Brood reduction and adoption in Ring-billed Gulls (*Larus delawarensis*): the potential for intergenerational conflict.

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Abstract

Patterns of intra-clutch egg size variation and intra-clutch hatch intervals in the Ring-billed gull (Larus delawarensis) were documented during the peak nesting period of two consecutive breeding seasons, at a colony near Port Colborne, Ontario. Egg size decreased with laying order; third laid eggs were significantly smaller than first laid eggs. Hatching of the third egg was delayed from that of first and second eggs. Intra-clutch egg size differences established initial size disparities among chicks at hatch. Hatch intervals further exaggerated size disparities during the early post brood completion period. Competitive asymmetries among chicks were associated with increased mortality rates among third hatched chicks despite the lack of evidence of a sibling feeding hierarchy. Fledging success in 1987 was greater than in 1988. A "brood reduction strategy" appears to have enabled parents in 1987, to obtain an extra unit of reproductive fitness, while in 1988 parents were often unable to raise the entire brood and third chicks likely represented insurance reproductive value.

Experimental broods (1988) were created in which hatch intervals were double those of natural intervals. The size disparities among chicks were significantly greater than in control broods, and the pattern of mortality among chicks suggested that first chicks benefited at a cost to second and third chicks. Parents of peak experimental broods achieved a fledging success rate similar to that of control broods.

Characteristics of chick adoptions were also recorded. In each study year, 9 chicks abandoned their natal territories, 6 of which were adopted. Chicks consistently established themselves into broods where they were older than resident chicks. No direct evidence of cost to foster parents, or benefits to adopted chicks was obtained, although fledging success of adopted chicks was high.
ACKNOWLEDGEMENTS

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Introduction:

Trivers (1974) suggested that sexual reproduction leads to an evolutionary conflict between parents and offspring over optimal strategies to maximize lifetime reproductive fitness. Conflict arises as each offspring is more closely related to itself than to its siblings, while each parent is equally related to each offspring. Selection favours parental control over patterns of investment that enable parents to maintain somatic condition while maximizing their inclusive fitness. However, selection also favours selfish behaviour in offspring since they are completely related to themselves while sharing (on average) only 50% of their genes with siblings. Offspring are expected to, 1) demand more parental investment than the parent is selected to give and 2) attempt to skew parental investment in their direction as long as the cost to siblings multiplied by the relatedness factor (0.5 in full sibs) is less than the benefit obtained by the selfish individual (Trivers 1974). Interests of parents and offspring, in terms of maximized lifetime reproductive fitness, are likely to differ. The relative strengths of opposing selective forces on parents and offspring respectively determine the outcome of such conflicts.

In many temperate nesting larid species, the typical clutch size is three. The interests of parents and chicks are expected to differ at hatch, in terms of strategies to maximize lifetime reproductive fitness. The way in which such conflicts are resolved, in the context of natural selection, is of great interest.

Intra-clutch Egg Size and Hatch Intervals:

Variation in intra-clutch egg size patterns and hatching intervals are commonly reported in many species of birds. Intra-clutch egg size patterns range from eggs increasing in size with laying order (Eudyptes
to eggs decreasing in size with laying order (*Larus spp.*) (Clark and Wilson 1981, Slagsvold et al. 1984). The adaptive value of intra-clutch egg size variation has received considerable attention since distinctly different patterns are observed among different species (Parsons 1976). In many temperate nesting larid species, the typical clutch size is three and the third or last laid egg is generally smaller in length, breadth and mass than previously laid eggs (*L. argentatus*; Parsons 1975, *L. atricilla*; Hahn 1981, *L. delawarensis*; Chardine and Morris 1983, *L. occidentalis*; Pierotti and Bellrose 1986). Also, intra-clutch hatch intervals lengthen as the breeding season progresses; eggs in clutches initiated early in the breeding season hatch more synchronously (on average) than those initiated later in the breeding season (Nisbet and Cohen 1975, Parsons 1975, Chardine and Morris 1983).

