledged did not increase with clutch size. In fact, three-egg clutches were more productive than the most common clutch size of four eggs. The IOH appears to be unsupported for this population, at least up until the time of fledging. We suggest a potential insurance value exists for the fourth-laid egg, thus explaining the maintenance of a modal clutch size of four eggs in this species.

*Key words: Individual optimization; clutch-size variation; clutch-size manipulations; brood enlargement.*

## INTRODUCTION

Intraspecific variation in clutch size is considerable among altricial birds. Since clutch size and fitness are closely linked (see Price and Liou 1989, Cooke et al. 1990), the maintenance of so much variation within a single population appears puzzling. Lack (1954, 1966) argued that within a population, the most productive clutch size (that which maximizes the number of offspring surviving to breed) would evolve through natural selection to be the most common. However, many passerine species exhibit greater productivity with unmanipulated clutches that are larger than the most common clutch size (e.g., Bryant 1975, Perrins and Moss 1975, De Steven 1980, Richter 1984, Haydock and Ligon 1986, Gustafsson and Sutherland 1988, Briskie and Sealy 1989). It thus appears plausible that more than one optimal (best) clutch size exists within a population (Högstedt 1980, Nur 1987). This would explain why clutch size variation is maintained in many species.

The individual optimization hypothesis (IOH) proposes that different females have different optima which permit individual differences in maximizing reproductive output (Högstedt 1980, Nur 1986), making variation adaptive. Accordingly, each female lays a clutch of the size that is best suited to her ability to rear nestlings (Perrins and Moss 1975, Schifferli 1978, Richter 1984, Power et al. 1989) under prevailing conditions of her physiology (Drent and Daan 1980) or territory quality (Högstedt 1980). The critical prediction is that 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 fitness than with a clutch of "x + 1" or "x − 1" eggs (Nur 1986). Thus females that lay a particular clutch size would have greater fledging success than females of experimentally enlarged or reduced broods. Alternatively, females raising experimentally enlarged broods may fledge the same number of offspring as do the controls, but these enlarged broods may fledge either a smaller proportion of offspring (have increased nestling mortality) or lighter and smaller offspring than in the control broods. A secondary prediction of the IOH is that females laying larger clutches are more capable of rearing nestlings than those laying smaller clutches (Nur 1986), and thereby would have greater fitness (Nur 1987). Evidence for this prediction alone, however, would not conclusively support the IOH (Nur 1986).

Despite frequent post-hoc appeals of the IOH in explaining results, little conclusive evidence

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exists to support it (Nur 1987). Högstedt's (1980) work on the Black-billed Magpie (*Pica pica*) and that of Pettifor et al. (1988) and Tinbergen and Daan (1990) on Great Tits (*Parus major*) are evidently the only studies that supported the critical prediction of this hypothesis. Nur (1986) rejected the IOH in his study of Blue Tits (*Parus caeruleus*) as did Dhondt et al. (1990) with Great and Blue Tits. Further studies are needed to test the IOH by manipulating and comparing clutch size relative to the original clutch size (Andersson 1978, Nur 1987).

The purpose of this study is to determine if the IOH can explain the evolution of clutch size by examining a current reproductive attempt in Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*). We tested the central prediction of the IOH by comparing fledging success, proportion fledged, nestling mass and size among control, enlarged and reduced broods. We also tested the secondary prediction by assessing fledging success and proportion fledged among control clutches of three, four, and five eggs. This study is valuable since so few tests of the critical predictions of the IOH exist.

## METHODS

Field work was carried out in 1988 at Crescent Pond, near Delta, in south-central Manitoba (50°7′N, 99°19′W). Crescent Pond covers 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). Crescent Pond is surrounded predominantly by cattail (*Typha* spp.).

Yellow-headed Blackbirds are brood-reducing icterids that build their nests among cattail in deep-water marshes. They are socially polygynous with males having between two and five females in a territory. This species is single-brooded. Females lay between two and five eggs, with clutches of four eggs being the most common. In 1988, the frequency of clutches was as follows: 2 eggs—1.4%, 3 eggs—32.4%, 4 eggs—62.6%, 5 eggs—3.6%. During late incubation, we randomly selected experimental and control clutches within each of the most common natural clutch sizes of three and four eggs. Clutches were enlarged by adding one egg to clutches of three and four eggs to create clutches of four and five eggs respectively (designated as 3 → 4, 4 → 5). Clutches from which an egg was removed were reduced to either two or three eggs (3 → 2, 4 → 3). 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 control three- (C3), four- (C4) and five-egg (C5) clutches were handled on the day of laying, then monitored daily along with the experimental nests. Abandoned nests and those in which nestlings were depredated were not included in this analysis, since our focus was to determine whether a female is best able to feed the number of nestlings that corresponds to the clutch size she laid. Predation levels were similar across all clutch sizes and treatments. Our final sample consisted of 12 enlarged, 31 control and 29 reduced broods.

