

BROOD REDUCTION AND THE INSURANCE-EGG HYPOTHESIS IN TWO
FACULTATIVE BROOD REDUCING SPECIES, THE HERRING GULL
AND THE DOUBLE-CRESTED CORMORANT

BY

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Abstract

A study was conducted in 1991 and 1992 at Kaweenakumik Lake, Manitoba, to determine if last-laid eggs contribute to reproductive success because they replace older siblings that fail to survive (the insurance-egg hypothesis) in two facultative brood reducing species, the herring gull (Larus argentatus) and the double-crested cormorant (Phalacrocorax auritus). Mock and Parker's (1986) formula was used for partitioning reproductive value of last-laid eggs into insurance value and, if all chicks survive, extra-reproductive value. It was found that in 1991 the insurance value of the last-laid herring gull egg was 53.3% higher than its extra-reproductive value, while in 1992 it was 11.5% lower. When control clutches (those that contained all n eggs), were compared to experimental clutches ($n-1$ eggs), it was found that the control clutches had a significantly greater nest productivity. To determine if this increased productivity at control nests was due to insurance or extra-reproductive value, the data was partitioned into potential insurance nests, if one or more older siblings failed, or potential extra-reproductive value if all ($n-1$) older siblings had survived. It was found that in 1991 the last-hatched offspring only added significantly as extra-reproductive value, whereas in 1992 it added significantly as both insurance and extra-reproductive value. When a correction factor was used to take account of instances where surviving last-hatched young that had lost an older sibling might have survived even if their older siblings had not failed, insurance values were reduced, and were not significant in either year.

In 1991 both 3 and 4-egg double-crested cormorant clutches were examined. Insurance value of the last-laid egg in three egg clutches was 50% of the total reproductive value, whereas in clutches of four, obligate brood reduction occurred and young from last-laid eggs survived only as insurance. When 3-egg control clutches were compared to experimental clutches ($n-1$ eggs), it was found that the last-laid egg added

significantly as both insurance and extra-reproductive value, but as for herring gulls the insurance value was no longer significant when the correction factor was used. In 4-egg clutches the control nests exhibited a significantly enhanced nest productivity, all due to insurance value. Observations in 1992 showed that both facultative and obligate elimination of the last-hatched chick in cormorants appeared to be the result of its inability to compete with its older, larger siblings for food. Siblicide, typical of many obligate brood reducers, was not observed.

This study obtained the first known experimental evidence in support of the insurance-egg hypothesis for a facultative brood reducing species. The level of insurance value in herring gulls and cormorants was low, however, and was not sufficiently robust to endure at a significant level after potential insurance chicks that might have survived even if their older siblings had not failed were removed from the insurance value group. As shown previously for pelicans, a significant level of insurance value was shown experimentally under obligate brood reduction conditions, in 4-egg cormorant clutches.

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General Introduction

The adaptive significance of avian brood reduction as proposed by Lack (1947, 1954), suggests that females lay as many eggs as they can raise to fledging during a 'favorable' year. This optimum number of eggs is often referred to as the optimistic clutch size (Lack 1947; Magrath 1990). If food proves to be scarce during a particular breeding season, then the sequential elimination of young (last hatched to first hatched) results. Asynchronous hatching is believed to facilitate this process by placing the youngest chicks in the brood at a competitive disadvantage (Parsons 1975; Howe 1976, 1978; Ryden and Bengtsson 1980; Bengtsson and Ryden 1981; Hahn 1981), thereby ensuring that only the most viable young survive.

The brood reduction hypothesis, although conceptually straight forward, has been difficult to test under natural conditions, and alternative interpretations have been advanced. The most common criticisms of the brood reduction hypothesis arise from alternative interpretations of hatch asynchrony with which the hypothesis is usually associated. In general, it is argued that if hatch asynchrony has other functions or causes, then brood reduction may be simply an effect (*sensu* Williams 1966), possibly maladaptive (Clark and Wilson 1981) of asynchrony which results in the competitive demise of the youngest chick. Alternative interpretations of hatch asynchrony include: (1) the peak-demand reduction hypothesis (Hussell 1972) which proposes that asynchronous hatching increases the reproductive potential of a brood by spreading out its feeding demands; (2) the sibling rivalry reduction hypothesis (Hahn 1981) which proposes that asynchronous hatching is a mechanism which creates a stable dominance hierarchy to prevent needless energy expenditure when competing for food; (3) the nest-failure hypothesis (Clark and Wilson 1981) which proposes that asynchronous hatching minimizes predation on nestlings; (4) the hurry-up hypothesis

(Clark and Wilson 1981, Slagsvold 1986) which proposes that asynchronous hatching is the result of early incubation which is a way of hurrying up the hatching of the young to utilize declining food resources; (5) the sexual conflict hypothesis (Slagsvold and Lifjeld 1989) which proposes that asynchronous hatching is a female strategy to increase male parental investment. It has also been suggested that asynchrony is an epiphenomenon arising from joint hormonal control of incubation and ovulation (Mead and Morton 1985).

A somewhat related, but more direct criticism of the brood reduction hypothesis was the suggestion (Amundsen and Stokland 1988) that even if hatch asynchrony did facilitate beneficial pruning of surplus offspring in years when food was scarce, any such benefit would be more than negated by competitive losses of youngest brood members in years when food was abundant. Although this may be true under certain conditions, recent theoretical studies (Temme and Charnov 1987; Pijanowski 1992) have demonstrated that benefits received during poor food years could in fact outweigh costs endured during good food years. Moreover, experimental tests in which both food and asynchrony were manipulated (Magrath 1989) provide direct empirical support for the hypothesis.

In some species brood reduction is obligate, that is, the second hatched nestling almost always dies (Edwards and Collopy 1983), making Lack's hypothesis as originally formulated, difficult to apply. For these species an extension of the brood reduction theory has been developed, called the insurance-egg hypothesis. This was first proposed by Dorward (1962) to explain why white (Sula dactylatra) and brown boobies (S. leucogaster) lay two eggs and yet only rarely raise both young to fledging. The hypothesis states that birds using this strategy will lay an 'extra' egg to insure against the loss or infertility of the first egg or the early death of the first chick (Cash and Evans 1986). If an older sibling does indeed die, then it is the function of the insurance-egg to replace it, and by doing so, maintain the parent's reproductive fitness.

If the first chick is healthy, then the second chick must be eliminated (brood reduction), often as a result of sibling aggression (Mock 1984; Mock et al. 1990). The insurance-egg hypothesis has been primarily confined to explaining the evolution of two egg clutches in obligate brood reducing species such as the white and brown booby (Dorward 1962; Anderson 1990), the whooping crane (Grus americana) (Novakowski 1966), the great white pelican (P. onocrotalus) (Brown and Urban 1969), the pink-backed pelican (P. rufescens) (Burke and Brown 1970; Din and Eltringham 1974), rockhopper (Eudyptes chrysocome) and macaroni penguins (E. chrysolophus) (Williams 1980), the American white pelican (Pelecanus erythrorhynchos) (Cash and Evans 1986), ground hornbills Bucorvus spp. (Lamey and Mock 1991), and a number of falconiform species (see Meyburg 1974; Gargett 1978; Edwards and Collopy 1983; Simmons 1988).

Mock and Parker (1986) and Forbes (1990) have proposed that the insurance-egg hypothesis is also applicable to species practicing facultative brood reduction as in the species originally considered by Lack in his brood reduction hypothesis. In multi-sibling broods, the last-hatched chick can act as insurance against the death of an older nestmate in less than favorable conditions, while serving as a potential extra unit of reproductive output during favorable conditions. When death does occur in these species it is usually as a consequence of starvation rather than siblicide (Mock et al. 1990) (for exceptions see Procter 1975; Fujioka 1985; Mock 1984, 1985; Drummond and Chavelas 1989). To date, few studies have looked at the insurance-egg hypothesis with regard to this type of reproductive adaptation (but see Graves et al. 1984; Mock and Parker 1986; Beissinger and Waltman 1991), and none has tested it experimentally.

This study tested the insurance-egg hypothesis experimentally in two brood reducing species, the double-crested cormorant (Phalacrocorax auritus) (Drummond 1987), and the herring gull (Larus argentatus) (Paludan 1951; Parsons 1975).

The herring gull was selected as an apparently conventional facultative brood reducing species for which an insurance function of the last, or third, egg has been suggested (Graves et al. 1984).

Brood reduction status in the double-crested cormorant is more problematical. Clutch size is variable, ranging from 1 to 9 eggs (Lewis 1929; Mcleod and Bondar 1953), and it has been suggested that brood reduction varies with clutch size (Desgranges 1982). Preliminary observations of cormorant nests in Manitoba (East Shoal Lake, Evans pers. comm.; Kaweenakumik Lake, pers. obs.) suggested that for clutches of 4 or 5, brood reduction was essentially obligate, whereas it was facultative for clutches of 3 eggs. The possibility of testing the insurance-egg hypothesis under both conditions in the same species prompted me to select cormorants as a second species in which to test this hypothesis.

The thesis is written in the form of two manuscripts, one for each species. Additional herring gull data taken from the study nests but only peripherally relevant to the assessment of the insurance-egg hypothesis, are for completeness included in Appendix I.

Chapter 1: Brood Reduction and the Insurance-egg Hypothesis in Herring Gulls (Larus argentatus)

Introduction

Many species of birds lay more eggs than they can raise to independence (Ricklefs 1965; Seel 1970; Clark and Wilson 1981; Mock 1984). Lack (1947) suggested that birds lay as many eggs as they can possibly raise during a 'favorable' year, when food is abundant. During a poor breeding season when food is scarce the last-hatched young is eliminated, which reduces demands on the parents. This adaptive interpretation of chick loss is commonly known as brood reduction (Ricklefs 1965). Integral to the brood reduction hypothesis is the further assumption that asynchronous hatching facilitates the process by placing the youngest chick at a competitive disadvantage (Lack 1947; Parsons 1975; Howe 1976; Ryden and Bengtsson 1980; Hahn 1981), thereby ensuring that only the most viable young survive. As developed by Lack (1947, 1954), brood reduction is adaptive because when food is plentiful, the entire brood is successfully raised, while if it is scarce, the brood is reduced to a number the parents can successfully rear. The adaptiveness of brood reduction has been questioned (eg. Clark and Wilson 1981; Slagsvold 1982), but recent studies have provided both empirical (Magrath 1989) and theoretical (Temme and Charnov 1987; Pijanowski 1992) support for an adaptive interpretation.

An adjunct to brood reduction theory is the insurance-egg hypothesis, first proposed by Dorward (1962). Birds utilizing this strategy are thought to lay an 'extra' egg that survives only when there is loss or infertility of an older egg or the accidental death of an elder chick (Cash and Evans 1986). More recently, Mock and Parker (1986) and Forbes (1990), have suggested that the insurance-egg hypothesis is also applicable to facultative brood reducing species in which the last-hatched chick can act either as a unit of extra reproductive output during favorable conditions, or serve a potential insurance function during less

favorable conditions when an older nestmate has either failed to hatch or suffered an early death (Nisbet and Cohen 1975; Forbes 1990). For the laying of an insurance egg to function as an efficient parental strategy, a hatchling produced from it must be quickly eliminated (brood reduction) during those times when food is scarce and older siblings do not fail.

The herring gull (Larus argentatus) is a facultative brood reducing species that usually lays three eggs (Paludan 1951; Harris 1964; Kadlec and Drury 1968; Burger 1984). After studying the effects of food supplementation on chick growth, Graves et al. (1984) suggested that the third egg functions primarily as potential insurance against the loss of the first or second egg. Their study showed that the third chick had a very low probability of fledging unless one of the first two eggs failed to hatch or the chicks suffered an early death. Although plausible, the insurance-egg hypothesis has not been tested experimentally in herring gulls or any other facultative brood reducing species. In this study I examined the insurance-egg hypothesis in herring gulls by determining offspring survivorship and growth at experimentally manipulated and natural control nests.

In typical obligate brood reducing species where the insurance-egg hypothesis was first developed, last-hatched offspring that survive do so only as insurance. In facultative brood reducing species such as the herring gull, the expected reproductive value (RV) (Fisher 1958) of the last-hatched offspring may be made up of two components (Mock and Parker 1986): the fraction of its survivorship which is independent of its siblings' fates, and the fraction that does depend critically on their fates. These components are termed extra-reproductive value (R_{Ve}), and insurance reproductive value (R_{Vi}) respectively (Mock and Parker 1986). R_{Ve} represents an additional unit of reproductive success for the parents whereas R_{Vi} is a replacement unit of parental fitness. In this study I assess R_{Ve} and R_{Vi} following the methodology of Mock and Parker (1986), then introduce a new correction term that provides a more generalized

method of calculating these values.

Methods

Study Site

The study was conducted in the spring of 1991 and 1992 at Kaweenakumik Lake (formerly Kawinaw Lake), which is situated approximately 450 km north of Winnipeg, Manitoba Canada, between Lake Winnipeg and Lake Winnipegosis, at 52° 50'N latitude and 99° 29'W longitude (Vermeer 1969; for map see O'Malley and Evans 1980). The four islands on which the bird colonies reside are part of the Manitoba Ecological Reserves Program. Only one of the islands supported the main herring gull population between 1990-1992 (pers.obs.) as well as in previous years (Vermeer 1970; Evans pers. comm.). There were approximately 180 active nests in the main colony in each of 1991 and 1992.

The herring gull colony resides on a treeless rocky island with relatively sparse vegetation consisting mainly of burning nettle (Urtica dioica var. procera), and squirrel tail grass (Hordeum jubatum). Other avian species found nesting on the island included white-winged scoters (Melanitta deglandi) and a single Canada goose (Branta canadensis). The study island could only be reached once the ice had left the lake, by which time some herring gulls had laid their first egg. My first visits occurred on 15 May, 1991 and on 13 May 1992.

Field methodology

In 1991 the herring gull colony was not visited on a regular basis until laying had been completed (30 May). Sixty nests with full three-egg clutches were marked with numbered stakes and the last-laid (C) egg identified by relative size. According to Harris (1964), Parsons (1972), and Davis (1975), the C egg has a significantly smaller volume than either the A or B eggs (for exceptions see Meathrel et al. 1987). To facilitate correct identification of the C egg, length (L) and breadth (B) of all

eggs in each clutch were taken with vernier calipers ($\pm 0.05\text{mm}$), and volumes (V) calculated using the equation $V=0.476LB^2$ (Harris 1964). The egg with the smallest volume was labelled C with an indelible ink felt marker.

In 1992 the herring gull colony was entered daily during the laying period. Nests with new eggs were marked with a numbered stake and A, B or C eggs were labeled according to their laying order. Once laying was complete, length and breadth measurements were taken and volumes calculated as in 1991.

To reduce chick loss due to human-induced movements of mobile young (Haymes and Morris 1977; Evans 1980), wire enclosures were placed around the nests using 63.5 centimeter high, 2.54 cm mesh poultry wire. After preliminary testing, a circumference of approximately 10 meters around each nest was selected to ensure relatively normal chick and parent behavior. Only nests with protective cover (vegetation or rocks) were used, to reduce the probability that predation rates were inflated due to the decrease in total area available to the chicks.