Intra-clutch egg size variation in larids is often explained in terms of energetic constraints on laying females (Mills 1979, Winkler and Walters 1983, Pierotti and Bellrose 1986). However, despite the availability of supplemental food resources, patterns of intra-clutch egg size variation often remain unchanged (see Karlsson 1983, in Slagsvold et al. 1984). Therefore, researchers have suggested that patterns of egg size variation are not solely due to the depletion of energetic reserves in the laying female; females may be capable of exerting some control over the pattern of resource apportionment to eggs within a clutch (Quinn and Morris 1986).

Hatching intervals between siblings within a brood can range from a single day to a week depending on the species (Lack 1954, Nisbet 1973, Parsons 1975). Intra-clutch hatch intervals are determined, to a great extent, by the point at which parents begin incubation of the clutch. By beginning incubation prior to clutch completion, parents are able to spread out the hatch of each egg thus providing first laid eggs with a developmental advantage over last laid eggs (Chardine and Morris 1983).
Slagsvold et al. (1984) proposed that birds possess several mechanisms that enable them to adjust the magnitude of their reproductive effort relative to environmental conditions as well as their own breeding condition. Such mechanisms include hatching patterns (Ricklefs 1965) and intra-clutch egg size variation (Ojanen et al. 1981). The adaptive value of intra-clutch egg size variation may be closely linked to the hatching pattern of the brood (Slagsvold et al. 1984).

Decreases in egg size with laying order along with asynchronous hatching are often associated with an increased mortality rate among later hatching offspring (Lack 1954, Nisbet 1973, Parsons 1975). Last hatched offspring are smaller and younger than previously hatched offspring and are therefore at a competitive disadvantage with respect to older and larger siblings. This competitive disadvantage often translates into reduced growth rates and a reduced rate of survival (Pierotti and Bellrose 1986, Hebert and Barclay 1986). In species with a typical clutch size of three, this phenomenon is most often referred to as the "Third Chick Disadvantage".

Several functional interpretations have been proposed to explain the adaptive basis of the "Third Chick Disadvantage". The "Sibling Rivalry Reduction" hypothesis suggests that competitive asymmetries among chicks in the brood establish a sibling feeding hierarchy such that excessive and potentially wasteful intrabrood competition for resources is reduced (Hahn 1981, Braun and Hunt 1983, Slagsvold et al. 1984). Energy that may have otherwise been used for nestling growth is consumed by sibling rivalry and may represent a significant burden on parental fitness (Hamilton 1964, Hahn 1981). By reducing intra-brood competition for resources, parents are able to maximize their efficiency and thereby their reproductive success (Mock and Ploger 1987).

The "Insurance" hypothesis suggests the smaller last egg provides a form of insurance against the loss of a previously laid egg, or the loss of
an older nestling (Howe 1978). The insurance value of such an egg would be highest in species which have a high rate of egg infertility, or where chicks are at an extremely high risk during the early nestling stage. According to this hypothesis, the third chick would represent a replacement unit of reproductive fitness, having virtually no chance of surviving unless another sibling died or an egg failed to hatch (Graves et al. 1984, Mock and Parker 1986).

Further interpretations suggest that asynchronous hatching in passerines, functions to spread out the times of peak food demand within the brood (Bryant 1978). Hussell (1972) suggested that the asynchronous hatch interval staggers periods of peak food demand such that parents are better able to meet the needs of the entire brood.

In species that suffer heavy nest predation, asynchronous hatching may be adaptive in that it reduces the period between laying and hatching. By beginning incubation before clutch completion, parents are able to speed up the time to hatching of the first chick and thereby the time to fledging (Tyrvainen 1969).

The most widely accepted hypothesis pertaining to intra-clutch egg size variation and asynchronous hatch intervals is the "Brood Reduction" hypothesis. Through decreased egg size with laying order and an asynchronous hatching pattern, parents establish a sibling feeding hierarchy within the brood which enables them to adjust brood size according to available food resources or environmental conditions prevalent during the nestling period (Lack 1954, Stearns 1976). Braun and Hunt (1983) suggested that female birds breeding under conditions such as unpredictable food supply, lay clutches of a size appropriate for a good food year. Therefore, parents initially create more nestlings than they are capable of supporting under average or poor ecological conditions (Mock and Parker 1986). The brood reduction strategy enables parents to adjust the number of offspring later in the nestling stage when conditions can be
assessed (Slagsvold et al. 1984). Through the establishment of a sibling feeding hierarchy, parents are able to rely on sibling competition to effectively adjust the number of offspring to a size that can be successfully reared under prevalent conditions (Howe 1976, O'Connor 1978). During periods of food stress, parents are able to 'cut their losses' by quickly eliminating the smallest and youngest chick in the brood, which represents the minimum of already invested energy (Lack 1954, Ricklefs 1965, Howe 1976). Conditions of unpredictable food supply will likely favour parents that are able to maximize their reproductive success by favouring some offspring at the expense of others (Alexander 1974).