Adding or removing an egg from a clutch had no effect on its viability. The hatching success of transferred eggs (84.2%, $n = 19$ nests) was not significantly different from that of control eggs (88.5%; $n = 26$ nests) ($\chi^2 = 0.17$, df = 1, $P > 0.5$). Eggs that failed to hatch were replaced with newly hatched nestlings in both the experimental and control groups to maintain the required designated brood size. Nestlings that died after hatching were not replaced.

Nestlings were individually marked on the day of hatching with blue and black fingernail polish applied to their toes (J. Blank, pers. comm.). 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. To determine on which day the nestlings hatched, since they could have hatched at any time between successive daily visits, we used the following method to assign birds a hatching date. Mean hatching mass and mean mass gained per hour were first calculated for a sample of eight nestlings of known hatching time that had also been measured the following day. Negligible mass gain was assumed between 22:00 and 05:00 hr. To determine hatch time of 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 main gain was divided by the mean mass gained per hour, which gave the number of hours since the nestling's hatch, and allowed us to backdate to the time of hatch. If the predicted time of hatch fell between 22:00 and 05:00 hr, the hatch was assigned to the previous day.

TABLE 1. Summary of *P*-values for Mann-Whitney *U* tests for fledging success, day 9 mass and tarsal size among the predicted comparisons of the individual optimization hypothesis.

| | C4 > 4 –> 5 | C3 > 3 –> 4 | C4 > 4 –> 3 | C3 > 3 –> 2 |
|---|---|---|---|---|
| Number of fledglings | 0.02† | 0.45 | 0.23 | 0.01* |
| Proportion fledged | 0.18 ∧ | 0.049* | na | na |
| Nestling mass (female) | 0.50 ∧ | 0.23 | na | na |
| Nestling mass (male) | 0.50 ∧ | 0.04* | na | na |
| Nestling tarsus (female) | 0.50 ∧ | 0.27 | na | na |
| Nestling tarsus (male) | 0.42 ∧ | 0.25 | na | na |
| | C5 > C4[1] | C4 > C3[1] | 4 –> 3 > C3[1] | C4 > 3 –> 4[1] |
| Number of fledglings | — | 0.25 | 0.43 | 0.23 |
| Proportion fledged | — | 0.01Δ | na | 0.23 |
| Nestling mass (female) | na | na | 0.44 | 0.21 |
| Nestling mass (male) | na | na | 0.14 | 0.11 |
| Nestling tarsus (female) | na | na | 0.35 | 0.29 |
| Nestling tarsus (male) | na | na | 0.29 | 0.11 |

* = Significant differences ($P < 0.05$).
† = Significant difference, but in the direction opposite to the IOH prediction.
Δ = Significant difference where IOH predicts none.
na = Not applicable. Not predicted by the IOH.
— = Sample size too small to warrant statistical tests. Includes all C5 > 4 –> 5 results (not shown).
∧ = Not enough statistical power to detect small differences.
[1] = Derived from the secondary prediction that females laying larger clutches have a greater ability to raise young.

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. Tarsus measurements were taken with dial calipers to the nearest 0.1 mm. Timing of measurements was randomized among the different groups and usually occurred between 08:00 and 17:00 hr. Nests were monitored until all nestlings either fledged or died. When 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 fledging time of 10–11 days for this species at Delta, and falls within the range of 9–12 days found by previous researchers (Fautin 1941, Willson 1966). If eight days old or younger, the nestling 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).

We monitored nestling survival until fledging. Since the data were not normally distributed, we used non-parametric statistics, and corrected for ties. Kruskal-Wallis tests were performed on fledging success and fledging proportion data of the three treatments (reduced, enlarged and controls). One-way Mann-Whitney *U* tests were done on the a priori predictions of the IOH (Table 1). Sample sizes were very low for both C5 ($n = 3$) and 4 → 5 ($n = 4$) groups, thus results for the C5 vs. 4 → 5, and the C4 vs. C5 comparisons were not included in Table 1. We did power tests on the results of the C4 vs. 4 → 5 predictions, using the LSD method (Steel and Torrie 1980) to determine whether the sample size of 4 → 5 was sufficient to detect true differences. The "na" ("not applicable") in Table 1 denotes that these particular comparisons are not relevant to the testing of the IOH. For example, the IOH makes no definitive prediction about the proportion of nestlings fledged between control and experimentally reduced broods, but does so for control and enlarged broods.