Nests were randomly selected as either experimentals or controls. Five days prior to the time of hatch, C eggs were removed from experimental nests ($n=30$ in 1991, 41 in 1992) and fostered to nests not used in the insurance-egg experiment. Fifty eight staked nests in 1992 not used in the experiment and not manipulated were retained as unpenned control nests.

At the onset of hatching, daily nest checks were initiated in both years. Newly hatched chicks (day 0) were fitted with a temporary numbered plastic leg band (domestic chick size) and weighed ($\pm 0.05\text{g}$, Ohaus electronic balance). It was noted whether they were wet, slightly wet (most of body wet but some drying had occurred), nearly dry (most of body dry but still some damp feathers), or dry. Chicks were subsequently weighed every second day, up to day 8. Daily weighings were avoided to reduce disturbance to the colony. Ending the measurements on day 8 was

considered valid because the greatest mortality for herring gull chicks normally occurs within the first seven days after hatching (Paynter 1949; Harris 1964; Kadlec and Drury 1968; Parsons 1975). When the colony was visited, the number, position, and weight of dead chicks were recorded, and dead bodies collected for a post mortem examination.

Partitioning Expected Reproductive Value

Each surviving offspring has a particular amount of expected reproductive value (RV) that it adds to its parents overall fitness. When dealing with the last-hatched chick, RV was partitioned into either extra-reproductive value (R_{Ve}) or insurance-reproductive value (R_{Vi}), based on its survival and the fate of its siblings. To calculate the R_{Ve} and the R_{Vi} of a last-hatched offspring in unmanipulated control broods, I used the formulas devised by Mock and Parker (1986)

$$R_{Ve} = q(P_e) \quad (1)$$

$$R_{Vi} = (1-q)P_i \quad (2)$$

where q is the proportion of broods in which the youngest was not predeceased by an elder sibling, P_e is the fraction of q in which the youngest survived, and P_i is the fraction of youngest offspring that survived in the other $(1-q)$ broods.

In addition, R_{Vi} was partitioned into insurance-egg values (R_{Vie}), and insurance-chick values (R_{Vic}). R_{Vie} was represented by those nests in which the last-laid egg served as a unit of replacement for an earlier laid egg within the clutch that failed to hatch, while R_{Vic} was represented by those nests in which replacement occurred when an older sibling failed after hatching. These two values were calculated as

$$R_{Vie} = e R_{Vi} \quad (3)$$

$$R_{Vic} = c R_{Vi} \quad (4)$$

where e and c represent the proportion of failed elder siblings that did not hatch (e) or died as chicks (c), ($e + c = 1$).

Experimental Tests for RVe and RVi

Each brood from the control and experimental samples was designated as either belonging to a potential RVe group or a potential RVi group. A particular nest (control or experimental) was classified as potential RVe if an elder sibling had not died by 8 days, whereas a nest in which one or both elder siblings died, was classified in the potential RVi group. Brood size at 8 days of age was then compared for the experimental potential RVe group versus the control potential RVe group and also for the experimental and control potential RVi groups. This enabled me to determine whether the last-hatched chick significantly increased the parent's reproductive fitness through either increased RVe, RVi, or both.

Calculation of RVe and RVi Correction Factors

Although Mock and Parker's (1986) pioneering analysis of reproductive value in the context of brood reduction enables one to determine the relative magnitudes of RVe and RVi, their calculations do not allow for the possibility that some last-laid eggs (C) in broods where an elder sibling died, would have survived even if their nestmates had lived. Mock and Parker's concept of RVe and RVi can be further developed to take account of these young by noting that surviving C-chicks in the (1-q) sample may be divided into two classes: those that owe their survival directly to the demise of an older sibling (insurance offspring), and those that might have survived even if not predeceased (extra units of reproduction). The latter class could include, for example, robust terminal offspring that were thriving at the nest but failed to qualify, operationally, as extra units of reproduction merely because of the untimely accidental death of an older sibling just before survival data were collected. Any such C-offspring that do not owe their survival directly to the death of an older sibling would not represent replacement units of reproduction, hence should be factored out as a correction term (RVC), from any estimates of RVi.

Assuming that all subsamples of nests are drawn from the same population, an estimate of the proportion of last-hatched chicks in the (1-q) sample that might have survived even if all of their older siblings also survived is given by P_e , the proportion of C-offspring surviving with their older siblings in the sample of q nests. The correction term (RVC), is then

$$RVC = P_e(1-q) \quad (5)$$

Removal of RVC from R_{Vi} leaves the corrected estimate of insurance value, designated as R_{Vi}^*

$$\begin{aligned} R_{Vi}^* &= R_{Vi} - RVC \\ &= P_i(1-q) - P_e(1-q) \\ &= (1-q)(P_i - P_e) \end{aligned} \quad (6)$$

Since RVC represents the reproductive value of terminal eggs from the (1-q) sample that would have survived even if their older siblings had too, they can be thought of as units of extra-reproductive value. Therefore they can be added to R_{Ve} to give it an upwards corrected estimate designated as R_{Ve}^* .

$$\begin{aligned} R_{Ve}^* &= R_{Ve} + RVC \\ &= P_e(q) + P_e(1-q) \\ &= P_e \end{aligned} \quad (7)$$

Testing Corrected Insurance Value Experimentally

The correction factor can also be incorporated into the experimental test of the insurance-egg hypothesis. To do this, a proportion of nests representing the correction factor (RVC) must be subtracted from the (1-q) sample nests. $P_e(1-q)$ (eq.5) was used to estimate the number of nests in the (1-q) sample where C-chicks would have survived regardless of their older siblings' fates. These nests were then removed from the nests in the (1-q) sample where C-chicks were alive. Only nests from the (1-q) sample in which the terminal offspring survived could possibly represent R_{Ve} , since to be considered extra-reproductive value the last-hatched

chick must live. To apportion the reduction within the sub sample of nests having a live C-chick, the frequency with which either one or both of the A or B offspring were lost was determined, and the required number of nests, rounded to the nearest integer, removed in proportion to the relative occurrence of each category. At the remaining nests, all of the surviving C-offspring can be assumed to represent insurance (replacement) value. This remaining subsample was then combined with the other nests in the (1-q) sample (ie. those 1-q nests in which the terminal offspring did not survive) and the resulting sample compared statistically with the controls, as described below.

Statistical Analysis

Productivity at control and experimental nests was compared at the time of hatch and at 8 days of age using the non-parametric one-tailed Kruskal-Wallis test (direction of this effect was predicted by hypothesis; data were neither normally distributed nor continuous) (Zar 1974). Comparisons of brood size between experimental and control nests were conducted using one-tailed Kruskal-Wallis tests, for the same reasons noted above. All other tests, where the direction of the effect was not predicted by the hypothesis, were two-tailed. Hatching success, survival, and causes of death were compared at the egg and chick stages using $r \times c$ contingency tables and Chi-square tests. Weight comparisons at 8 days of age were made using t-tests. All calculations were performed with Statistix (version 3.5, Analytical Software, St. Paul, Minnesota). Probability values ≤ 0.05 were considered significant for all tests.

Results

Insurance and Extra-reproductive Values

Calculations of the proportion of reproductive value attributable to insurance (RVi) and extra-reproductive values (RVE) for the C eggs and chicks at control nests in 1991 and 1992 are listed in Table 1. Although

Table 1. Insurance (RV_i) and extra-reproductive (RVe) values¹ for last-laid eggs and last-hatched chicks at control nests (number of nests in parentheses).

	1991	1992
Extra-reproductive Value (RVe)		
A and B survive (n)	13 (26)	22 (35)
q	0.50	0.63
C also survives	4	9
Pe	0.30	0.41
RVe	0.15	0.26
RVe^*	0.31	0.41
Insurance Value (RV_i)		
A and/or B fails	13 (26)	13 (35)
(1-q)	0.50	0.37
C survives	6	8
Pi	0.46	0.62
RV_i	0.23	0.23
RV_i^*	0.08	0.08
Egg and Chick Components of RV_i		
RV_{ie} (e=egg)	0.16	0.12
RV_{ic} (c=chick)	0.07	0.11
RV_{ie}^*	0.06	0.04
RV_{ic}^*	0.02	0.04

¹ Calculations based on method of Mock and Parker (1986). See methods.

* Incorporates correction term, $RVC = Pe(1-q)$. $RVC = 0.15$ for both 1991 and 1992.

both RVe and RVi were present each year, RVi was 53.3% higher than RVe in 1991, but 11.5% lower in 1992. This yearly difference was due to a marked increase in RVe in 1992. RVi was the same (0.23) in both years.

As shown in the last part of Table 1, the 1991 insurance value of the last-hatched herring gull offspring was mainly due to the replacement of A or B eggs that failed to hatch (RVie), rather than to the loss of A or B chicks after hatching (RVic). About half of the insurance value occurred at each stage in 1992.

All of the above calculations of RVe and RVi were based on C-chick survival to 8 days. The relative values of RVe and RVi could be affected, however, if C-chick weights differed significantly, thereby raising the possibility that chicks had different probabilities of survival after 8 days of age. At 8 days of age, the mean weight of surviving RVe C chicks in 1991 was 123.7 ± 9.17 g (mean \pm SE), $n=4$, and the mean weight of surviving RVi C chicks was 191.5 ± 17.06 g, $n=6$. These differences were significant ($t=3.01$, $df=8$, $P=0.0168$). The same trend occurred in 1992 (RVe C chicks: 137.4 ± 20.96 g, $n=8$, RVi C chicks: 165.3 ± 16.58 g, $n=8$), but the variation was greater and the difference was not significant ($t=1.04$, $df=14$, $P=0.3157$).

Experimental Tests of Reproductive Values (RVi, RVe)

Not surprisingly, significantly more chicks hatched per brood from controls than from experimental broods (1991: controls= 2.0 ± 0.16 chicks/brood ($n=29$), experimentals= 1.4 ± 0.14 chicks/brood ($n=30$), $H=8.15$, $df=1$, $P=0.004$, 1992: controls= 2.4 ± 0.15 chicks/brood ($n=40$), experimentals= 1.5 ± 0.12 chicks/brood ($n=39$), $H=22.63$, $df=1$, $P<0.0001$). At 8 days of age, control broods (A, B and C chicks combined), were still significantly larger (160% in 1991 and 150% in 1992), than experimental broods (1991: controls= 1.6 ± 0.21 chicks/brood ($n=20$), experimentals= 1.0 ± 0.16 chicks/brood ($n=26$), $H=5.11$, $df=1$, $P=0.0119$, 1992: controls= 1.7 ± 0.15 chicks/brood ($n=40$), experimentals= 1.1 ± 0.14 chicks/brood ($n=37$), $H=6.68$, $df=1$, $P=0.0049$), indicating that the presence of the extra

(3rd) egg significantly increased nest productivity.

Whether the increased productivity at control nests was due to either or both RVi and RVe of C-offspring was analyzed by partitioning the control and experimental chicks into groups representing potential RVi (nests in which either or both A and B-offspring failed by 8 days of age) and potential RVe (nests in which neither the A nor B chicks failed). In 1991, the last-hatched offspring added significantly to nest productivity as RVe but not RVi (Table 2). In 1992, the last-hatched offspring added significantly to nest productivity as both RVe and RVi.

RVe and RVi values did not appear to be affected by differential hatchability among A, B, and C eggs (Table 3). There were no significant differences in hatchability among the experimental AB, control AB, and control C eggs in 1991 (2 X 3 contingency table $X^2=1.643$, $df=2$, $P=0.4398$) nor among the experimental, control, and unpenning A, B, or C eggs in 1992 (3 X 8 contingency table $X^2=4.498$, $df=7$, $P=0.7210$). Similarly, there were no significant differences among egg types in the number of eggs that died before hatching, were missing, or were addled, in either year (1991: 2 X 3 contingency table $X^2=0.1576$, $df=2$, $P=0.9242$, 1992: 8 X 3 contingency table $X^2=0.1568$, $df=14$, $P=0.3331$). The number hatching from the control nests in 1992 also showed no significant difference (two-tailed $H=0.43$, $df=1$, $P=0.4345$) from the unpenning control nests (Table 3).

RVe and RVi were also unaffected by differences between experimental and control A and B chick survival. There were no significant differences in survivorship among the experimental AB and control AB chicks in 1991 ($X^2=0.7290$, $df=1$, $P=0.39$) nor among the experimental and control A and B chicks in 1992 (4 X 2 contingency table $X^2=1.00$, $df=3$, $P=0.8012$). In addition, there were no significant differences in causes of death among the experimental or control A or B chicks for either year (1991: 2 X 4 contingency table $X^2=1.688$, $df=3$, $P=0.6397$, 1992: 4 X 4 contingency table $X^2=4.681$, $df=9$, $P=0.8611$) (Table 4).

Table 2. Experimental test for insurance and extra-reproductive value of herring gull C-offspring (mean \pm SE nest productivity, chicks reared to 8 days) (n nests in parentheses)

Nest Type	Year	Experimental	Control	H ¹	P
Potential R _{Ve}	1991	2.00 \pm 0.00 (8)	2.43 \pm 0.20 (7)	4.00	0.02
	1992	2.00 \pm 0.00 (16)	2.44 \pm 0.12 (18)	9.03	0.002
Potential R _{Vi}	1991	0.55 \pm 0.11 (22)	1.09 \pm 0.31 (22)	0.39	0.266
	1992	0.48 \pm 0.11 (21)	1.09 \pm 0.17 (22)	6.60	0.005

¹ Kruskal-wallis test, df=1.

Table 3. Numbers and fate (%) of herring gull eggs (A,B,C) at experimental, control, and unpenned control nests

Egg type	N	Hatched	Died ¹	Missing	Addled
<u>1991</u>					
Exp AB ²	54	40 (74.0)	7 (13.0)	0 (0.0)	7 (13.0)
Control AB	58	43 (74.1)	8 (13.8)	0 (0.0)	7 (12.1)
Control C	29	18 (62.1)	5 (17.2)	0 (0.0)	6 (20.7)
Total Control	87	61 (70.2)	13 (14.9)	0 (0.0)	13 (14.9)
<u>1992</u>					
Exp A	39	29 (74.4)	2 (5.1)	5 (12.8)	3 (7.7)
Exp B	39	30 (76.9)	4 (10.3)	3 (7.7)	2 (5.1)
Total Exp	78	59 (75.6)	6 (7.7)	8 (10.3)	5 (6.4)
Control A	40	35 (87.5)	0 (0.0)	5 (12.5)	0 (0.0)
Control B	40	31 (77.5)	1 (2.5)	7 (17.5)	1 (2.5)
Control C	40	29 (72.5)	1 (2.5)	6 (15.0)	4 (10.0)
Total Control	120	95 (79.1)	2 (1.7)	18 (15.0)	5 (4.2)
Unpenned A	58	44 (75.9)	2 (3.4)	10 (17.2)	2 (3.5)
Unpenned B	58	41 (70.7)	2 (3.4)	11 (19.0)	4 (6.9)
Unpenned C	58	42 (72.4)	1 (1.7)	13 (22.4)	2 (3.5)
Total Unpenned	174	127 (73.0)	5 (2.9)	34 (19.5)	8 (4.6)

¹ Contained dead embryo when opened 6-8 days after date of expected hatch.