Lack (1966) suggested that the production of more offspring than are normally reared functions to exploit a fluctuating food supply when food is plentiful. Under conditions of superabundant food supply, the third chick in the brood may represent an extra unit of reproductive fitness for the parent (Mock and Parker 1986).

The brood reduction hypothesis suggests that, in an unpredictable environment, parents able to control their pattern of reproductive expenditure, such that they are able to 'hedge bets', will be more likely to experience higher reproductive success than those losing an entire brood during a food shortage (Stearns 1976). If patterns of parental reproductive effort have any heritable component, then natural selection should favour, strongly, the subset of the population that is able to raise successfully some young (Howe 1978).

In larid species, the establishment of the sibling feeding hierarchy appears to represent an adaptation providing parents with initial control over potential conflicts at hatch (Slagsvold et al. 1984, Morris 1987). By producing competitive asymmetries among chicks in the brood, parents are able to exert control over the ability of chicks to solicit excess parental investment. Parents are able to control resource apportionment within the brood such that their inclusive fitness is maximized (Morris et al.
Brood reduction allows parents to increase their inclusive fitness by regulating the pattern of mortality among chicks in the brood (Hahn 1981). Therefore, parents are 'winning' the conflict.

Parental control over offspring survival may be dependent to some extent on the rate of development of chick mobility; once chicks become mobile, parental control decreases. Therefore, offspring receiving inadequate parental care in their natal brood, due to brood reduction or the loss of a parent, may have the behavioural option of seeking parental care elsewhere (Pierotti and Murphy 1987, Morris 1988).

**Adoption and Alloparental Care:**

In many larid species, the temporary or permanent abandonment of parents by offspring followed by the adoption of these offspring by adults other than their parents have been observed (Dawkins 1976, Waltz 1981, Graves et al. 1984, Pierotti and Murphy 1987). Many gulls are able to recognize their young, however, rates of chick recognition vary according to species, experience and habitat (Evans 1980). Rates of chick recognition also appear to correspond with the rate of development of chick mobility (Beer 1970, Miller and Emlen 1975). Despite the ability of parents to recognize their chicks, adoptions of foreign young are often observed. This type of apparently altruistic behaviour appears to be inconsistent with classic evolutionary theory. According to the theory of natural selection, selection should act against adults that adopt another individual's offspring and should favour adults capable of recognizing their own offspring and rejecting unrelated offspring (Wilson 1975, Waltz 1981, Wittenberger 1981).

Several hypotheses have been proposed to explain the occurrence of this apparently altruistic behaviour in larid species. These include 1) selfishness of the foster parent, 2) kin selection, 3) reciprocal altruism,
4) group selection, 5) reproductive error or maladaptation and 6) Intergenerational conflict.

Adoption is often considered to be a selfish act on the part of the adopting parent, rather than an altruistic act (Holley 1980). This interpretation suggests that individuals are able to gain parenting experience through adoption or are able to dilute the effects of predation by maintaining an additional chick in the brood. In species that show delayed breeding and extended parental care, individuals can greatly improve their reproductive success through experience gained early in their reproductive period. Individuals subjected to heavy nest predation may also improve the probability of survival of their own offspring.

Kin selection theory has also been applied to explain the occurrence of adoption in gulls (Holley 1980). Foster parents increase their inclusive fitness by adopting a related individual. This theory is applied to individuals breeding in close proximity to related individuals.

Reciprocal altruism has also been proposed to explain the occurrence of adoption. This hypothesis suggests that an individual that adopts an unrelated offspring is later reciprocated by having one of its own offspring adopted at some time in the future. Reciprocal altruism is most likely to occur between individuals that are relatively long-lived and have many opportunities to interact with the same individuals (Trivers 1971, Waltz 1981). Stringent checks against cheaters are required for such a system of reciprocity to evolve (Waltz 1981).