The sex of each nestling was determined by its mass on the last visit prior to 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 is considered reliable (Richter 1983). Due to this sexual dimorphism, results for mass and tarsus size were analyzed separately for males and females. We selected day 9 mass and tarsus measurements because this time is close to that of fledging, and it gave us a higher sample size than would day 10 or 11. Sine the nestlings hatch so asynchronously, many were not measured on day 9, but were measured on days 8 and 10. Therefore, we calculated a mean day 9 mass and tarsus for females and one for males in each nest in which more than one nestling of this age were present. Data were then analyzed in the same manner as that of fledging success. Results were considered significant if $P$-values were less than 0.05.

## RESULTS

Brood reduction occurred in 67% of the control and experimental nests combined, with a total of 30.1% of nestlings dying. Last-hatched nestlings typically died first, followed by the penultimate nestling, if two died. Last-hatched nestlings did survive in 6.3% of four- and five-egg clutches, but only when an earlier-hatched sibling died.

For the entire sample of nests, the amount of brood reduction varied among control, experimentally enlarged, and experimentally reduced broods (Kruskal-Wallis: $H = 5.91$, df = 2, $P = 0.052$, $n = 72$), with experimentally reduced broods fledging the highest proportion of offspring (Fig. 1A). The IOH prediction of controls fledging a greater proportion of nestlings than enlarged broods was not supported overall, since both groups fledged a similar proportion (Mann Whitney $U = 176.5$, $n_1 = 31$, $n_2 = 12$, median = 0.67, interquartile range = 0.5, 0.75, $P = 0.40$). Among the three control groups (C3, C4 and C5), there was a significant difference in the proportion of offspring fledged ($H = 6.66$, df = 2, $P = 0.036$, $n = 31$) with C3 fledging the highest proportion (Fig. 1B). The IOH predicts that all three control groups would fledge a similar proportion.

The a priori predictions of the IOH for number of fledglings, as summarized in Table 1, were supported in only one case: C3 fledged significantly more offspring than 3 → 2 ($U = 15$, $n_1 = 13$, $n_2 = 6$, median = 2.0, i.r. = 1.25, 3.0, $P = 0.01$) (Fig. 2). However, contrary to the IOH, 4 → 5 fledged significantly more offspring than did C4 ($U = 10.5$, $n_1 = 15$, $n_2 = 4$, median = 3.0, i.r. = 2.0, 3.0, $P = 0.02$). Nestlings from the 4 → 5 group were not significantly lighter or smaller in tarsal size than those from the C4 group, but sample size was small, reducing the statistical power for detection of small differences. All other predictions for fledging success (numbers fledged) were nonsignificant (Table 1).

For proportion of offspring fledged, only one prediction was supported: C3 fledged a higher proportion of offspring than did 3 → 4 ($U = 30$, $n_1 = 13$, $n_2 = 8$, median = 0.75, i.r. = 0.67, 1.00, $P = 0.049$) (Table 1, Fig. 3). The IOH predicts that females from control groups should fledge similar proportions of offspring, but females from C3 fledged a higher proportion of nestlings than did those from C4 (Table 1). There was not enough statistical power to detect any differences in the proportion fledged between C4 and 4 → 5 due to the low sample size of 4 → 5 (observed difference = 0.1, LSD = 0.21).