² A and B eggs were not distinguished in 1991.

Exp = experimentally reduced by removal of C egg.

Table 4. Number and fate (%) of herring gull chicks in 1991 and 1992¹

Chick type	N	Survived	Missing	Pecked	Starved	Other
<u>1991</u>						
Exp AB ²	40	28 (70.0)	6 (15.0)	1 (2.5)	1 (2.5)	4 (10.0)
Control AB	40	25 (62.5)	10 (25.0)	1 (2.5)	0 (0.0)	4 (10.0)
Control C	17	8 (47.1)	4 (23.5)	0 (0.0)	1 (5.9)	4 (23.5)
Total Cont	57	33 (57.9)	14 (24.6)	1 (1.8)	1 (1.8)	8 (14.0)
<u>1992</u>						
Exp A	29	21 (72.4)	4 (13.8)	1 (3.5)	2 (6.9)	1 (3.5)
Exp B	30	21 (70.0)	2 (6.7)	2 (6.7)	3 (10.0)	2 (6.7)
Total Exp	59	42 (71.2)	6 (10.2)	3 (5.1)	5 (8.5)	3 (5.1)
Control A	35	26 (74.3)	2 (5.7)	3 (8.6)	3 (8.6)	1 (2.9)
Control B	31	25 (80.7)	1 (3.2)	3 (9.7)	1 (3.2)	1 (3.2)
Control C	29	16 (55.2)	1 (3.5)	5 (17.2)	6 (20.7)	1 (3.5)
Total Cont	95	67 (70.5)	4 (4.2)	11 (11.6)	10 (10.5)	3 (3.2)

¹ Survivorship and fate are measured up to 8 days of age.

² A and B chicks were not distinguished in 1991. Exp = experimental, Cont = control.

Reproductive values at control nests were affected by differences in survival of C-chicks compared with their older siblings (Table 4). In 1992, the survival of the control C chicks (55.2%) was significantly less ($X^2=4.734$, $df=1$, $P=0.0148$ one-tailed) than the survival of the combined control A and B chicks (77.3%). The survival of control C chicks in 1991 was also less (47.1%) than for the control AB chicks (62.5%), but this difference was not significant ($X^2=0.9490$, $df=1$, $P=0.165$ one-tailed).

Calculation of Insurance and Extra-Reproductive Values Using the Correction Factor

To determine the effects of incorporating the correction factor, the 1991 and 1992 RVe and RVi values were recalculated using the values from Table 1 and formulae (5-7). This resulted in corrected values as follows: 1991 RVe*=0.31, 1991 RVi*=0.08, 1992 RVe*=0.41, 1992 RVi*=0.08 (Table 1). In both years the correction factor increased RVe* and decreased RVi* by approximately 0.15 (=RVc). Based solely on the calculation of reproductive values incorporating this correction factor, it is evident that the last-hatched chick's reproductive value came mainly from their extra-reproductive value. This is different from the uncorrected method which showed a low RVe value in 1991, and a high RVe value in 1992 (Table 1), and it is more consistent with the experimental test of insurance in 1991 which did not find the control RVi group to have significantly greater nest productivity than the experimental group (see above).

When the RVi* is partitioned into egg RVie* and chick RVic* components (see methods: Partitioning Expected Reproductive Value), the relative proportions remain the same, but the actual values are reduced (Table 1). Hence in 1991, the eggs were most important in terms of providing insurance reproductive value, whereas in 1992 eggs and chicks were equally important.

Experimental Tests of Reproductive Values (R_{Vi}) Using the Correction Factor

To take account of apparent insurance offspring that might have survived even if their elder siblings had survived too, the potential R_{Vi} data from 1991 and 1992 were reanalyzed after incorporating the correction factor. In both years the R_{Vc} = 0.15 (Table 1). In 1991, only 6 of the control potential R_{Vi} nests had the last-hatched chick survive to 8 days. Of these, an estimated $Pe(1-q)$, or 4 chicks could have survived even if their older siblings had not failed. When compared to the experimental potential R_{Vi} group, the 1991 data were still not significant (control=0.61±0.183 (n=18) young/nest, experimentals=0.55±0.109 (n=22) young/nest, H=0.0037, df=1, one-tailed P=0.4758), as would be expected since the correction factor reduces R_{Vi} and the result from the uncorrected data was not significant either (Table 2). In 1992, there were 8 nests in which the last-hatched C-chick survived to 8 days of age and of these nests, an estimated $Pe(1-q)$, or 5 were removed. When these were compared to the experimental potential R_{Vi} group there was no significant difference (control=0.83±0.177 (n=17) young/nest, experimentals=0.48±0.112 (n=21) young/nest, H=2.2186, df=1, one-tailed P=0.0682), although a trend towards significance was observed.

An experimental test of R_{Ve} using the correction factor could not be conducted since the addition of nests taken from the R_{Vi} sample, done to maintain symmetry, biases the results. It increases the sample size while lowering the mean productivity of the control nests and hence reduces the probability of obtaining a significant result.

Discussion

The presence of the third egg significantly increased herring gull nest productivity. Compared to experimentals, the control nests had larger brood sizes at the time of hatch, as well as at 8 days of age. The greater nest productivity that the controls exhibited was the result of

the surviving C offspring providing both extra-reproductive value (R_{Ve}) and insurance reproductive value (R_{Vi}). When the total reproductive value data of the control group was partitioned into R_{Ve} and R_{Vi} in 1991 and compared to the experimental groups, it was found that nest productivity was significantly greater only in the control R_{Ve} group. However in 1992, nest productivity in both the R_{Ve} and R_{Vi} groups was significantly greater in the controls. The difference between years was a result of a decrease, in 1992, of 12.7% in mean nest productivity at experimental nests, in which one or both of the older siblings failed (potential R_{Vi} nests). Productivity remained constant between years in the corresponding control nests.

To function fully as either R_{Ve} or R_{Vi}, the last-laid egg must have a high probability of hatching. If this probability was low in the terminal egg, then the potential to serve as insurance, in cases where an elder sibling suffers an early death, would also be low. I found that reproductive values of C-offspring were unaffected by hatchability differences among eggs: experimental and control, as well as A, B, and C eggs all had equal probabilities of hatching. This was also found by Parsons (1970). The percentage of eggs that hatched for both controls and experimentals (70-80%) in the present study, is within the range others have documented for this species (Erwin 1971; Ryder and Carroll 1978; Burger 1984).

There were no differences between the experimentals and controls in A or B chick survival, but as predicted by the brood reduction hypothesis (Lack 1947, 1954), C chicks exhibited greater mortality compared to A and B offspring. This trend was observed in 1991, and in 1992 (with a larger sample size) the greater C chick mortality was found to be significant (see also Parsons 1975; Hebert and Barclay 1986). Graves et al. (1984) suggested that this mortality not only occurs because the C chick is unable to compete successfully with its older siblings, but also because in the first two days after hatching the relatively immobile C chick is

put at a further disadvantage by the parents who feed the other chicks up to 1m away from the nest. Thus the older and larger chicks are able to follow the parents more closely and obtain more feedings than the C chick. This 'third chick disadvantage' (Coulter 1977) in gulls, is akin to the situation in passerines in which nestlings compete for preferred feeding positions in the nest (Lockie 1955; Ryden and Bengtsson 1980; Greig-Smith 1985; Gottlander 1987).

It was also found that in 1991, C chicks at control nests where one or both older siblings had failed were significantly heavier than C chicks within full 3-chick broods. This trend also occurred in 1992, although not significant that year. Presumably C chicks from broods of three exhibited slower weight gain as a result of fewer feeds (Hebert and Barclay 1986) than received by C chicks in broods of two. Bollinger et al. (1990) found this to be the case with common terns (*Sterna hirundo*). It is possible that lower weight in C-chicks from broods of three could lower their chances of survival (Graves et al. 1984). If so, my estimates of RVe would be correspondingly too large. However, because growth is rapid until about 30-35 days of age (Kadlec et al. 1969), it remains possible that the C chicks from broods of three 'caught up' to the C chicks in broods of two (Haymes and Morris 1977).

The above effects on C-chick survival and weight highlight the similarity between the brood reduction hypothesis and the insurance-egg hypothesis. According to the brood reduction hypothesis, surplus offspring provide the parent with optimal reproductive value during favorable food years. The insurance-egg hypothesis, in contrast, states that surplus offspring provide the parent with optimal reproductive value by acting as a unit of replacement (insurance) against the unexpected failure of an older sibling (Forbes 1990). In both cases, the optimum parental strategy will be to eliminate any chicks which are surplus to their needs while attempting to maximize the brood size within the limits set by available food resources. In either situation, the parent need not

be an active participant in actual offspring reduction (O'Connor 1978).

Effect of the RVi and RVe Correction Factors

When using the highly conservative corrected measure of insurance value, the C egg in herring gull clutches was found to not significantly add to nest productivity as insurance reproductive value in either year. In both years, RVe* made up the greatest proportion of the chicks' total reproductive value.

A major assumption of the correction factor is that P_e , derived from the sample of q nests where all older siblings did survive, is an adequate estimate of the probability that a terminal egg would have survived in the $(1-q)$ sample even if all of its elder siblings had lived. This assumption is biologically reasonable if the mortality in the A and B eggs or chicks arises from accidental (congenital defects, infertility, predation, parasitism) events (Forbes 1990), as assumed by the insurance-egg hypothesis. This assumption is supported by the hatchability of A and B eggs from RVe and RVi nests (nests with complete clutch failure were not included), which was not significantly different (two-tailed Fisher exact tests, A eggs: $P=1.00$, B eggs: $P=0.2105$).

Use of the correction factor, RVC, in studies of insurance value seems justified for several reasons. First, RVi* represents an estimate based on the proportion of nests for which it can be reasonably claimed that their last-laid eggs owe their survival to replacement of a failed older sibling, as required by the insurance-egg hypothesis. Of perhaps equal importance, it is intuitively evident from equation (6) that $P_i > P_e$ must occur for a positive insurance value to result. This requirement means that the youngest chick must be more likely to survive when an older sibling dies first, than when it does not. This interpretation fits well with the notion of insurance value, and avoids the anomaly, possible in the uncorrected versions, of a positive insurance value being calculated when the chances of a C-offspring surviving was unchanged or even reduced

when predeceased by an older sibling.

Because the insurance-egg hypothesis was developed for obligate brood reduction and is most easily conceptualized and tested in that context, it is relevant to determine whether RVi^* is applicable to the obligate situation. When obligate brood reduction occurs, terminal offspring are not expected to survive as extra-reproductive value, and hence RVe will be equal or close to 0. As a result, the correction factor (RVc), used to derive RVi^* , simply drops out of the equation because $Pe=0$, hence for the obligate case,

$$\begin{aligned} RVi^* &= (1-q) (Pi-Pe) \\ &= Pi (1-q) \quad [Pe=0] \quad (8) \end{aligned}$$

This is identical to Mock and Parker's (1986) RVi formula. Evidently their calculated RVi is directly applicable without modification to cases of obligate brood reduction. Discrepancies in insurance value would be small when applied to species approaching the obligate situation (for examples see Mock et al. 1990). RVi^* thus emerges as a general formulation for estimating insurance value which can be applied without contradiction to either obligate or facultative brood reducing species.

For herring gulls then it appears that although low levels of RVi do exist, it is not significantly robust when the correction factor is used. However, because there was a strong trend towards significance ($P=0.0682$) in 1992, and a relatively small sample size (experimentals $n=21$, controls $n=17$), a bootstrapping technique was employed to ensure that the probability value resulting from the correction factor was not simply a result of the sample size. Using the shift method adapted from Noreen (1989), artificial samples were drawn from the existing non-normally distributed data with replacement. Ten separate runs each consisting of 10,000 iterations resulted in a mean P value=0.044, and a range of P values 0.040-0.048, thereby providing a measure of support for the insurance-egg hypothesis. The bootstrapping technique was also performed with the nonsignificant 1991 correction factor data ($P=0.4758$). In this

instance the result remained not significant (mean $P=0.370$, range of P values $0.360-0.377$). Although variation between years remains evident, bootstrap results from 1992 suggest that it would be premature to reject the hypothesis that the last-laid egg functions as insurance following the accidental death of an elder sibling, even when assessed using the conservative correction factor.

Chapter 2: Clutch Size Dependant Brood Reduction in Double-crested Cormorants (Phalacrocorax auritus): Implications for the Insurance-egg Hypothesis

Introduction

Avian egg and chick failure arises from many factors, ranging from egg infertility, predation, or accidental loss (Ricklefs 1969) to highly competitive brood size dependent competition between siblings over food provided by parents (Mock 1984). This competitive mortality, which selectively affects the youngest sibling, has been widely documented in birds (Lack 1954) under the more familiar term brood reduction (Ricklefs 1965; Mock 1984; Magrath 1990; Amundsen and Slagsvold 1991; Pijanowski 1992).

Lack's (1947, 1948, 1954) brood reduction hypothesis states that birds lay as many eggs as they can possibly raise during a favorable year, and that hatching asynchrony is an adaptation to unpredictable conditions which may arise during the breeding season. If the food supply becomes insufficient to raise the entire brood, hatching asynchrony produces a competitive feeding hierarchy within the brood (Dyrce 1974; Nisbet and Cohen 1975; Parsons 1975; Howe 1976; Ryden and Bengtsson 1980) which results in the sequential elimination of young (last-hatched to first-hatched). However if conditions are favorable, then the entire brood will be raised. By placing the youngest chicks at a competitive disadvantage, asynchronous hatching ensures an orderly and rapid demise when food is inadequate.

Brood reduction can be divided into two basic groups; obligate and facultative. Obligate brood reduction has been found to occur in some species of boobies (Sulidae) (Dorward 1962; Anderson 1990), eagles (Accipitridae) (Brown et al. 1977; Simmons 1988), penguins (Spheniscidae) (Williams 1980; Lamey 1990), and pelicans (Pelecanidae) (Cash and Evans

1986). Facultative brood reduction is much more common, occurring in many avian taxa (Clark and Wilson 1981; Magrath 1990). Obligate brood reducing species typically lay two eggs and if the first chick is healthy, then the second chick will be eliminated (>90% of the time, Simmons 1988), usually as a result of sibling aggression (Mock 1984; Mock et al. 1990).

Since obligate brood reduction does not seem dependent on environmental conditions as Lack (1947, 1954) had suggested, an adjunct to the brood reduction hypothesis, termed the insurance-egg hypothesis, has been proposed (Dorward 1962). The insurance-egg hypothesis states that birds utilizing this strategy lay an 'extra' egg to insure against the hatching failure or early death of an elder sibling (Cash and Evans 1986; Forbes 1990). The parents are hypothesized to benefit from these insurance offspring because of their replacement (insurance) value for older offspring which do not survive. Several studies of obligate brood reducing species are consistent with the insurance-egg hypothesis (reviewed in Anderson 1990), and it has been verified experimentally in the American white pelican (*Pelecanus erythrorhynchos*) (Cash and Evans 1986).