Group selection has also been suggested as a driving selective force behind adoption. Individuals adopt strange chicks indiscriminately, thereby increasing the fitness of the colony or population as a whole. Group selection explanations are often unsatisfactory, since selection at the individual level is likely to overcome opposing selection at the group level (Williams 1966).
The above hypotheses suggest that foster parents are benefiting, either directly or indirectly, by adopting an unrelated individual. Alternative hypotheses are based on observations that evidence of benefits to foster parents are lacking while costs are abundantly apparent. The loss in time and energy that does not contribute to inclusive fitness (Waltz 1981, Reidman 1982) and the propagation of competing genotypes in the population (Hamilton 1964) represent potential costs to foster parents. Further costs, in terms of lost reproductive fitness through reduced survival among the foster parents own chicks, or the loss of future reproductive fitness due to reduced fecundity resulting from the depletion of energy reserves, have also been observed (Nisbet and Drury 1972, Carter and Spear 1986). Parents should, therefore, attempt to prevent the possibility of investing in unrelated offspring. The finding that 20% of wandering larid chicks are killed by adults suggests that parents do attempt to prevent adoption (Mock 1984, Pierotti and Murphy 1987).

Based on observations that adoption represents a cost to foster parents, adoption is often considered to be maladaptive, resulting from errors in recognition when the offspring are small and the ability of parents to recognize their offspring is not fully developed (Holley 1981, 1984). As adoption in gulls can occur at relatively high frequencies (2%-15%; Hebert 1988) and at an age exceeding that at which recognition has developed (Graves and Whiten 1980), such explanations are often unsatisfactory.

An alternative hypothesis suggests that selection favours chicks that are able to solicit effectively parental investment from adults other than their parents. Pierotti and Murphy (1987) suggested that adoption may represent an intergenerational conflict between disadvantaged chicks and unrelated adults. The conflict arises as a result of advantages to adults capable of recognizing their own offspring and rejecting unrelated
offspring (Wilson 1975, Dawkins 1976), and advantages to chicks that are able to solicit and obtain parental care outside of their natal territory when their chances of survival are low.

Poor environmental conditions such as food stress may significantly reduce the probability of a chick surviving on its natal territory. Gauthreaux (1978) showed that chicks suffering food deprivation showed increased locomotory activity, while Hunt and McLoon (1975) found that poorly fed Glaucous-winged gull (L. glaucescens) chicks wandered about their territories more than well fed chicks. The loss of a parent increases chick disadvantage, as chicks are more likely to be subjected to food stress and to attacks by intruding adults or predators (Hunt and McLoon 1975, Graves and Whiten 1980, Holley 1980).

Despite the risks involved in abandoning the natal territory (Graves and Whiten 1980), disadvantaged gull chicks that successfully invade a foreign territory, experience increased growth rates, feeding rates, and probability of survival relative to those remaining in the natal territory (Pierotti and Murphy 1987). On average, 65% of chicks that obtain adoption status survive to fledge (Parsons 1971, Graves and Whiten 1980, Holley 1981, Carter and Spear 1986).

Although foster parents incur a cost by adopting an unrelated individual, this cost may be devalued by the related cost of mistakenly rejecting one of its own offspring (Pierotti and Murphy 1987). Selection acting on disadvantaged offspring may be powerful enough to overcome selection on adults to reject unrelated offspring (Pierotti and Murphy 1987). An intergenerational conflict is apparent in terms of opposing selective forces acting on parents and offspring respectively. The outcome of this conflict will be determined by the relative strengths of selection acting on foster parents and disadvantaged offspring.

The Ring-billed gull (L. delawarensis) is an ideal organism for studies related both to brood reduction and adoption. Peak nesting Ring-
billed gulls lay a typical clutch of three eggs and intra-clutch hatch intervals lengthen as the breeding season progresses. Third laid eggs are typically smaller than previously laid eggs and, although peak clutches hatch relatively synchronously, the hatch of the third egg is often delayed from that of first and second eggs (Chardine and Morris 1983). Also, Ring-billed gull chicks have been observed abandoning their natal territory and establishing themselves in foreign territories where they are fed and cared for by adults other than their parents (pers. obser.).