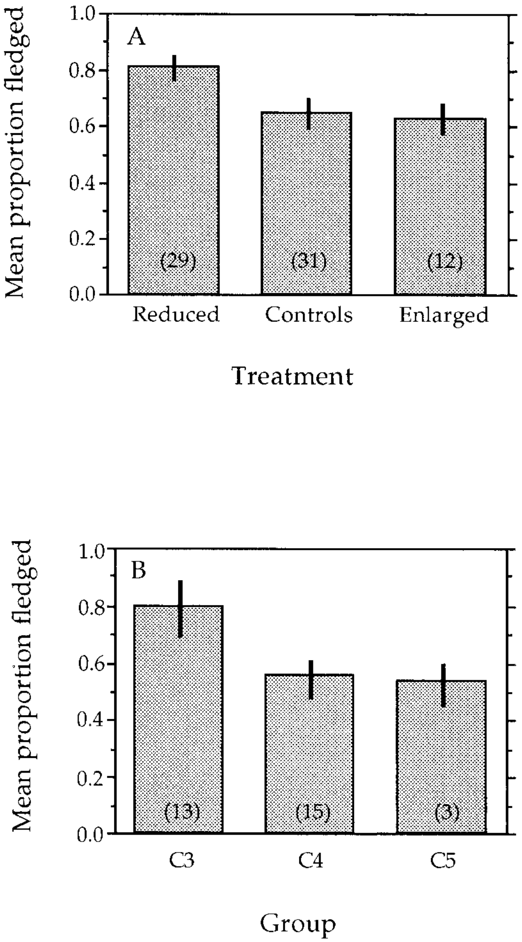

FIGURE 1. Mean proportion (±SE) of nestlings fledging from A) reduced, control and enlarged clutches, and B) within control clutches of three, four, and five eggs. Sample size of nests is in brackets.

For the entire nest sample, nestling mass on day 9 did not differ significantly among control, enlarged, and reduced broods for females ($H = 1.1$, df = 2, $P = 0.59$, $n = 40$) or males ($H = 3.1$, df = 2, $P = 0.21$, $n = 33$). Similarly, nestling tarsal size (day 9) did not differ significantly among controls, enlarged and reduced broods for

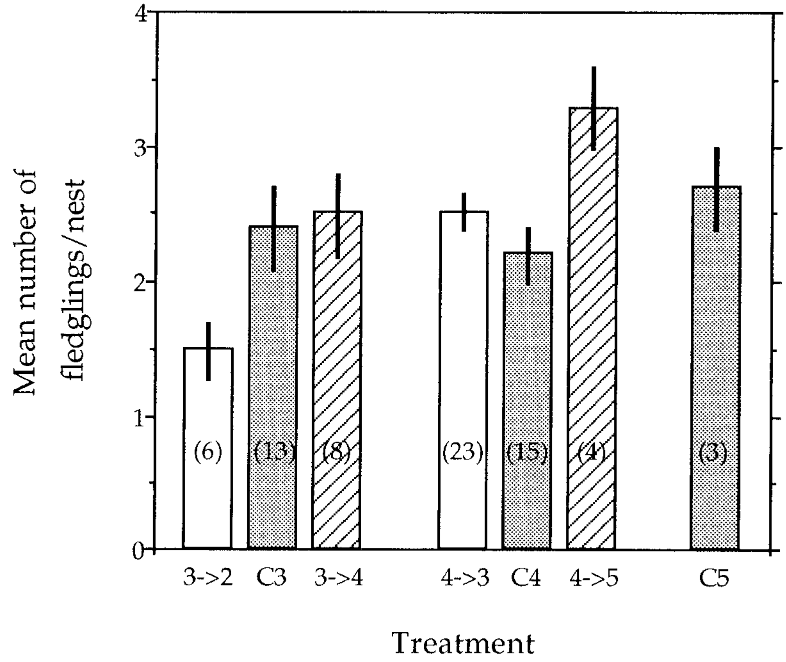

FIGURE 2. Mean number (±SE) of fledglings per nest within the different treatments. Sample size of nests is in brackets.

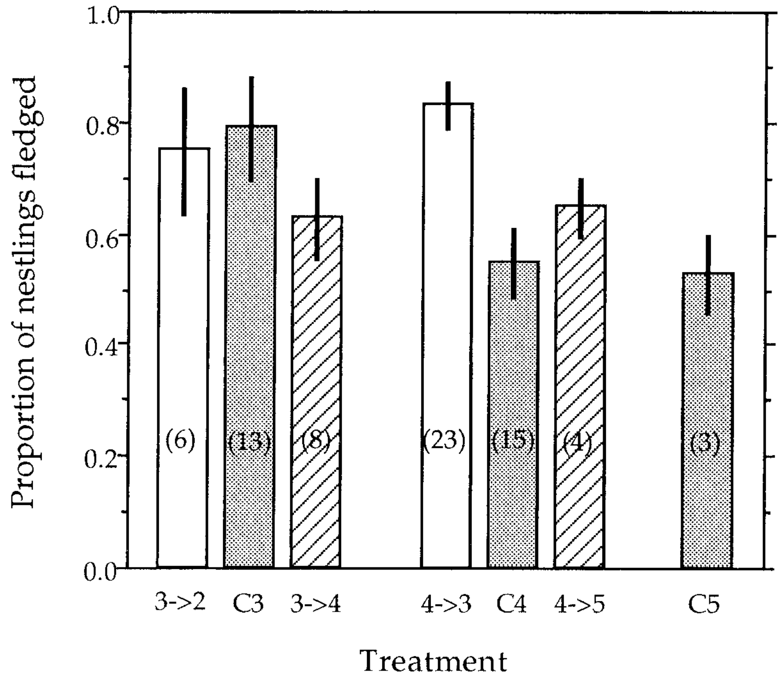

FIGURE 3. Mean proportion (±SE) of nestlings fledging within the different treatments. Sample size of nests is in brackets.