More recently it has been suggested (Nisbet and Cohen 1975; Graves et al. 1984; Mock and Parker 1986; Forbes 1990) that the insurance-egg hypothesis is also applicable to facultative brood reducing species in which the last-hatched chick may act either as a unit of extra-reproductive output during favorable conditions, or serve a potential insurance function during less favorable conditions when an older nestmate has either failed to hatch or suffered an early death. Hence, in facultative brood reducing species, unpredictable hatching success and an unpredictable food supply may both be operating to determine whether brood reduction occurs (Magrath 1990).

The double-crested cormorant (*Phalacrocorax auritus*) is considered a facultative brood reducing species (Drummond 1987) that lays a clutch of 3-4 eggs, rarely 5, (Bent 1922; Lewis 1929; Pilon et al 1983). Eggs hatch

over a period of 2-4 days (Lewis 1929). This species also possesses those characteristics thought to be required for a facultative brood reducing species to produce an insurance-egg (Forbes 1990): a) a relatively large clutch size, which increases the likelihood that at least one offspring will fail, b) a high offspring failure rate (Drent et al. 1964; Post and Seals 1991), and c) a mechanism, asynchronous hatching, to facilitate removal of surplus offspring. This last point is critical for efficient brood reduction since the elimination of surplus offspring not required for insurance is a fundamental part of an adaptive insurance-egg parental strategy (Forbes 1990).

Although brood reduction in double-crested cormorants is legitimately considered to be facultative in that it sometimes occurs and sometimes does not (Drummond 1987), preliminary observations of chick survival in this species, at two colonies in Manitoba, Canada (Evans pers. comm.; pers. obs.) indicated that brood reduction may be brood-size dependent. We noted that the youngest sibling in 4-egg clutches rarely if ever survived at nests where all 3 older siblings were alive and growing. These observations are consistent with the hypothesis that double-crested cormorants are an obligate brood reducing species when 4 eggs are laid. Three-egg clutches appeared to exhibit the typical pattern of a facultative species. Experimental tests of the insurance-egg hypothesis for either situation are lacking.

In this study I tested the insurance-egg hypothesis experimentally for both the facultative (3-egg clutches) and obligate (4-egg clutches) brood reduction situations for double-crested cormorants, by comparing levels of productivity between control and manipulated experimental nests. In addition, I calculated insurance and extra-reproductive values of last-hatched offspring following Mock and Parker's (1986) method as well as with a correction factor (see Chapter 1 methods). I also examined the proximate causes of brood reduction in an attempt to determine how the last-hatched chick was eliminated.

Methods

Study Site

The study was conducted in the spring of 1991 and 1992 at Kaweenakumik Lake (formerly Kawinaw Lake), which is situated approximately 450 km north of Winnipeg, Manitoba Canada, between Lake Winnipeg and Lake Winnipegosis, at 52° 50'N latitude and 99° 29'W longitude (Vermeer 1969; for map see O'Malley and Evans 1980). The four islands on which bird colonies reside are part of the Manitoba Ecological Reserves Program. However only two of the islands supported double-crested cormorants between 1990-1992, with a minimum of 350 nests estimated to be on the two islands combined (pers.obs.). This is a dramatic increase from Vermeer's report of observing only four nests on one of the islands in 1969. The cormorant colonies reside on relatively flat islands with one or two rocky uprisings favored by the cormorants. The study islands can be reached once the ice has left the lake, before the cormorants begin to lay. My first visits to the colonies occurred on 18 May and 8 June in 1991 and 1992 respectively.

Field Methodology

In 1991 the double-crested cormorant colonies were not visited on a regular basis until after laying had been completed. At this time, the completed three and four egg nests were marked with numbered stakes (N=36 three egg nests, N=84 four egg nests). Nests with odd-numbers were arbitrarily selected as experimentals, even-numbered nests as controls. Since the purpose of the experiment was to determine if an insurance-egg increased parental productivity, a randomly selected egg was removed from the experimental nests and fostered to unused nests within the colony. This was based on the assumption of an equal probability of hatch failure for each egg within a clutch. This has been found to be true in herring gulls (Larus argentatus) (Parsons 1970; see Chapter 1 results), European

starlings (*Sturnus vulgaris*) (Stouffer and Power 1990), and green-rumped parrotlets (*Forpus passerinus*) (Beissinger and Waltman 1991). Daily nest checks began one week later, near the estimated time of hatch, based on the incubation of double-crested cormorant eggs as approximately 27-28 days (van Tets 1959; Drent et al 1964; Brechtel 1983). Newly hatched chicks were first marked with a piece of non-damaging colored carpet tape around the leg to identify their position in the hatch sequence. Later in their first week, the tape was replaced with numbered domestic chick wing tags. To reduce disturbance to the colony (Kury and Gochfield 1975), chicks were weighed upon hatch and then only every second day thereafter ($\pm 0.05g$, Ohaus electronic balance up to 300g, then $\pm 10.0g$ up to 1500g using Pesola Scales). The measurements were not continued past day 12, which encompasses the period of greatest mortality in this species (Robertson 1971; Desgranges 1982; Leger and McNeil 1987). Also after 12 days, handling increased the likelihood of chicks fleeing the nest (pers. obs.), which could be detrimental to their survival. Upon each visit to the colony, the number, position, and weight of any dead chicks was also recorded. Each visit to the colony lasted no more than one hour.

Partitioning Reproductive Values

Each surviving offspring adds a particular amount of reproductive value (RV) to its parents overall fitness. When dealing with the last-hatched chick, RV can be partitioned into either extra-reproductive value (R_{Ve}) or insurance-reproductive value (R_{Vi}), based on its own survival and the survival of its siblings. To calculate the R_{Ve} and the R_{Vi} of a last-hatched offspring in unmanipulated control broods, Mock and Parker (1986) devised the formulas

$$R_{Ve} = q(P_e) \quad (1)$$

$$R_{Vi} = (1-q)P_i \quad (2)$$

where q is the proportion of broods in which the youngest was not predeceased by an elder sibling, P_e is the fraction of q in which the

youngest survives, and P_i is the fraction of youngest offspring that survives in the other $(1-q)$ broods.

An extension of the above values can also be calculated (see Chapter 1) to allow for the possibility that some last-hatched eggs in broods where an older offspring failed, would have survived even if their nestmates had survived. Mock and Parker's (1986) formulations thus include in R_{Vi} , a proportion, estimated as P_e , of youngest offspring that would have survived even if their older siblings had too. This part of their R_{Vi} value can therefore be considered to contribute to R_{Ve} instead of R_{Vi} . The true insurance value would then be R_{Vi} (derived from Mock and Parker's 1986 formula) minus the proportion, R_{Vc} , that would have survived as R_{Ve} in the absence of prior loss of an older sibling, where

$$R_{Vc} = P_e(1-q) \quad (3)$$

The corrected values are then (see Chapter 1),

$$R_{Ve}^* = R_{Ve} + R_{Vc} \quad (4)$$

$$= P_e$$

$$R_{Vi}^* = R_{Vi} - R_{Vc} \quad (5)$$

$$= (1-q) (P_i - P_e)$$

Using either Mock and Parker's equation or the corrected version, R_{Vi} can also be partitioned into insurance-egg values (R_{Vie}), or insurance-chick values (R_{Vic}), depending on which stage of life the last-offspring's older sibling(s) fail. R_{Vie} is represented by those nests in which the last-laid egg serves as a unit of replacement for an earlier laid egg within the clutch that fails to hatch, while R_{Vic} is represented by those nests in which replacement occurs when an older sibling dies following hatching. These two values can be calculated as

$$R_{Vie} = e (R_{Vi}) \quad (6)$$

$$R_{Vic} = c (R_{Vi}) \quad (7)$$

where e and c represent the proportion of failed elder siblings that did not hatch (e) or died as chicks (c), respectively ($e+c=1$). For corrected values, R_{Vi}^* replaces R_{Vi} in (6) and (7).

To test the insurance-egg hypothesis experimentally, a brood (control or experimental) was designated as either belonging to, (1) a potential RVe group, if all elder siblings were alive by 12 days of age, or (2) a potential RVi group, if at least one elder sibling had failed by 12 days of age. Brood sizes at 12 days of age were then compared for the experimental and control broods for the potential RVe groups and also for the potential RVi groups. This method allowed me to determine whether the last-hatched chick significantly increased the parent's reproductive fitness through either increased RVe, RVi, or both.

The experimental test of the insurance-egg hypothesis was also conducted using the correction factor (see above). The data were partitioned as above, then a proportion of potential RVi control nests in which the last-hatched chick survived, corresponding to the proportion represented by the correction term R_{Vc}, were removed. This was done by multiplying P_e , an estimate of the probability that the last-hatched chick would have survived regardless of its elder siblings' fates, by the number of nests in the (1-q) sample and removing this number of nests from the RVi sample in which the youngest chick survived. Since either one or more than one of the elder siblings could have died at these nests, nests were removed in proportion to the number of nests experiencing each level of sibling failure. The result was a new frequency distribution, of RVi* nests, in which all of the Nth (last-laid) eggs could be assumed to represent true insurance (replacement) value (see Chapter 1).

Mechanism of Brood Reduction

In 1992, a separate double-crested cormorant colony was used to determine the proximate mechanisms involved in the brood reduction of the last-hatched chick. A 4' x 4' wooden blind on a 4' x 4' x 4' high platform was placed approximately 4 meters from the colony periphery. Access to the blind was gained through an approximately 28 meter long tunnel built similar to that described by Cairns et al. (1987). The blind and tunnel

were erected near the time of hatch, when nest tenacity is high, to avoid nest desertion by the parents.

Nests nearest the blind (N=30) were recorded on a hand-drawn map of the colony, and nest contents identified daily. Exact ages of most chicks were not known, but it was assumed that the smallest chick in the nest was the youngest. This has been observed to be true for shags (Phalacrocorax aristotelis) (Snow 1960; Stokland and Amundsen 1988), crowned cormorants (P. coronatus) (Williams and Cooper 1983), and double-crested cormorants (Leger and McNeil 1987; this study). At no time after erection of the blind did I enter the colony. Observations were performed daily from June 23 to June 30, using the focal subgroup sampling technique as described by Altmann (1974). Nest observation times ranged from 8:00 am to 9:30 pm. Snow (1963) found in her study on shags that very few feedings occurred before 8:00 am. A total observation time of 375 nest hours was completed by observing approximately 15 nests simultaneously over one hour time intervals.

During each observation period I recorded the time at which feeds occurred, which chick was fed (based on size), whether the fed chick was actively begging (described by van Tets 1959), its relative proximity to the parent (bill to bill), if it was a successful feed, and any aggression amongst the chicks. A feed was classified as successful if any of the following characteristics were observed; a distended throat as food passed down the oesophagus of the chick, swallowing motions, or the cessation of high intensity begging (Robertson 1971).

Statistical Analysis

Productivity and reproductive values, as defined above, at 3-egg and 4-egg clutches were analyzed separately. Productivity at control and experimental nests was compared at the time of hatch and at 12-days of age using the non-parametric one-tailed Kruskal-Wallis test (direction of the effect was predicted by hypothesis; data was neither normally distributed

nor continuous) (Zar 1974). Comparisons of brood size between experimental and control nests, were conducted using one-tailed Kruskal-Wallis tests, for the same reasons noted above. Egg hatchability of experimental and control groups was compared using Chi-square tests. To determine if hatch asynchrony affected mortality, two-tailed Fisher tests were used. Chick mortality was compared between experimental and control broods using contingency table Chi-square tests. Intra-brood comparisons of frequency data were by Chi-square tests. Weight comparisons at the time of hatch were made using repeated measures ANOVAs, and if needed, multiple comparisons of means were performed using Tukey's technique. Chi-square tests were used for observational data comparisons, such as presence of begging, proximity of feeding chick to the parent, and number of successful feeding attempts. All calculations were performed with Statistix (version 3.5, Analytical Software, St. Paul, Minnesota). Probability values ≤ 0.05 were considered significant for all tests.

Results

Insurance and Extra-reproductive Values

Calculations of the proportion of reproductive value attributable to insurance (R_{Vi}) and extra-reproductive values (R_{Ve}) for the C eggs in control 3-egg clutches and the D eggs in control 4-egg clutches are listed in Table 1. In 3-egg clutches R_{Ve} and R_{Vi} were equal (0.23). With the incorporation of the correction factor, R_{Ve}* increased by approximately 65% to 0.38, while R_{Vi}* decreased to only 0.08, representing only 17% of the total reproductive value (Table 1).

In 4-egg control clutches, the D-chick survived only if an elder sibling predeceased it. Hence, the reproductive value of the D-chick was composed entirely of R_{Vi}, with R_{Vi}=R_{Vi}* (Table 1). R_{Ve} and R_{Ve}* were both equal to 0.00.

As shown in the last 4 lines of Table 1, R_{Vi} was due mainly to the replacement value of earlier laid eggs which did not hatch (R_{Vi}^e), rather

Table 1. Insurance (R_{Vi}) and extra-reproductive (R_{Ve}) values for last-hatched chicks at control nests (number of nests in parentheses)

	3-Egg Clutches	4-Egg Clutches
Extra Reproductive Value		
Elder sibs survive	8 (13)	19 (36)
q	0.62	0.53
Nth ¹ chick survives	3	0
P _e	0.38	0.00
R _{Ve} ²	0.23	0.00
R _{Ve} *	0.38	0.00
Insurance Value		
Elder sib(s) fail	5 (13)	17 (36)
(1-q)	0.38	0.47
Nth chick survives	3	11
P _i	0.60	0.65
R _{Vi} ²	0.23	0.31
R _{Vi} *	0.08	0.31
Egg and Chick Components of Insurance Value		
R _{Vi_e}	0.18	0.22
R _{Vi_c}	0.05	0.09
R _{Vi_e} *	0.06	0.22
R _{Vi_c} *	0.02	0.09

¹ Represents last-hatched chick.

² Calculations based on Mock and Parker (1986) (see methods).

* Incorporates correction term, $R_{Vc} = P_e(1-q)$. $R_{Vc} = 0.15$ for 3-egg clutches, $R_{Vc} = 0.00$ for 4-egg clutches.

than to older siblings which hatched but did not survive (RVic). RVie represented 78% of the total RVi in the 3-egg clutches and 71% of the total RVi in the 4-egg clutches. These proportions were only marginally affected by the use of the correction factor.

All of the above conclusions of reproductive values were based on the number of last-hatched chicks surviving to 12 days of age. The relative values of RVi and RVe could be affected, however, if the last-hatched chick weights differed significantly (for a particular clutch size), thereby raising the possibility that these chicks had different probabilities of survival after 12 days of age (Robertson 1971). At 12 days of age, the mean weight of surviving RVe C-chicks from control 3-egg clutches was 358.2 ± 91.8 (mean \pm SE), and the mean weight of surviving RVi C-chicks was 485 ± 13.23 . Although these means suggest surviving RVe chicks may have been at a disadvantage, they represent a very small sample, only three chicks survived in each group.

In the 4-egg control clutches, no RVe D-chicks survived to 12 days of age. Of the RVe D-chicks that died ($n=13$), 11 (84.6%) showed both a decrease in weight and an emaciated body condition prior to their deaths, suggesting that they died as a result of starvation. When the last recorded weight of the D-chicks was compared to the weight of its siblings at that same age, the elder siblings were found to weigh significantly more ($T=7.28$, $df=50$, $P<0.0001$). The median age of death for the last-hatched chicks was 9 days.