The objectives of my study were to determine the effects of natural and experimentally doubled hatch intervals and egg size variation on 1) the pattern of within brood chick mortality, 2) feeding rates to chicks relative to hatch order, 3) pattern of chick abandonment of natal territories with respect to hatch order and 4) parental reproductive success. A further objective was to quantify the characteristics of adoptions in terms of costs and benefits to foster parents and chicks.

According to the Brood Reduction Hypothesis, the following predictions were made:

1) Third hatched chicks are expected to be disadvantaged with respect to feeding and survival rates.
2) Third chick disadvantage should be most apparent in a poor year as opposed to a good year.
3) In a poor year, the demise of the third chick should increase the probability of survival of siblings and thereby increase parental reproductive success.

In experimental broods, where hatching intervals are artificially manipulated:

1) If natural selection has favoured natural hatch intervals, then extended hatch intervals should not increase parental reproductive success, and may decrease parental fitness.
2) Pattern of mortality of chicks in experimental broods should differ from that in control broods.

Based on the hypothesis of adoption as an intergenerational conflict:
1) As third chicks are expected to be at the greatest disadvantage, they should be most likely to abandon natal territories.
2) Chicks abandoning their natal territories, should move to broods where they are at least as large as the largest chicks in the brood in order to increase their competitive ability within the foreign brood.
3) Chicks that are adopted should increase their probability of survival.
4) Foster parents should incur a cost when adopting an unrelated offspring.
Methods:

1. The Study Area

The study was conducted at a Ring-billed gull colony located in Port Colborne Ontario (42 53' N, 79 16' W) near the Lake Erie terminus of the Welland Canal. Ring-billed gulls nested on a man-made rock pile adjacent to the western leg of the concrete breakwater complex located approximately one kilometre from the northern shore of Lake Erie. The nesting substrate consisted of rocks and stones. No vegetation was present. Refer to Morris and Haymes (1977) for a detailed description of the study colony.

In 1987 and 1988, the study area was located on the north side of the rock pile. This area was chosen based on visibility of nests and accessibility with a minimum of disturbance.

2. Data Collection

In 1987 and 1988, an observation blind was erected 5 metres from the edge of the study area prior to the laying of the earliest eggs in the study area (13-15 April). The blind was set up in a position that allowed maximum visibility of the study area and ensured minimum disturbance when entering the blind. Access to the blind was possible by taking three to four steps from a boat landing site, up the rock pile behind the blind.

Daily counts of new clutches were made in the study area to determine the onset of the peak period of clutch initiation. All eggs laid on and subsequent to 17 April 1987 and 18 April 1988 were numbered with indelible magic marker according to laying sequence. Three-egg study clutches were then chosen from the larger sample of clutches initiated during the peak nesting period and were numbered using spray paint directly on an adjacent rock or numbered aluminum plates fixed to an adjacent rock. All eggs in peak three-egg study clutches were
measured for length (mm) and breadth (mm) using vernier calipers and volumes calculated as $V=0.51 \, L \, B^2$ (Hoyt 1979).

During the incubation period, study clutches were checked once weekly to ensure numbers on eggs remained visible. Otherwise, the peak study area was not entered from 4-20 May 1987 and 28 April -10 May 1988. As study clutches approached the end of the incubation period, they were checked once every second day for signs of hatching.

In 1987, following the observation of first pipping eggs in peak study clutches, nest checks were conducted once daily, weather permitting, to determine the intervals between the hatch of successive eggs. The hatching stage of eggs were recorded as star pip, pipped or holed, based on the extent of hatching observed. Chicks were recorded as wet or dry based on the condition of their plumage when first observed in the study brood. In 1988, study clutches were monitored twice daily for hatching. Nest checks were conducted once in the morning and once in the late afternoon, weather permitting, in order to increase the accuracy of recorded hatch intervals. Recording procedures were the same as those used in 1987. All chicks in peak study broods were individually colour banded at hatch using plastic split-ring colour bands. Colour band codes included up to four bands per chick (maximum of two per leg), which identified the chicks natal brood and hatching order within that brood. In 1987, banding began on 20 May and was completed on 24 May. In 1988, banding began on 11 May and was completed on 19 May. Termination of banding was determined by the development of chick mobility within the area.