females ($H = 1.1$, df $= 2$, $P = 0.57$, $n = 40$) or males ($H = 1.7$, df $= 2$, $P = 0.42$, $n = 33$).

When examining nestling differences in female mass, female tarsus, or male tarsus, none of the predictions of the IOH were supported (Table 1). For male mass, only one prediction was supported: male nestlings in C3 were significantly heavier than those in 3 → 4 broods ($U = 5$, $n_1 = 7$, $n_2 = 4$, median = 46.1, i.r. = 44.25, 50.15, $P = 0.045$). There was not enough statistical power to determine small differences in female or male nestling mass/tarsus for the C4 vs. 4 → 5 comparison. Of the 22 relevant comparisons made, three supported the IOH, two were opposite to what was predicted, and 17 had non-significant results (Table 2).

TABLE 2. Tests of the predictions of the individual optimization hypothesis (IOH). The number of comparisons under: "Yes" are those in agreement with the IOH ($P < 0.05$), "No" are against the IOH ($P < 0.05$), and "Neither" have non-significant results ($P > 0.05$).

| The IOH predicts: | Yes | No | Neither |
|---|---|---|---|
| 1. More fledglings from controls than from enlarged[1] or reduced clutches. | 1 | 1 | 2 |
| 2. More fledglings from larger control clutch sizes. | 0 | 0 | 1 |
| 3. More fledglings from<br>a) 4 -> 3 than C3 and<br>b) C4 than 3 -> 4. | 0 | 0 | 2 |
| 4. A higher proportion fledged from control than enlarged broods. | 1 | 0 | 0 |
| 5. A similar proportion fledged from C3, C4 and C5 broods. | 0 | 1 | 0 |
| 6. A higher proportion fledged from C4 than 3 -> 4. | 0 | 0 | 1 |
| 7. Greater nestling mass/tarsal size in C3 than 3 -> 4. | F: 0<br>M: 1 | 0<br>0 | 2<br>1 |
| 8. Greater nestling mass/tarsal size in<br>a) 4 -> 3 than C3<br>b) C4 than 3 -> 4. | F: 0<br>M: 0 | 0<br>0 | 4<br>4 |
| | 3 | 2 | 17 |

[1] Each enlarged and reduced group is compared to its corresponding control group (i.e., x + 1, x − 1 vs. Cx).

## DISCUSSION

The IOH proposes that a female lays the number of eggs that maximizes the number of nestlings she can fledge throughout her lifetime. Nestling quality constitutes an alternative estimate of fitness, and thus an additional means of evaluating the IOH. Heavy fledglings are thought to be of better quality than light ones since a high mass at fledging usually increases the changes of post-fledging survival (Murphy 1978, Howe 1979, Fiala 1981, Nur 1984a, Tinbergen and Boerlijst 1990, Magrath 1991, but see Nur and Clobert 1988). Therefore, adding an extra egg to a female's clutch should curtail her reproductive output through lowered fledging success, lower proportion of fledglings, or lighter/smaller fledglings. It may also result in future costs to the parents (Williams 1966, Charnov and Krebs 1974) consisting of reduced parental survival (Askenmo 1979, Nur 1984b, Reid 1987, Dijkstra et al. 1990, but see Pettifor et al. 1988) or reduced female fecundity (Røskaft 1985, Nur 1988a, Gustafsson and Sutherland 1988, Gustafsson and Pärt 1990, but see Pettifor et al. 1988). These last two variables may yield support for the IOH, but it was beyond the scope of our study to test them. Instead, we addressed the first three of these predictions, involving current reproductive effort and success up to the time of fledging.

Contrary to the IOH, larger natural clutch sizes in Yellow-headed Blackbirds did not result in more fledglings being produced than smaller clutch sizes. Our results differ in this regard from those of Willson (1966) and Richter (1984), where higher fledgling production was found in the larger clutch sizes in this species. Our results also fail to support Lack's (1954) prediction that the most common clutch size (four eggs in Yellow-headed Blackbirds: Willson 1966, Richter 1984, pers. obs.) would also be the most productive, since three-egg clutches fledged as many nestlings as four-egg clutches.