Experimental Test of Insurance and Extra-Reproductive Values

Significantly more chicks hatched per brood from 3-egg and 4-egg controls than from the reduced experimental broods (Table 2). At 12 days of age the 4-egg control clutches were still significantly larger than the experimentals, but the 3-egg controls clutches were not. The fourth egg in the control 4-egg clutches significantly increased nest productivity, while the third egg in control 3-egg clutches seemingly did not, although

Table 2. Experimental test for insurance and extra-reproductive value of last-hatched double-crested cormorant offspring. Mean \pm SE chicks reared to 12 days of age (n nests in parentheses)

Nest Type	Clutch Size	Experimental	Control	Statistic ¹	P
Initial Brood Size	3	1.44 \pm 0.20 (18)	2.01 \pm 0.26 (18)	4.93	0.013
	4	2.33 \pm 0.14 (40)	3.12 \pm 0.17 (41)	18.49	0.000
12 Days of Age	3	0.61 \pm 0.22 (18)	1.22 \pm 0.29 (18)	2.59	0.054
	4	1.53 \pm 0.16 (40)	2.22 \pm 0.17 (41)	9.59	0.001
Partitioned RV					
Potential R _{Ve}	3	2.00 \pm 0.00 (5)	2.50 \pm 0.22 (6)	3.13	0.039
Potential R _{Vi}	3	0.08 \pm 0.08 (13)	0.58 \pm 0.26 (12)	2.81	0.047

¹ One-tailed Kruskal-Wallis test, df=1.

it approached significance ($P=0.054$, Table 2).

Since the fourth egg in the control 4-egg clutches only survived if one or more of its elder siblings died, the increased productivity observed at the control nests could only have been due to RVi (see above). Thus cormorants with 4-egg clutches were, in effect, obligate brood reducers, and there was no need to partition the data, for further analysis, into potential RVi and potential RVe groups (see Statistical Analysis). This partitioning was done for 3-egg clutches, where both RVe and RVi were present (see above). Control broods were significantly larger at 12 days for both potential RVe nests and potential RVi nests (Table 2, last 2 lines).

To take account of apparent insurance offspring that might have survived even if their elder siblings had survived too, the potential RVe and RVi data from 3-egg clutches were reanalyzed after incorporating the correction factor. For 3-egg clutches, $RVC = 0.15$ (Table 1). Only three of the 3-egg control potential RVi nests had the last-hatched (C) chick survive to 12 days. Of these, an estimated $Pe(1-q)$, or two, could have survived even if older siblings had not failed. Accordingly, two nests were removed to form the potential RVi* control group. When compared to the experimental potential RVi group, there was no longer a significant difference in nest productivity ($H=0.7221$, $df=1$, $P=0.1978$).

RVe and RVi were both unaffected by differences in hatchability (Table 3). There were no significant differences between experimental and control eggs (3-egg control clutches: $X^2=0.31$, $df=1$, $P=0.5770$, 4-egg control clutches: $X^2=0.01$, $df=1$, $P=0.9124$). There were also no significant differences in total nest failure (ie. nest fledged no young) between the experimental and control groups (failed 3-egg clutch, controls= 8 (44.4%) nests, experimentals= 12 (66.7%) nests, $X^2=1.8$, $df=1$, $P=0.1797$: 4-egg clutch, controls= 5 (12.1%) nests, experimentals= 10 (25.0%) nests, $X^2=2.2$, $df=1$, $P=0.1380$). There was however a significantly greater probability of the 4-egg control nests fledging at least one young, (36 nests, 87.8%)

Table 3. Numbers and fate (%) of double-crested cormorant eggs (A,B,C,D) at experimental and control nests

Egg Type	N eggs	Hatched	Died ¹	Missing	Addled
3-Egg Nests					
Exp AB ²	36	26 (72.2)	0 (0.0)	9 (25.0)	1 (2.8)
Cont ABC	54	36 (66.7)	1 (1.9)	14 (25.9)	3 (5.5)
4-Egg Nests					
Exp ABC	120	93 (77.5)	2 (1.7)	15 (12.5)	10 (8.3)
Cont ABCD	164	128 (78.1)	2 (1.2)	21 (12.8)	13 (7.9)

¹ Contained dead embryo when opened 7-12 days after date of expected hatch.

² Eggs were not distinguished by laying order for experimental or control nests.

Exp = experimentally reduced by removal of one random egg.

Cont = unmanipulated control clutches.

than the 3-egg control nests (10 nests, 55.6%), ($X^2=7.57$, $df=1$, $P=0.0059$). Eggs missing and presumed predated, accounted for most egg failures (Table 3). 4-egg clutches also had a relatively high frequency (8.1%) of addled eggs, but this was not significantly different from the 3-egg clutches ($X^2=1.2$, $df=1$, $P=0.2732$).

RVe and RVi were also unaffected by differences between experimental and control A and B (3-egg control clutches), or A, B, and C (4-egg control clutches) chick survival (Table 4) (position determined by hatch order). There were no significant differences in survivorship among the experimental or control A or B chicks for 3-egg clutches (4×2 $X^2=3.512$, $df=3$, $P=0.3192$), or among experimental or control A, B, or C-chicks in 4-egg clutches (6×2 $X^2=10.79$, $df=5$, $P=0.0556$).

According to brood reduction theory, offspring losses should mainly affect the youngest chick. In agreement with this prediction, reproductive values were affected by differences in survival of C (in 3-egg control nests) or D-chicks (in 4-egg control nests), compared to their older siblings. At the 3-egg control nests, the survival of the control C-chicks (37.5%) was significantly less ($X^2=3.2$, $df=1$, $P=0.0368$ one-tailed) than the combined survival of the control AB-chicks (75%). Similarly, the survival of the last-hatched D-chicks (21.1%) from 4-egg control nests was also significantly less ($X^2=24.34$, $df=1$, $P<0.0001$) than the survival of the combined ABC-control chicks (82.5%). The D-chick only survived in nests where it was predeceased by one or more of its elder siblings.

There was a significant difference in day 0 weights among chicks in broods of three ($F_{2,14} = 7.47$, $P=0.0062$). The C-chick (34.3 ± 1.01) weighed significantly less ($P<0.05$) than the B chick (37.9 ± 0.85), but neither A (35.5 ± 1.21) and B, nor A and C differed significantly. In the 4-chick broods a significant difference in day 0 weights was also found ($F_{3,54} = 11.16$, $P<0.0001$). The D-chick (31.8 ± 0.66) weighed significantly less ($P<0.05$) than the A (34.5 ± 0.85) and the B (35.6 ± 0.65) chicks. The C-chick (33.5 ± 0.66) was not significantly different from either the D-chick or the

Table 4. Numbers and fate (%) of double-crested cormorant chicks

Chick Type	N	Survived ¹	Died ²
3-Egg Clutch			
Exp A	12	6 (50.0)	6 (50.0)
Exp B	12	5 (41.7)	7 (58.3)
Cont A	8	6 (75.0)	2 (25.0)
Cont B	8	6 (75.0)	2 (25.0)
	Statistic ³	$\chi^2=3.512$	P=0.32
4-Egg Clutch			
Exp A	21	14 (66.7)	7 (33.3)
Exp B	21	18 (85.7)	3 (14.3)
Exp C	21	11 (52.4)	10 (47.6)
Cont A	19	14 (73.7)	5 (26.3)
Cont B	19	16 (84.2)	3 (15.8)
Cont C	19	17 (89.5)	2 (10.5)
	Statistic ³	$\chi^2=10.79$	P=0.06

¹ Survivorship and fate are measured up to 12 days of age.

² Died includes chicks missing from the nest.

³ rxc Chi-square tests.

Exp = experimentally reduced nests.

Cont = unmanipulated control nests.

A-chick, but it did weigh significantly less than the B-chick. A and B-chicks did not differ.

Proximate Mechanisms of Brood Reduction

Only chicks that begged (542 of 542 cases at N=20 nests) obtained food. Under the assumption that the smallest chick in the brood was the youngest, it was found that the youngest chick in broods of three and four received most of its feedings (85.7%) when it was the only chick begging ($X^2=71.42$, $df=1$, $P<0.0001$). The youngest was significantly less successful in obtaining food during a feeding attempt (3-chick brood: 21.3%, 2 X 2 contingency table $X^2=20.27$, $df=1$, $P<0.0001$, 4-chick brood: 27.7%, 2 X 2 contingency table $X^2=22.88$, $df=1$, $P<0.0001$) than the older siblings (59.2% and 69.7%, respectively). Failure to successfully complete an attempted feed was sometimes the result of the parent regurgitating such a large bolus of food that the chick could not swallow it. With very young chicks (less than one week old), which could only lift their heads slightly off the ground, the parent was often not able to successfully guide the young chick's bill into its mouth. In broods of two (not necessarily from a natural clutch, more probably a result of early predation or brood reduction), there was no significant difference ($X^2=0.0392$, $df=1$, $P=0.8431$) in the number of successful feeds between the largest and the smallest chick.

In 491 of 499 (98%) observations, the chick which was closest to the parent (bill to bill) prior to the feeding attempt received the bolus of food. This was found to be significant for all clutch sizes (2-chick brood: $X^2=173.34$, $df=1$, $P<0.0001$, 3-chick brood: $X^2=176.19$, $df=1$, $P<0.0001$, 4-chick brood: $X^2=128.03$, $df=1$, $P<0.0001$). Because the median A-C chick hatch asynchrony for 3-egg clutches at Kaweenakumik Lake was 3 days, and the median A-D chick hatch asynchrony in 4-egg clutches was 5 days, a size hierarchy was created. This size disparity allowed the older chicks to move and position themselves nearer to the parent, whereas the last-

hatched chick could not move as easily and was often trapped underneath its siblings. This was usually the case in broods of four in which the youngest chick could often not be seen during a feeding bout.

Pecking of the youngest chick was never observed, nor were any other aggressive behaviors directed towards the smallest chick. At the end of my observations, 75% of the last-hatched chicks in broods of 4 had died, probably as a result of starvation. The other 25% were noticeably emaciated (very small, slow moving, baggy skin), which was usually a precursor to death.

Discussion

At the time of hatch, it was found that the controls had significantly greater nest productivity, in both 3-egg and 4-egg clutches, than the experimentals. This would be expected given that one egg was removed from the experimental nests, and that hatchability did not differ among eggs in the laying sequence. At 12 days of age, greater nest productivity still remained at the 4-egg control than at the experimental clutches. This increased productivity of control nests was due entirely to the insurance value of the D-chick, as shown in the calculation of RVi (Table 1). The last-hatched chick only survived if one or more of its elder siblings failed. These results support the interpretation that 4-egg clutches represent an obligate brood reducing strategy in double-crested cormorants, with the last-laid egg functioning as an insurance offspring.

Brood reduction in 4-egg clutches is by no means a universal finding for this species. Hobson et al. (1989) have described a colony in which the average number of fledged chicks/nest was 4, suggesting that the degree of brood reduction varies from place to place and presumably year to year. This makes intuitive sense since the double-crested cormorant is a known facultative brood reducer (Drummond 1987), where brood size is determined by the availability of specific resources (Nisbet and Cohen

1975). In 1991, and possibly in 1990 and 1992 (pers. obs.), in the region of Kaweenakumik Lake, food provisioning may have been inadequate to successfully raise broods of four. This could have arisen from an actual shortage in fish stocks, or from the inability of the parents to locate or capture food. Both are quite probable for this particular colony since the cormorants leave the shallow waters of Kaweenakumik Lake where fish are scarce (Vermeer 1969), to forage further away, (eg. Cedar Lake or Lake Winnipeg). The brood reduction exhibited here thus differs from the true obligate brood reducing strategy in that the elimination of surplus chicks appears to be dependant on environmental conditions. True obligate brood reduction is not a response to poor food conditions, but rather is a direct result of the successful hatch of both siblings under conditions where parents appear chronically unable to feed both (all) young (Dorward 1962; Cash and Evans 1986).

The final nest productivity at 3-egg nests did not differ significantly between control and experimental nests. Because there was a significant difference between the two groups at the time of hatch, the 3-egg control nests must have experienced a greater chick mortality than did the reduced experimental nests, prior to 12 days of age. However, the result was very close to being statistically significant ($P=0.054$), and may have been due to a small sample size or high variance.

To test for the effects of sample size on productivity, I performed a bootstrap resampling of the data using the shift method as described by Noreen (1989). Ten thousand artificial samples were drawn (with replacement) from the original sample in each of 10 separate runs. By this method, control 3-egg clutches showed a significantly greater final nest productivity than the experimental clutches (mean $P=0.041$, range of P values 0.032-0.047). When the total RV was partitioned, it was found that the control 3-egg nests had greater nest productivity than the experimentals, both as R_{Ve} and R_{Vi} . Using the bootstrap resampling technique with the data partitioned into potential R_{Ve} and potential R_{Vi}

groups (Table 2), the statistical significance was maintained for both RVE (mean $P=0.008$, range of P values $0.016-<0.001$) and RVi (mean $P=0.024$, range of P values $0.022-0.026$). However, when RVi was corrected downwards to account for cases where C-chicks might have survived even if their older siblings had not failed, the insurance value (RVi*) was no longer significant (mean $P=0.143$, range of P values $0.135-0.149$). This was also the case when the corrected RVi data was analysed for nest productivity using the Kruskal-Wallis test (see above).

As predicted by the brood reduction hypothesis (Lack 1947, Ricklefs 1965), the last-hatched offspring in both 3-chick and 4-chick clutches survived significantly less often than their elder siblings. This result would be expected if food conditions were poor, since the brood would be reduced (from smallest to largest) to a size which could be optimally supported. In addition, although sample size was small, the mean weight in 3-egg clutches was lower than for the C-chicks in broods where an elder sibling died. Thus a larger brood size seemed to increase the food demands on the parents, and the last-hatched chicks weighed less. This occurred although the food requirements of the chicks at this time are not very high (Dunn 1975).

Day 0 weights of the last-hatched chicks were significantly less than the hatch weights of the first chick in 3-egg clutches, and the first two (A and B) chicks in 4-egg clutches. Hatch weight has been correlated to egg size for a number of species (Howe 1978; Shaw 1985; Hebert and Barclay 1988), but Bretchel (1983) found that egg size did not differ based on position in the laying sequence for double-crested cormorants. It may be that the different day 0 weights were due to different amounts of feeding prior to my daily visits to the colony, rather than different egg sizes. Williams and Cooper (1983) found that feeding of crowned cormorant chicks occurred within 24 hours of hatching and as a result, day 0 weights differed within the hatch sequence.

The lower weight of the last-hatched chick, in conjunction with the

relatively large hatching asynchrony, should facilitate elimination of that chick when food conditions are poor. This is presumably of benefit to the parents since the sooner a chick dies, the less amount of parental investment is 'wasted' (Forbes 1990). In addition, an early, rather than a late death, is of benefit to the surviving elder siblings, if the last-hatched chick increases the likelihood of predation, or reduced food availability (O'Connor 1978; Forbes 1990).