From 25 May - 16 June 1987, study clutches that hatched three chicks were observed daily from the observation blind for three consecutive hours, 0600-0900 or 1800-2100, corresponding to peak periods of feeding activity. Each study brood was observed for the number of feeds delivered by parents over the three hour observation period. The number of feeds obtained by each chick in a brood with respect to hatching
order was also recorded. Chicks were recorded as having received a feed if they obtained any part of the regurgitated bolus.

During daily observation periods, a census of study broods was conducted. Chicks were recorded as 1) present, 2) dead (if observed in the study area) and 3) disappeared (if not visible in the natal brood or anywhere in the study area or surrounding visible areas). Any obvious abnormal conditions of chicks were also recorded (e.g. visible head injuries).

Chick movements from natal territories were monitored. Nests were checked for the presence of foreign chicks (having bands corresponding to another brood, or having no bands in a brood of banded chicks). Where possible, the natal brood of the foreign chick was recorded. Any subsequent movements of these chicks to other broods were recorded. Feeding rates to, and fates of foreign chicks were also recorded, visibility permitting. Survival of chicks in broods that adopted a chick were monitored.

In 1988, all procedures used were the same as for 1987 except that all chicks in three-chick study broods were weighed at hatch and again on the last day of entry into the study area (19 May), using a 100 gram Pesola Spring Scale.

3. Experimental Manipulation of Intra-clutch Hatch Intervals

In 1988, peak experimental broods were produced by manipulating intra-clutch hatch intervals to double those of natural hatch intervals.

Ten peak experimental study broods were selected from the larger sample of peak three-egg clutches according to visibility from the blind and hatch initiation date. When first eggs showed signs of hatching (in the star pip stage), the second and third eggs were checked for any signs of hatching. If they showed no signs of hatching they were left in the clutch. If the second egg showed any signs of hatching, it was removed...
from the clutch and replaced by a donor egg from a non study clutch that showed no signs of hatching. On the following day (24 hours later), the donor second egg was replaced by an egg that was in the advanced pipping stages or was holed. This egg then hatched in the experimental brood. The same procedure was carried out for the third egg. The manipulation procedure produced hatch intervals from 36-48 hours between the hatch of first and second eggs and second and third eggs, approximately double those of natural hatch intervals. Chicks were banded, weighed and monitored as for control broods.

4. Statistical Analyses

Egg volume data conformed to assumptions of parametric testing, having a normal distribution (D'Agostinos Test, Zar 1984) and homogeneity of variances (Bartlett's Test, Zar 1984). Comparisons of egg volumes with respect to laying order, within peak control (1987, 1988) and peak experimental (1988) groups, were conducted using Repeated Measures Analysis of Variance. Comparisons of egg volumes between groups, such as peak control 1987 and peak control 1988, were conducted using Unpaired T-Tests. All other data were analysed using non-parametric statistics as sample size often precluded tests of normality and homogeneity of variances.

Comparisons within peak control or peak experimental groups were conducted using pairwise non parametric tests. If two samples were compared, then Wilcoxon Signed Rank was used. If three samples were compared, then Freidmans Anova was used; pairwise comparison test statistic q (according to Zar 1984,p230). Chick survival data were compared using Cochrans Q Test for dichotomous nominal scale data; pairwise comparison statistic s (according to Zar 1984, pp 231-233).

If sample sizes were too small for the use of pairwise comparisons then unpaired tests were used. When two samples were compared; Mann-
Whitney U-test. When three samples were compared; Kruskal-Wallis (nonparametric analogue to ANOVA).

Comparisons between peak control 1987 and 1988 or between control 1988 and experimental 1988 were compared using unpaired non-parametric statistics including Mann-Whitney U-tests, Fisher Exact Probability and Chi-Square Contingency Tables.
Results:

1. Brood Reduction

A. Egg Volumes

Comparative volume data are presented in Table 1. In 1987, the volumes of the first and second laid eggs were significantly different from that of the third laid egg (Repeated Measures ANOVA, F=25.49, p=0.0001; FPLSD=1094.48, p<0.05). In 1988, all eggs were significantly different in volume measurements (Repeated Measures ANOVA, F=80.45, p=0.0001; FPLSD=1095.99, p<0.05). The volumes of second and third eggs laid in 1987 were significantly different from those laid in 1988; eggs laid in 1988 had smaller volumes than those laid in 1987 (Unpaired T-tests, egg 2; t=3.33, df=63, p<0.05, egg 3; t=3.97, df=63, p<0.05).