We found that the enlarged 4 → 5 broods fledged more nestlings than C4 (four-egg control) broods, contrary to the prediction. These fledglings did not have lower masses or smaller tarsi (although sample size was small), than those in the C4 broods. C3 broods did not fledge more offspring than those of 3 → 4, although in agreement with the IOH, male nestlings from C3 were heavier than males from 3 → 4. Also in support of the IOH, C3 fledged a higher proportion of nestlings than 3 → 4. Thus, although females from the C3 and 3 → 4 groups raised similar numbers of offspring, those from the 3 → 4 group would presumably have wasted valuable energy in attempting to raise an extra nestling that they had not intended to raise. A possible confounding effect on enlarged broods is the extent of paternal care. For example, males might provide relatively more care to noisily begging nestlings in enlarged broods. However, if they did so, the effect should also show up through greater fledging success in larger control nests, which did not occur.

Removal of an egg from a clutch should also result in a reduced reproductive output through the production of fewer possible fledglings. Although fledging success is predicted to be lower in reduced broods than in controls, the proportion of young fledged would likely be as high as in controls, simply due to the increased probability of these females raising the remaining young. As expected, the 3 → 2 group did fledge fewer nestlings than the C3 group (Fig. 2).

Overall, the fledging success data supported the IOH in only one of the four main predictions. Additional support from proportion fledged and mass/size comes from only two of ten comparisons of the primary prediction (although five comparisons did not have enough statistical power to detect differences), and none of the thirteen comparisons of the secondary prediction. The results thus provided little support for individual optimal clutch sizes, but do suggest an advantage in having a minimum clutch size of three eggs. Care must be taken when interpreting studies of short duration such as ours (Nur 1988b). Although these results are perhaps not as conclusive as those of a longer-term study, they do pose significant problems for the generality of the IOH.

Why then does such large clutch-size variation exist within this species, given that large clutches may fledge as many nestlings as a smaller one? It may be age-related. Crawford (1977) observed that yearling Yellow-headed Blackbird females laid smaller clutches than older females, and fledged fewer young. Although we were unable to age adult females, we did not observe a similar increase in fledging success with clutch size.

Clutch-size variation may also be maintained by variations in breeding conditions that favor different clutch sizes in different years (the fluctuating selection pressure hypothesis, van Noordwijk et al. 1980). Unlike our study, others on this species in different areas have documented increased fledging success with increasing clutch size (Willson 1966, Richter 1984). Variable breeding conditions could make it difficult for females to predict and lay an optimal clutch size. Failing the ability to predict future environmental conditions when laying eggs, females may lay an optimistic number of eggs, rather than an optimal number (i.e., it may not be the most productive clutch size in a given year). The extent of male help in feeding is yet another variable which may make it difficult for a female to predict and lay an optimal clutch size. Females could still be selected to lay a clutch size that maximizes lifetime fitness, but this clutch size may only be optimal in a given year or habitat. 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 nestlings. Although somewhat controversial (see Magrath 1990 for review), brood reduction is commonly thought to be an adaptation to unpredictable environments (Pijanowski 1992, Konarzewski 1993). Since Yellow-headed Blackbirds are brood-reducers, the IOH, as currently developed, may not readily apply to this species.

Finally, the "waste" of laying a fourth egg may be functional when evaluated in light of the insurance-egg hypothesis (Dorward 1962, Forbes 1990). 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). Therefore, the benefits incurred by laying an extra egg would exceed the costs of producing and incubating it (Anderson 1990). Forbes (1990) examined this hypothesis from a theoretical perspective and concluded that the insurance-egg hypothesis can provide an explanation for larger clutch sizes in species exhibiting facultative brood reduction, such as Yellow-headed Blackbirds. In our study, last-hatched nestlings survived in only 6.3% of four- and five-egg clutches, and in each case, only in those clutches in which an earlier-hatched nestling had died. In addition, only one female ever fledged four nestlings (interestingly, they were all female: the smaller sex), and no female fledged five nestlings. 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 6.3%, because as part of our experimental design, we replaced eggs that failed to hatch. For control clutches, 88.5% of eggs laid, hatched. Given that hatchability was not affected by clutch size or laying order (Barber 1991), the probability of at least one of the first three eggs of a four-egg clutch not hatching while the fourth did would be 0.272. 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, even when four nestlings are rarely fledged.

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