Observations of Brood Reduction

It was found in both clutches of 3 and 4 that the last-hatched chick had significantly less feeding success than its older siblings and it was usually fed last. This was probably a result of hatching asynchrony which gave the A chick a 3-5 day headstart on the development of begging behavior over the last-hatched chick.

The feeding of very young cormorant chicks is initiated by the chick peeping and waving its head in an uncoordinated manner (Dunn 1975; pers. obs). The parent responds by attempting to place its open mouth over the entire head of the chick (see van Tets 1959). Older chicks on the other hand, stand with bills outstretched towards the parent's bill, uttering a hoarse begging call. Often they flap their wings and hit the parent's gular pouch with their bills (Dunn 1975; pers. obs.). Because the older chicks begin to develop this more aggressive feeding behavior by the time the last-hatched chick first emerges, and since the parent appears to selectively feed the most prominently begging chick, the elder siblings can outcompete the younger one(s).

The fact that selective feeding of particular nestlings does not seem to occur in double-crested cormorants is not unusual. Many species feed those nestlings which gape the highest and are positioned closest to the parent (Lockie 1955; Ricklefs 1965; Bengtsson and Ryden 1981; for an exception see Stamps et al. 1985). Thus for most species feeding appears to be simply a direct result of a scramble competition amongst the chicks,

with the largest chicks receiving food first. When food is in short supply, the youngest chick receives proportionately less food, and is quickly eliminated.

Although Lewis (1929) reported instances of sibling aggression in the double-crested cormorant, none was observed in this study, nor in the study by Hanbidge (1989). Mock et al. (1990) noted that five characteristics were common to all siblicidal birds; 1) competition between siblings for food, 2) the provisioning of food to the chicks in small units, 3) adequate weaponry (eg. strong bill) for the chicks to intimidate or damage one another, 4) spatial confinement of the chicks (in the nest), and 5) competitive disparities between siblings. Although all of these characteristics appear to be present in double-crested cormorants (this study, see also van Tets 1959), siblicide has been rarely reported. It may be that under most circumstances the length of hatching asynchrony is large enough to permit elimination of last-hatched chicks by begging competition, so that elder siblings are not selected to expend significant energetic costs of siblicidal aggression (Gargett 1978; Mock 1984).

General Discussion

Experimental evidence has shown that the insurance-egg hypothesis is applicable to obligate brood reducing species (Cash and Evans 1986). However, although Mock and Parker (1986) and Forbes (1990) have proposed that this hypothesis may also operate in facultative brood reducing species, it had never been formally tested until now.

For this study, insurance and extra-reproductive values of last-laid eggs were calculated based on Mock and Parker's (1986) equations, and a nest productivity experiment was designed to compare the final brood sizes of nests possessing the last-laid egg with those in which the last-laid egg had been removed. In addition, because Mock and Parker did not differentiate between last-hatched chicks which survived as insurance and those chicks that would have survived regardless of their elder siblings' fates, a correction factor (RVC) was developed based on Mock and Parker's (1986) original equations and included in the analysis. This conservative correction factor made the analysis of whether a last-laid egg served an insurance function more applicable to the facultative brood reducing species.

Herring gulls are a conventional facultative brood reducing species which usually lays three eggs (Paludan 1951; Harris 1964). Using Mock and Parker's (1986) original equations it was found that the insurance value (R_{Vi}) of the last-laid egg (0.23) was lower than the extra-reproductive value (R_{Ve}) (0.26) in 1992, but not in 1991 (0.23 versus 0.15 respectively). When the experimental data were tested in 1992, it was determined that nests possessing the third egg had significantly greater nest productivity than those nests in which the last-laid egg had been removed, both as R_{Ve} ($P=0.002$) and R_{Vi} ($P=0.005$). However in 1991 greater nest productivity was only observed in nests defined as R_{Ve} nests ($P=0.02$). It was not found in the comparison between R_{Vi} nests ($P=0.266$).

Using the correction factor (RVC), it was found that R_{Vi} was lower than R_{Ve} in both 1991 and 1992, and that nest productivity in the form of

RVi was not significantly greater in nests with the third egg present ($P=0.4758$ for 1991, $P=0.0682$ for 1992). However because there was a trend towards significance in the 1992 data, a bootstrapping technique was employed to ensure that the P value was not simply the result of a small sample size. This statistical method of drawing artificial samples (with replacement) from the sample itself, resulted in a mean P value equal to 0.044. This suggested that the third egg may actually be adding to the nest productivity as RVi and therefore serving an insurance function. Further studies, possibly in which food is more critical and hence RVe lower (Graves et al. 1984), could give a stronger insurance effect if present.

Double-crested cormorants were also examined, but because they lay clutch sizes of 1 to 9 eggs (McLeod and Bondar 1953), the study was more problematical. It was decided that only clutches of 3 and 4 would be tested since they were the most common at this location. Using Mock and Parker's (1986) equation it was found that the last-laid egg in 3-egg cormorant clutches represented equal amounts of insurance and extra-reproductive value (0.23). In the 4-egg clutches, there was only an insurance reproductive value (0.31), which is characteristic of obligate brood reduction. When an experimental test of nest productivity was performed, it was found that the last-laid egg contributed significantly as both RVi ($P=0.047$) and RVe ($P=0.039$) in the 3-egg clutches, and as RVi in the 4-egg clutches.

When the correction factor was applied to the calculation of RVi and RVe values in 3-egg cormorant clutches, it was found that RVi (0.08) was approximately one-fifth the value of RVe (0.38). Within 4-egg clutches both RVi and RVe remained unchanged. The latter finding makes intuitive sense because in 4-egg clutches there were no last-hatched chicks which would have survived regardless of their siblings' fates, and therefore RVi should not be adjusted downwards. When the correction factor was used at 3-egg clutches to compare the nest productivity at potential RVi nests, it

was found that there was no longer a significant difference between the experimental and control groups ($P=0.1978$). This result was verified using the bootstrapping technique (mean $P=0.143$, range of P values 0.135-0.149).

In conclusion, when using the conservative correction factor it appears that the third egg in herring gull clutches adds mainly to the nest productivity as extra-reproductive value, although the hypothesis that it may also serve an insurance function cannot be ruled out. Double-crested cormorants that lay clutches of four eggs benefit solely from the insurance value of their last-laid egg, while cormorants which lay clutches of three eggs appear to receive no insurance benefit at all. Results of this study support the view (Mock and Parker 1986; Forbes 1990) that the insurance-egg hypothesis can be applied to facultative brood reducing species and is amenable to experimental testing, but support for the hypothesis remains equivocal. Further testing, especially of herring gulls during years when food is scarce, would be useful.

References

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behavior* 49:227-267.
- Amundsen, T. and Slagsvold, T. 1991. Hatching asynchrony: facilitating adaptive or maladaptive brood reduction? *Acta XX Congressus Internationalis Ornithologici Vol 3*, pp.1707-1719.
- Amundsen, T. and Stokland, J. N. 1988. Adaptive significance of asynchronous hatching in the shag: a test of the brood reduction hypothesis. *J. Anim. Ecol.* 57:329-344.
- Anderson, D. J. 1990. Evolution of obligate siblicide in boobies. 1. A test of the insurance-egg hypothesis. *Am. Nat.* 135:334-350.
- Beissinger, S. R. and Waltman, J. R. 1991. Extraordinary clutch size and hatching asynchrony of a neotropical parrot. *Auk* 108:863-871.
- Bengtsson, H. and Ryden, O. 1981. Development of parent-young interaction in asynchronously hatched broods of altricial birds. *Z. Tierpsychol.* 56:255-272.
- Bent, A. C. 1922. Life histories of North American petrels and pelicans and their allies. *U.S. Nat. Museum Bull.* 121.
- Bollinger, P. B., Bollinger, E. K., and Malecki, R. A. 1990. Tests of three hypotheses of hatching asynchrony in the common tern. *Auk* 107:696-706.
- Brechtel, S. H. 1983. The reproductive ecology of double-crested cormorants in southern Alberta. M. Sc. Thesis, Univ. of Alberta, Edmonton, Alberta.
- Brown, L. H. and Urban, E. K. 1969. The breeding biology of the great white pelican (*Pelecanus onocrotalus roseus*) at Lake Shala, Ethiopia. *Ibis* 111:199-237.
- Brown, L. H., Gargett, V. and Steyn, P. 1977. Breeding success in some African eagles related to theories about sibling aggression and its effects. *Ostrich* 48:65-71.
- Burger, J. 1984. Pattern, mechanism, and adaptive significance of

- territoriality in herring gulls (Larus argentatus). Ornithological Monographs No.34.
- Burke, V. E. M. and Brown, L. H. 1970. Observations on the breeding of the pink-backed pelican. *Ibis* 112:499-512.
- Cairns, D. K., Bredin, K. A. and Birt, V. L. 1987. A tunnel for hidden access to blinds at high latitude seabird colonies. *J. Field Ornithol.* 58:69-72.
- Cash, K. J. and Evans, R. M. 1986. Brood reduction in the American white pelican (Pelecanus erythrorhynchos). *Behav. Ecol. Sociobiol.* 18:413-418.
- Clark, A. B. and Wilson, D. S. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Q. Rev. Biol.* 56:253-277.
- Coulter, M. C. 1977. Growth, mortality, and the third chick disadvantage in the western gull, Larus occidentalis. Ph.D. dissertation, University of Pennsylvania, Philadelphia Pennsylvania.
- Davis, J. W. F. 1975. Age, egg-size and breeding success in the herring gull Larus argentatus. *Ibis* 117:460-473.
- Desgranges, J. -L. 1982. Weight growth of young double-crested cormorants in the St. Lawrence estuary, Quebec. *Colonial Waterbirds* 5:79-86.
- Din, N. A. and Eltringham, S. K. 1974. Breeding of the pink-backed pelican (Pelecanus rufescens) in Rwenzori National Park, Uganda. *Ibis* 116:477-493.
- Dorward, D. F. 1962. Comparative biology of the white booby and the brown booby (Sula spp.) at Ascension. *Ibis* 103:174-220.
- Drent, R. H. 1967. Functional Aspects of Incubation in the Herring Gull. E. J. Brill., Leiden, the Netherlands.
- Drent, R. H., van Tets, G. F., Tompa, F., and Vermeer, K. 1964. The breeding birds of Mandarte Island, British Columbia. *Can. Field-Nat.* 78:208-263.

- Drummond, A. 1987. A review of the parent-offspring conflict and brood reduction in the Pelecaniformes. *Colonial Waterbirds* 10:1-15.
- Drummond, H. and Chavelas, C.G. 1989. Food shortage influences sibling aggression in the blue-footed booby. *Anim. Behav.* 37:806-819.
- Dunn, E. H. 1975. Caloric intake of nestling double-crested cormorants. *Auk* 92:553-565.
- Dyrzcz, A. 1974. Factors affecting the growth rate of nestling great reed warblers and reed warblers at Milicz, Poland. *Ibis* 116:330-339.
- Edwards, T. C. and Collopy, M. W. 1983. Obligate and facultative brood reduction in eagles: an examination of factors that influence fratricide. *Auk* 100:630-635.
- Erwin, R. M. 1971. The breeding success of two sympatric gulls, the herring gull and the great black-backed gull. *Wilson Bull.* 83:152-158.
- Evans, R. M. 1980. Development of behavior in seabirds: an ecological perspective. In: Burger J, Olla B, Winn H (eds) *Behavior of Marine Animals Vol.4*. Plenum Publishing, pp271-322.
- Fisher, R. A. 1958. *The Genetical Theory of Natural Selection*. Dover Publications Inc., New York.
- Forbes, L. S. 1990. Insurance offspring and the evolution of avian clutch size. *J. Theo. Biol.* 147:345-359.
- Fujioka, M. 1985. Food delivery and sibling competition in experimentally even-aged broods of the cattle egret. *Behav. Ecol. Sociobiol.* 17:67-74.
- Gargett, V. 1978. Sibling aggression in the black eagle in the Matopos, Rhodesia. *Ostrich* 49:57-63.
- Gottlander, K. 1987. Parental feeding behavior and sibling competition in the pied flycatcher Ficedula hypoleuca. *Ornis Scand.* 18:269-276.
- Graves, J., Whiten, A. and Henzi, P. 1984. Why does the herring gull lay three eggs? *Anim. Behav.* 32:798-805.

- Greig-Smith, P. 1985. Weight differences, brood reduction, and sibling competition among nestling stonechats (Saxicola torquata) (Aves: Turdidae). J. Zool. Lond. 205:453-465.
- Hahn, D. C. 1981. Asynchronous hatching in the laughing gull: cutting losses and reducing rivalry. Anim. Behav. 29:421-427.
- Hanbidge, B. A. 1989. Diet, growth and reproductive success of double-crested cormorants (Phalacrocorax auritus) at Dore Lake, Saskatchewan. M. Sc. Thesis, Univ. of Saskatchewan, Saskatoon, Saskatchewan.
- Harris, M. P. 1964. Aspects of the breeding biology of the gulls Larus argentatus, L. fuscus and L. marinus. Ibis 106:432-456.
- Haymes, G. T. and Morris, R. D. 1977. Brood size manipulations in herring gulls. Can. J. Zool. 55:1762-1766.
- Hebert, P. N. and Barclay, R. M. R. 1986. Asynchronous and synchronous hatching: effect on early growth and survivorship of herring gull, Larus argentatus, chicks. Can. J. Zool. 64:2357-2362.
- Hebert, P. N. and Barclay, R. M. R. 1988. Parental investment in herring gulls: clutch apportionment and chick survival. Condor 90:332-338.
- Hobson, K. A., Knapton, R. W. and Lysack, W. 1989. Population, diet and reproductive success of double-crested cormorants breeding on Lake Winnipegosis, Manitoba, in 1987. Colonial Waterbirds 12:191-197.
- Howe, H. F. 1976. Egg size, hatching asynchrony, sex, and brood reduction in the common grackle. Ecology 57:1195-1207.
- Howe, H. F. 1978. Initial investment, clutch size, and brood reduction in the common grackle (Quiscalus quiscula). Ecology 59:1109-1122.
- Hussell, D. J. T. 1972. Factors affecting clutch size in Arctic passerines. Ecol. Mono. 42:317-364.
- Kadlec, J. A. and Drury, W. H. 1968. Structure of the New England herring gull population. Ecology 49:644-676.
- Kadlec, J. A., Drury, W. H., and Onion, D. K. 1969. Growth and mortality of herring gull chicks. Bird Banding 40:222-233.