In peak experimental broods, volumes of eggs prior to clutch manipulation were compared in order to determine if intra-clutch egg size patterns were similar to peak control broods. Volumes of first and second laid eggs were significantly different from that of third laid eggs (Repeated Measures ANOVA, F=20.83, p=0.0001; FPLSD 1920.05, p's<0.05). There were no significant differences in the volumes of eggs in peak control and peak experimental clutches (Unpaired T-tests, p's>0.05).

B. Hatch Intervals

Mean intra-clutch hatch intervals were determined for peak control broods in 1987 and peak control and experimental broods in 1988 (Table 2). Mean hatch intervals of control clutches in 1987 and 1988 were not significantly different (Mann-Whitney U-tests, p's>0.05). Within 1988 peak control broods, the interval between the hatch of first and second eggs was significantly different from the interval between the hatch of second and third eggs (Wilcoxon Signed Rank, T+=189, T-=42, n=21, p<0.05). Manipulated hatch intervals of 1988 peak experimental broods were significantly different from those of peak control broods (Mann-
Table 1. Volumes of eggs (±1SD) in 1987 and 1988 peak clutches with respect to laying order. All statistical comparisons are between 1987 and 1988 control, and 1988 control and 1988 experimental.

<table>
<thead>
<tr>
<th>Year of Study (no. of study clutches)</th>
<th>Egg Volumes (mm$^3$ ± 1SD) (x 10$^4$)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Egg 1</td>
</tr>
<tr>
<td></td>
<td>5.39 ± 0.36 (n=30)</td>
</tr>
<tr>
<td>1987 Control (n=30)</td>
<td>5.45 ± 0.31 (n=30)</td>
</tr>
<tr>
<td>1988 Control (n=35)</td>
<td>5.38 ± 0.42 (n=35)</td>
</tr>
<tr>
<td></td>
<td>5.18 ± 0.35 (n=35)</td>
</tr>
<tr>
<td>1988 Experimental (n=10)</td>
<td>5.17 ± 0.37 (n=10)</td>
</tr>
<tr>
<td></td>
<td>5.00 ± 0.28 (n=10)</td>
</tr>
<tr>
<td></td>
<td>4.60 ± 0.20 (n=10)</td>
</tr>
</tbody>
</table>

Notes:
1. Volumes in rows without a letter in common are significantly different (ANOVA, p's<0.05)
2. Volumes in columns without a letter in common are significantly different (Unpaired T-tests, p's <0.05)
Table 2. Intra-clutch hatch intervals ($\bar{x} \pm 1SD$) of peak 1987 and 1988 study clutches.

<table>
<thead>
<tr>
<th>Year of Study</th>
<th>Egg 1-2</th>
<th>Egg 2-3</th>
<th>Egg 1-3</th>
</tr>
</thead>
<tbody>
<tr>
<td>1987</td>
<td>0.53 ± 0.52</td>
<td>1.07 ± 0.59</td>
<td>1.6 ± 0.74</td>
</tr>
<tr>
<td>Control</td>
<td>(n=15)</td>
<td>(n=15)</td>
<td>(n=15)</td>
</tr>
<tr>
<td>1988*</td>
<td>0.41 ± 0.44</td>
<td>0.84 ± 0.74</td>
<td>1.18 ± 0.83</td>
</tr>
<tr>
<td>Control</td>
<td>(n=31)</td>
<td>(n=28)</td>
<td>(n=36)</td>
</tr>
<tr>
<td>1988</td>
<td>1.94 ± 0.64</td>
<td>1.75 ± 0.93</td>
<td>3.69 ± 0.53</td>
</tr>
<tr>
<td>Experimental</td>
<td>(n=10)</td>
<td>(n=10)</td>
<td>(n=10)</td>
</tr>
</tbody>
</table>

* see appendix 1
Whitney U-tests, egg1-2, U'=305, n1=31, n2=10, p<0.05; egg 2-3, U'=225, n1=28, n2=10, p<0.05; egg 1-3, U'=360, n1=36, n2=10, p<0.05).