- Kury, C. R. and Gochfeld, M. 1975. Human interference and gull predation in cormorant colonies. *Biol. Conserv.* 8:23-34.
- Lack, D. 1947. The significance of clutch size. I, II. *Ibis* 89:302-352.
- Lack, D. 1948. The significance of clutch size. Pt. III. *Ibis* 90:25-45.
- Lack, D. 1954. *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford.
- Lamey, T. C. 1990. Hatch asynchrony and brood reduction in penguins. *Penguin Biology* (ed. L. S. Davies and J. Darby), pp.399-416. Academic Press Inc,
- Lamey, T. C. and Mock, D. W. 1991. Nonaggressive brood reduction in birds. *Acta XX Congressus Internationalis Ornithologici Vol 3*, pp. 1741-1751.
- Leger, C. and McNeil, R. 1987. Brood size and chick position as factors influencing feeding frequency, growth, and survival of nestling double-crested cormorants, (*Phalacrocorax auritus*). *Can. Field-Nat.* 101:351-361.
- Lewis, H. F. 1929. *The Natural History of the Double-crested Cormorant*. Ru-Mi-Lou Books, Ottawa, Canada.
- Lockie, J. D. 1955. The breeding and feeding of jackdaws and rooks with notes on carrion crows and other Corvidae. *Ibis* 97:341-369.
- Magrath, R. D. 1989. Hatching asynchrony and reproductive success in the blackbird. *Nature* 339:536-538.
- Magrath, R. D. 1990. Hatching asynchrony in altricial birds. *Biol. Rev.* 65:587-622.
- Mcleod, J. A. and Bondar, G. F. 1953. A brief study of the double-crested cormorant on Lake Winnipegosis. *Can. Field-Nat.* 67:1-11.
- Mead, P. S. and Morton, M. L. 1985. Hatching asynchrony in the mountain white-crowned sparrow (*Zonotrichia leucophrys oriantha*): a selected or incidental trait. *Auk* 102:781-792.
- Meathrel, C. E., Ryder, J. P. and Termaat, B. M. 1987. Size and composition of herring gull eggs: relationship to position in the

- laying sequence and the body condition of females. Colonial Waterbirds 10:55-63.
- Meyburg, B. U. 1974. Sibling aggression and mortality among nestling eagles. Ibis 116:224-228.
- Mock, D. W. 1984. Infanticide, siblicide and avian nestling mortality. In: Hausfater G, Hrdy SB (eds) Infanticide: comparative and evolutionary perspectives. Aldine, New York, pp3-30.
- Mock, D. W. 1985. Siblicidal brood reduction: the prey size hypothesis. Am. Nat. 125:327-343.
- Mock, D. W. and Parker, G. A. 1986. Advantages and disadvantages of egret and heron brood reduction. Evolution 40:459-470.
- Mock, D. W., Drummond, H. and Stinson, C. H. 1990. Avian siblicide. Am. Sci. 78:438-449.
- Nisbet, I. C. T. and Cohen, M. E. 1975. Asynchronous hatching in common and roseate terns, (Sterna hirundo) and (S. dougallii). Ibis 117:374-379.
- Noreen, E. W. 1989. Computer-intensive Methods For Testing Hypothesis: an Introduction. John Wiley and Sons, Toronto.
- Novakowski, N. S. 1966. Whooping crane population dynamics on the nesting grounds, Wood Buffalo National Park, Northwest Territories, Canada. Can Wildl Serv Rep Ser 1 Ottawa, Ontario
- O'Connor, R. J. 1978. Brood reduction in birds: selection for fratricide, infanticide and suicide? Anim. Beh. 26:79-96.
- O'Malley, J. B. E. and Evans, R. M. 1980. Variations in measurements among white pelican eggs and their use as a hatch date predictor. Can. J. Zool. 58:603-608.
- Paludan, K. 1951. Contributions to the breeding biology of Larus argentatus and Larus fuscus. Ejnar Munksgaard, 6, Norregade, Copenhagen.
- Parsons, J. 1970. Relationship between egg size and post-hatching chick mortality in the herring gull (Larus argentatus). Nature 228:1221-

1222.

- Parsons, J. 1972. Egg size, laying date and incubation period in the herring gull. *Ibis* 114:536-541.
- Parsons, J. 1975. Asynchronous hatching and chick mortality in the herring gull (Larus argentatus). *Ibis* 117:517-520.
- Paynter, R. A. Jr. 1949. Clutch-size and the egg and chick mortality of Kent Island herring gulls. *Ecology* 30:146-166.
- Pijanowski, B. C. 1992. A revision of Lack's brood reduction hypothesis. *Am. Nat.* 139:1270-1292.
- Pilon, C., Burton, J. and McNeil, R. 1983. Reproduction du grand cormoran (Phalacrocorax carbo) et du cormoran a aigrettes (P. auritus) aux iles de la Madeleine, Quebec. *Can. J. Zool.* 61:524-530.
- Post, W. and Seals, C. A. 1991. Breeding biology of a newly established double-crested cormorant population in South Carolina, USA. *Colonial Waterbirds* 14:34-38.
- Procter, D. L. C. 1975. The problem of chick loss in the south polar skua (Catharacta maccormicki). *Ibis* 117:452-459.
- Ricklefs, R. E. 1965. Brood reduction in the curve-billed thrasher. *Condor* 67:505-510.
- Ricklefs, R. E. 1969. an analysis of nesting mortality in birds. *Smithson. Contr. Zool.* 9:1-48.
- Robertson, I. 1971. The influences of brood-size on reproductive success in two species of cormorant, (Phalacrocorax auritus and P. pelagicus) and its relation to the problem of clutchsize. M.Sc. Thesis, University of British Columbia, Vancouver, British Columbia.
- Ryden, O. and Bengtsson, H. 1980. Differential begging and locomotory behavior by early and late hatched nestlings affecting the distribution of food in asynchronously hatched broods of altricial birds. *Z. Tierpsychol.* 53:209-224.

- Ryder, J. P. and Carroll, T. R. 1978. Reproductive success of herring gulls on Granite Island, northern Lake Superior, 1975 and 1976. *Can. Field-Nat.* 92:51-54.
- Seel, D. C. 1970. Nestling survival and nestling weights in the house sparrow and tree sparrow (Passer spp.) at Oxford. *Ibis* 112:1-14.
- Shaw, P. 1985. Brood reduction in the blue-eyed shag (Phalacrocorax atriceps). *Ibis* 127:476-494.
- Simmons, R. 1988. Offspring quality and the evolution of cainism. *Ibis* 130:339-357.
- Slagsvold, T. 1982. Clutch size, nest size, and hatching asynchrony in birds: experiments with the fieldfare (Turdus pilaris). *Ecology* 63:1389-1399.
- Slagsvold, T. 1986. Asynchronous versus synchronous hatching in birds: experiments with the pied flycatcher. *J. Anim. Ecol.* 55:1115-1134.
- Slagsvold, T. and Lifjeld, J. T. 1989. Hatching asynchrony in birds: the hypothesis of sexual conflict over parental investment. *Am. Nat.* 134:239-253.
- Slagsvold, T., Sandvik, J., Rofstad, G., Lorentsen, O., and Husby, M. 1984. On the adaptive value of intraclutch egg-size variation in birds. *Auk* 101:685-697.
- Snow, B. 1960. The breeding biology of the shag (Phalacrocorax aristotelis) on the island of Lundy, Bristol Channel. *Ibis* 102:554-575.
- Snow, B. 1963. The behavior of the shag. *British Birds* 56:77-103, 164-186.
- Stamps, J., Clark, A., Arrowood, P. and Kus, B. 1985. Parent-offspring conflict in budgerigars. *Behavior* 94:1-39.
- Stokland, J. N. and Amundsen, T. 1988. Initial size hierarchy in broods of the shag: relative significance of egg size and hatching asynchrony. *Auk* 105:308-315.
- Stouffer, P. C. and Power, H. W. 1990. Density effects on asynchronous

- hatching and brood reduction in European starlings. *Auk* 107:359-366.
- Temme, D. M. and Charnov, E. 1987. Brood size adjustment in birds: economical tracking in a temporally varying environment. *J. Theo. Biol.* 126:137-148.
- van Tets, G. F. 1959. A comparative study of the reproductive behaviour and natural history of three sympatric species of cormorants, (Phalacrocorax auritus, P. penicillatus and P. pelagicus) at Mandarte Island, British Columbia. M.A. Thesis, Univ. of British Columbia, Vancouver, British Columbia.
- Vermeer, K. 1969. The present status of double-crested cormorant colonies in Manitoba. *Blue Jay* 27:217-220.
- Vermeer, K. 1970. Aquatic park proposal for Lake Winnipegosis, Kaminaw and Pelican Lakes. *Blue Jay* 28:66-67.
- Williams, A. J. 1980. Offspring reduction in macaroni and rockhopper penguins. *Auk* 97:754-759.
- Williams, A. J. and Cooper, J. 1983. The crowned cormorant: breeding biology, diet and offspring-reduction strategy. *Ostrich* 54:213-219.
- Williams, G. C. 1966. *Adaptation and Natural Selection: A Critique of Some Evolutionary Thought*. Princeton University Press, Princeton.
- Zar, J.H. 1974. *Biostatistical Analysis*. Prentice-Hall Inc., Englewood Cliffs New Jersey.

Appendix 1

Additional Herring Gull Life History Data

Because control and experimental herring gull nests were selected at random, differences that might have confounded the results would presumably have been equally distributed between the samples, thereby exerting negligible impact on the conclusions. In this appendix I examine several possible effects on egg and chick survival to determine more directly whether they could potentially have confounded the assessment of both the experimental test and the calculated levels of RVe and RVi.

Nesting dates and incubation period In 1992, herring gulls had begun to lay by 13 May and most had complete clutches by 22 May. Of 153 nests there were 134 three-egg clutches (87.6%), 18 two-egg clutches (11.7%), and 1 single-egg clutch (0.6%) which was predated shortly after being laid. There were no significant differences in A-B or B-C (prior to removal) egg laying intervals among the experimental and control nests (two-tailed Kruskal-Wallis test, A-B interval: $H=0.0898$, $df=1$, $P=0.7645$, B-C interval: $H=0.1205$, $df=1$, $P=0.7285$). When the control, experimental, and unpenned control nests were combined, the mean \pm SE laying intervals were 1.83 ± 0.16 days between the A and B egg, and 2.08 ± 0.07 days between the B and C egg.

Incubation periods recorded in 1992 (Table 5) averaged 26.8 ± 0.07 for all eggs combined. Experimental and control incubation periods analyzed separately showed no significant differences (two-tailed Kruskal-Wallis test, A egg: $H=0.0064$, $df=1$, $P=0.9361$, B egg: $H=0.0779$, $df=1$, $P=0.7802$). For all eggs combined there was a significant difference in incubation periods (two-tailed Kruskal-Wallis test, $H=14.91$, $df=2$, $P=0.0006$) due to laying order, with A eggs taking longer to hatch than both B ($R=21.8$, $P<0.05$) or C ($R=22.6$, $P<0.05$) (Table 5). B and C eggs did

Table 5. Incubation periods (days) of herring gull eggs, 1992

Egg	Descriptive Statistics			
	N	Mean \pm SE	Range	Mode
A	26	27.4 \pm 0.24 ^a	25-30	28
B	59	26.7 \pm 0.01 ^b	26-28	27
C	49	26.5 \pm 0.01 ^b	26-28	26
Total	134	26.8 \pm 0.07	25-30	26

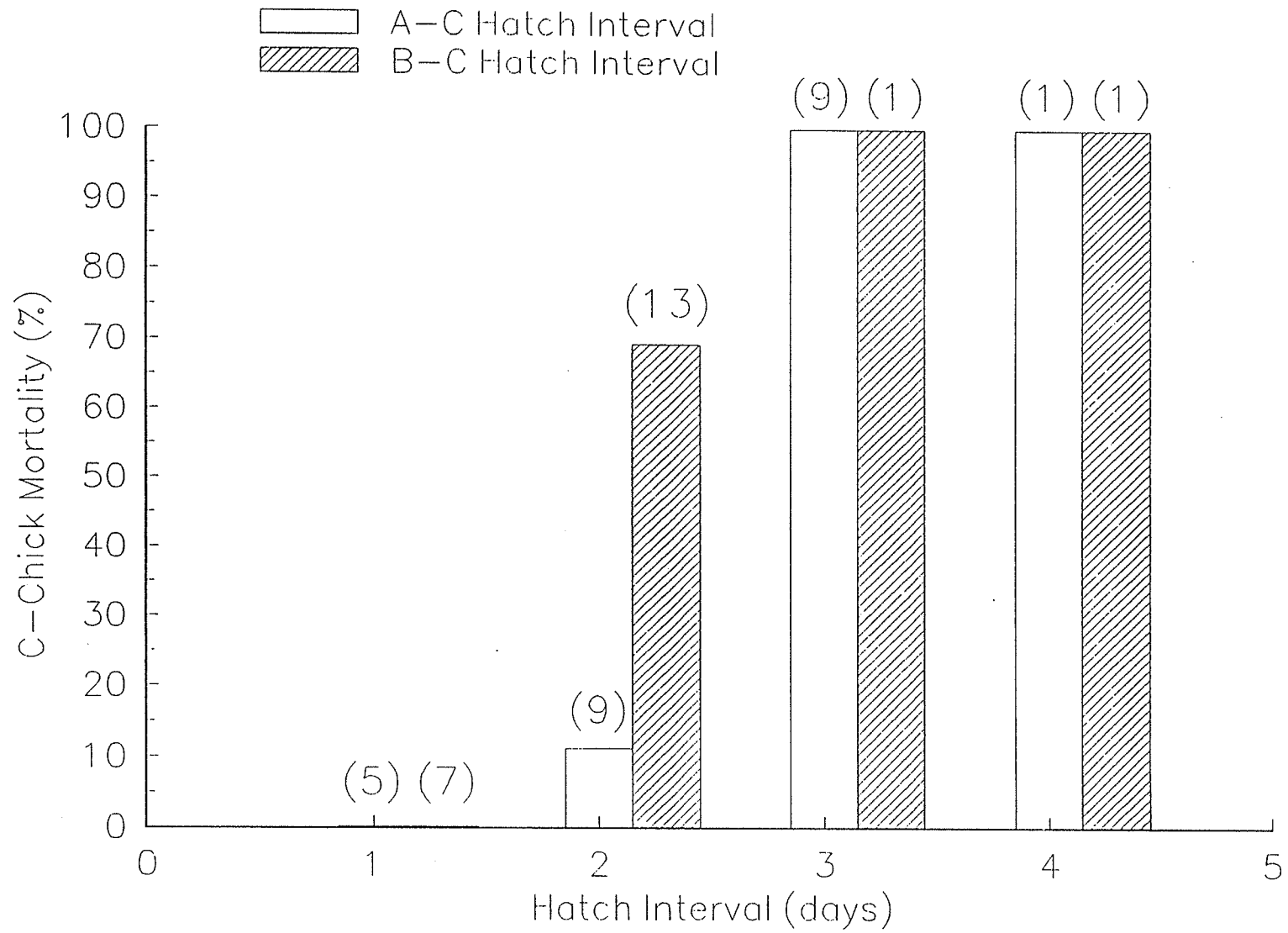
^{a,b} Values in columns having different superscripts are significantly different ($P < 0.05$) Kruskal-Wallis multiple comparison test.

not differ ($R=18.0$, $P>0.05$).

Hatching began on 6 June in both years, and was completed by 22 June in 1991, and by 19 June in 1992. The hatching peak was from June 13-17 in 1991 and June 9-13 in 1992. The mean time between hatching (all nests combined) of A and B eggs (A-B hatch interval) was 0.75 ± 0.95 days ($N=101$). B-C hatch interval was 1.68 ± 0.91 days ($N=57$). Modal hatch intervals were 1 day for A and B eggs, 2 days for B and C eggs. Experimental and control A-B hatch intervals were not significantly different (two-tailed Kruskal-Wallis test, $H=0.1213$, $df=1$, $P=0.7276$). Larger A-C hatch intervals (combined data) were associated with a significantly decreased probability of survival to 8 days for the C chicks ($X^2=20.26$, $df=1$, $P<0.0001$) (Figure 1), but it did not significantly alter the probability of A chick survival ($X^2=1.698$, $df=1$, $P=0.1926$). Experimental and control B-C intervals did not differ. For the combined sample a larger B-C hatch interval was also associated with a reduced C chick survival ($X^2=11.24$, $df=1$, $P=0.0008$), (Figure 1) while not changing the survival of the B chick ($X^2=1.84$, $df=1$, $P=0.175$). Different A-B hatch intervals had no influence on survival of either the A or B chicks (A chick: $X^2=0.0315$, $df=1$, $P=0.8592$, B chick: $X^2=0.0145$, $df=1$, $P=0.7039$).

Nearest Neighbor Distance Nearest neighbor distances, measured nest-cup to nest-cup, were calculated for both the experimental and control nests. There was no significant difference in the proximity of the closest nest (experimentals: 3.51 ± 0.16 meters, controls: 3.33 ± 0.18 meters, one-way ANOVA $F_{1,81}=0.49$, $P=0.4880$). In addition, a discrete regression analysis was performed on the control and experimental nests separately. This showed that there was no correlation between internest distances and survivorship for either group (experimentals: $T=-0.22$, $df=36$, $P=0.8304$, controls: $T=0.42$, $df=39$, $P=0.6775$).

Figure 1. The effect of hatch asynchrony on C-chick mortality in control clutches (N).



Egg Volumes The average lengths, breadths and volumes of experimental and control A and B eggs were compared and analyzed separately in 1992 to determine if these intrinsic egg parameters differed between the two groups (Table 6). No significant differences were found for any measurement using one-way repeated measures ANOVAs. Since the egg measurements for the experimental and control A and B eggs did not differ significantly, this could not have introduced a bias towards greater nest productivity in the control nests. The length, breadth and volume of A, B, and C eggs were then analyzed (as above, followed, where significant, by least significant difference comparison of means), with the experimental, control, and unpenning control egg measurements combined (Table 6). Egg breadth was found to be not significantly different between the A and B egg, but both were significantly greater than the C egg. In addition, the B egg had a significantly greater length than either the A egg or the C egg, neither of which were significantly different from one another. The volume of the C egg was significantly less than either the A or B eggs, which did not differ.

Probability of hatching was significantly affected by volume for the experimental eggs (log linear analysis, $X^2=12.22$, $df=4$, $P=0.0158$), but not for the control eggs (log linear analysis, $X^2=7.42$, $df=6$, $P=0.2835$). When the control data were combined with the control unpenning data, the probability of hatching was significantly affected by egg volume (log linear analysis, $X^2=13.48$, $df=6$, $P=0.0360$) (Figure 2). For a given volume, the position of the egg in the laying sequence, whether A, B, or C, had no effect (log linear analysis, experimentals: $X^2=7.26$, $df=3$, $P=0.0641$, controls: $X^2=8.72$, $df=6$, $P=0.19$, combined controls: $X^2=5.60$, $df=6$, $P=0.47$).

Egg volume was positively correlated to hatching weight using a linear regression, for the experimentals ($F_{1,54}=78.74$, $P<0.0001$), controls ($F_{1,78}=239.43$, $P=0.0001$), and experimental, control and unpenning controls combined ($F_{1,275}=512.93$, $P>0.0001$).

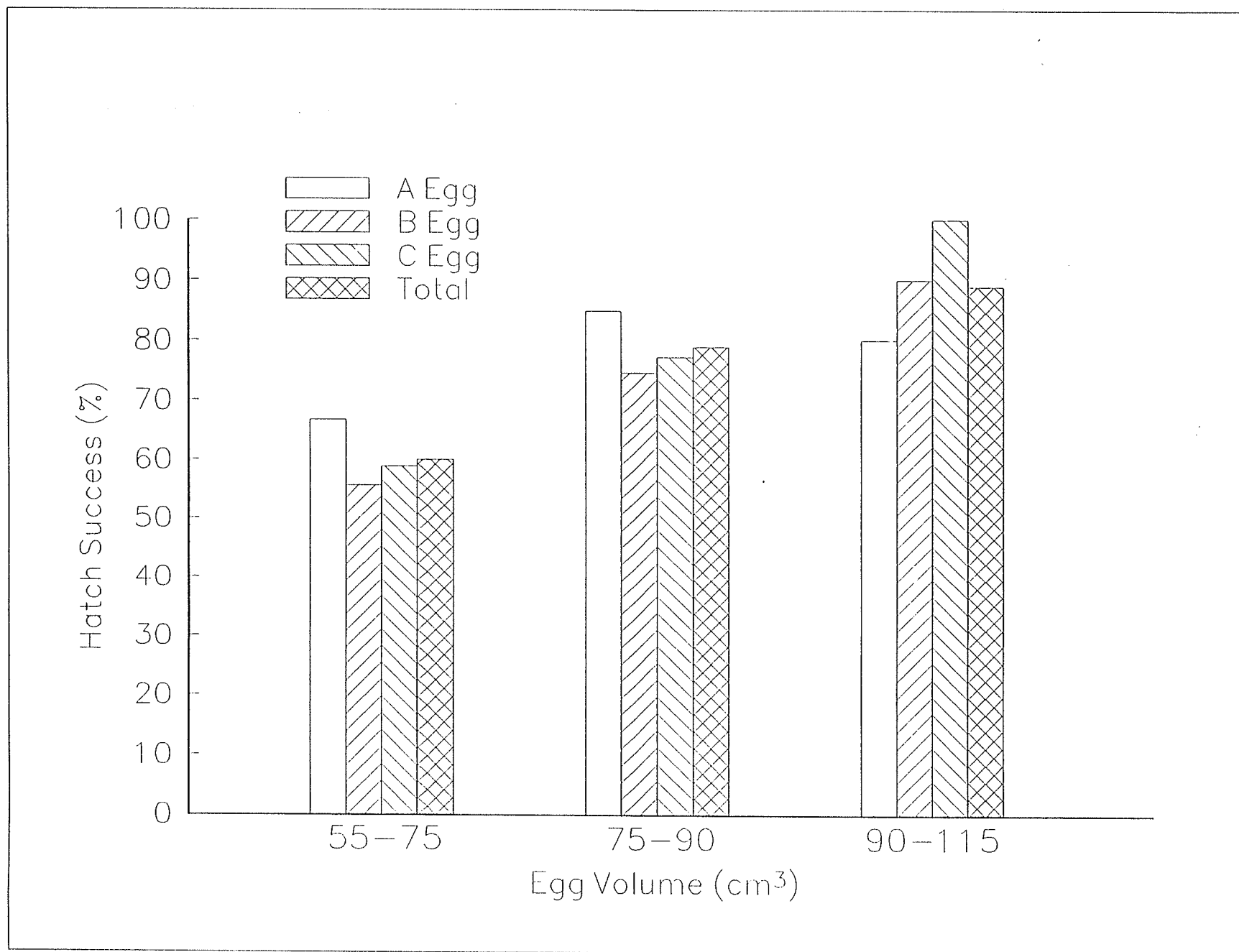
Table 6. Herring gull egg measurements (mean \pm SE) for 1992

Egg	Measurement		
	Length (mm)	Breadth (mm)	Volume (CC)
Experimental A	71.8 \pm 0.62	49.9 \pm 0.21	85.4 \pm 1.18
Control A	70.8 \pm 0.71	50.1 \pm 0.25	85.0 \pm 1.54
Statistic	$F_{1,71}=1.03$ ($P=0.31$)	$F_{1,71}=0.38$ ($P=0.54$)	$F_{1,71}=0.03$ ($P=0.86$)
Experimental B	72.5 \pm 0.60	50.2 \pm 0.22	87.2 \pm 1.22
Control B	72.1 \pm 0.65	50.2 \pm 0.28	86.9 \pm 1.58
Statistic	$F_{1,71}=0.21$ ($P=0.65$)	$F_{1,71}=0.00$ ($P=0.97$)	$F_{1,71}=0.03$ ($P=0.86$)
Combined ¹ A	71.2 \pm 0.33 ^a	49.8 \pm 0.13 ^a	84.2 \pm 0.70 ^a
Combined ¹ B	72.1 \pm 0.31 ^b	50.0 \pm 0.13 ^a	86.0 \pm 0.69 ^a
Combined ¹ C	71.2 \pm 0.28 ^a	49.0 \pm 0.13 ^b	81.6 \pm 0.67 ^b
Statistic	$F_{2,350}=3.26$ ($P=0.04$)	$F_{2,350}=21.70$ ($P<0.001$)	$F_{2,350}=12.86$ ($P<0.001$)

¹ Includes experimental, control, and unpenned control egg measurements

^{a,b} Values in columns having different superscripts are significantly different ($P<0.05$).

Figure 2. The hatching success of A, B and C herring gull eggs as a function of egg volume (1992).



Chick Weights In 1992 chick weights on the day of hatching (day 0) were not different for chicks that were still wet, slightly wet, nearly dry, or dry (A chicks: $F_{3,103}=0.45$, $P=0.7193$, B chicks: $F_{3,87}=1.08$, $P=0.3568$, C chicks: $F_{3,68}=0.97$, $P=0.4115$). All day 0 weights within controls or experimentals were therefore combined in subsequent weight analysis.

Weights of the control and experimental chicks measured every second day over the age range of 8 days, are shown in Table 7. All weight data was compared using repeated measures ANOVAs. In 1992, experimental A chicks were not significantly different from control A chicks ($F_{1,44}=0.79$, $P=0.3793$), and experimental B chicks were not significantly different from control B chicks ($F_{1,44}=1.78$, $P=0.1886$). At nests where all chicks survived, there were no significant differences between control and experimental chicks in 1991 (A chicks: $F_{1,8}=1.11$, $P=0.3193$, B chicks: $F_{1,8}=0.28$, $P=0.6105$) nor in 1992 (A chicks: $F_{1,22}=0.07$, $P=0.7882$, B chicks: $F_{1,23}=1.05$, $P=0.3165$). To equate brood size, the 1992 weights of experimental chicks from complete clutches (broods of 2) were then compared to the weights of chicks from naturally reduced (C-chick dead) control clutches. Again no significant differences in their 8-day weights were found (A chicks: $F_{1,23}=0.98$, $P=0.3315$, B chicks: $F_{1,28}=0.00$, $P=0.9908$). Weights of control A and B chicks from complete clutches also did not differ significantly from chicks at naturally reduced (C-chick dead) control clutches in 1992 (A chicks: $F_{1,17}=0.43$, $P=0.5197$, B chicks: $F_{1,21}=1.29$, $P=0.2687$, C chicks: $F_{1,13}=1.78$, $P=0.2056$).

Conclusions

There were no differences among the experimental and control nests with regard to egg laying intervals, inter-nest distances, incubation periods, hatch intervals, egg measurements, or chick weights. These results support the idea that these factors did not significantly confound interpretations of the experimental results. However, there were some

Table 7. Mean \pm SE weights(g) of herring gull chicks in 1992

Day	Chick	Average Weight of Broods		
		3 Chick Control	2 Chick Experimental	2 Chick Control ¹
0	A	67.5 \pm 2.64	65.8 \pm 4.00	65.0 \pm 1.78
	B	68.3 \pm 2.58	65.7 \pm 3.97	69.8 \pm 2.38
	C	64.9 \pm 2.73	-	68.0 \pm 2.78
2	A	76.9 \pm 2.36	75.1 \pm 4.40	77.6 \pm 4.00
	B	83.5 \pm 3.24	79.8 \pm 4.94	80.7 \pm 3.22
	C	72.8 \pm 5.60	-	84.9 \pm 5.29
4	A	101.7 \pm 4.88	101.2 \pm 6.61	96.6 \pm 5.50
	B	114.6 \pm 6.97	92.3 \pm 6.73	94.8 \pm 3.71
	C	90.9 \pm 9.20	-	109.0 \pm 8.27
6	A	130.6 \pm 7.51	123.9 \pm 8.07	128.8 \pm 6.43
	B	141.0 \pm 9.43	118.3 \pm 8.57	127.9 \pm 5.37
	C	110.9 \pm 13.15	-	135.0 \pm 12.62
8	A	158.9 \pm 6.87	161.0 \pm 11.28	147.3 \pm 11.13
	B	162.8 \pm 13.79	147.3 \pm 12.83	154.2 \pm 10.44
	C	137.4 \pm 20.96	-	165.3 \pm 16.58

¹ Control nests naturally reduced from 3 to 2 chicks by 8 days.

significant differences between A, B, and C eggs which will be briefly discussed.

The average incubation time of all eggs combined was 26.8 days which is similar to what others have documented (Paludan 1951; Parsons 1972). When eggs were analyzed according to their position in the laying sequence the A eggs' period of incubation was significantly longer. This provides further indirect evidence (Harris 1964; Drent 1967; but see Parsons 1972) that the parents do not begin full incubation of the A egg immediately after it is laid, especially since A and B eggs do not differ in volume and there was no difference in incubation period between the B and C eggs.

The modal hatch interval was one day for A-B eggs and two days for B-C eggs. It was found that larger A-C and B-C hatch intervals were associated with a decrease in the probability of C chick survival to 8 days (Figure 2). This illustrates the importance of hatch asynchrony as a mechanism for brood reduction. If food is in short supply then the parents would have to spend more time searching for food rather than incubating, and as a result, the hatching time of the youngest chick would increase. This would place the C chick at a greater than normal competitive disadvantage and it would be quickly eliminated. In this way the parents are not investing any unnecessary parental fitness in a chick that would ultimately die of starvation.

For all control eggs combined, the probability of hatching was significantly affected by egg volume (Figure 2). However, as mentioned above, the volume of the A and B eggs was significantly larger than the C eggs. Yet this difference did not translate into differences in hatchability within clutches. The reason for this apparent discrepancy is unknown. Because egg dimensions differed depending on their position in the laying sequence, there may be intrinsic egg differences within a clutch, but this would presumably not have differentially affected the nest productivity of the controls and experimentals.

Small C-eggs have been found in a number of other herring gull

studies (Harris 1964; Parsons 1972; Hebert and Barclay 1988; but see Meathrel et al. 1987). According to Slagsvold et al. (1984), this is an example of a 'brood-reduction strategy', whereby birds lay a small final egg so that adjustment of the number of offspring during adverse environmental conditions can be more readily accomplished. In my study, the order in the laying sequence had no effect on hatchability, but did affect survivorship (Chapter 1). The elimination of terminal young, brought about by hatch asynchrony which creates a size hierarchy within the brood, would be facilitated by producing smaller C eggs. Parsons (1970) found egg size to be inversely correlated to chick survivorship.

Overall, there were no potential confounding sources of variation between the experimental and control groups. The only observable differences were within clutches (ie. A, B, and C eggs and chicks), and these were present in both the experimental and control groups.