C. Mass of chicks at hatch and Post-brood completion

Chick mass at hatch with respect to hatching order is in Figure 1. In 1988 peak control broods, the mass of the third chick at hatch was significantly different from that of the first chick (Freidmans Test, $X^2_r=9.75$, df=2, p<0.05, pairwise comparisons; first vs. second, $q=1.06$, p>0.05; second vs. third, $q=3.18$, 0.10>p>0.05; first vs. third, $q=4.24$, p<0.05). In 1988 peak experimental broods, masses of chicks within a brood at hatch were not significantly different (Freidmans Test, $X^2_r=4.39$, df=2, p>0.05). Comparisons between masses of chicks at hatch in peak control and peak experimental broods, with respect to hatching order, revealed no significant differences (Mann-Whitney U-tests, p's>0.05).

In order to determine if the mass difference present at hatch persisted to the period from 0-4 days post brood completion, masses of chicks within a brood were compared with respect to hatching order (Figure 2). In peak control broods, the mass of the third chick at 0-4 days post brood completion was significantly different from that of first and second hatched chicks (Freidmans Test, $X^2_r=11.14$, df=2, p<0.05; pairwise comparisons, first vs. second, $q=1.13$, p>0.05; second vs. third, $q=3.40$, p<0.05; first vs. third, $q=4.54$, p<0.05). In peak experimental broods, the mass of the third chick at 0-4 days post brood completion was significantly different from that of the first chick (Freidmans $X^2_r=6.5$, df=2, p=0.05, pairwise comparisons; first vs. second, $q=2.50$, p>0.05; second vs. third, $q=1.00$, p>0.05; first vs. third, $q=3.50$, p<0.05). Chick mass at 0-4 days post brood completion were compared between chicks in peak control and peak experimental broods. The masses of first hatched chicks were significantly different (Mann-Whitney U-test, $U'=129$, n1=15, n2=10, p<0.05). No further significant differences were found (p's >0.05).
Figure 1: Mean mass at hatch ($\bar{x} \pm 1$SD) of peak control and peak experimental chicks with respect to hatching order.
Figure 2. Mean mass (\(\bar{x} \pm 1\text{SD}\)) of chicks in peak control and peak experimental broods at 0-4 days post brood completion (PBC) with respect to hatching order.
The mass disadvantage of second and third chicks at hatch and at 0-4 days post brood completion was quantified by subtracting their mass from that of first hatched chicks (Figure 3). In peak control broods, second chicks were at a greater mass disadvantage at 0-4 days post brood completion than at hatch (Mann-Whitney U-test, $U'=29$, $n_1=6$, $n_2=5$, $p<0.05$). The mass disadvantage of third chicks at hatch in peak control broods had also increased significantly by 0-4 days post brood completion (Wilcoxon Signed Rank, $T+=0$, $T-=91$, $p<0.05$).

In peak experimental broods, the mass disadvantage of second chicks at 0-4 days post brood completion was significantly different from that at hatch (Wilcoxon Signed Rank, $T+=0$, $T-=28$, $p<0.05$). The mass disadvantage of third chicks at 0-4 days post brood completion was also significantly different from that at hatch (Mann-Whitney U-test, $U'=25$, $n_1=5$, $n_2=5$, $p<0.05$).

The mass disadvantages of chicks in peak control and peak experimental broods at 0-4 days post brood completion were compared. The mass disadvantage of second hatched chicks in peak experimental broods was significantly different from that in peak control broods (Mann-Whitney U-test, $U'=35$, $n_1=5$, $n_2=7$, $p<0.05$). The mass disadvantage of third hatched chicks in peak control and peak experimental broods at 0-4 days post brood completion were also significantly different (Mann-Whitney U-test, $U'=35$, $n_1=7$, $n_2=5$, $p<0.05$).

D. Relationship between Egg Volume and Chick Mass at Hatch

There was a significant relationship between egg volume and the mass of chicks at hatch (Simple Linear Regression, $r^2=0.844$, $df=49$, $p=0.0001$) in 1988 peak study broods (Figure 4).
Figure 3: Mean mass disadvantage of the second and third chicks at hatch and at 0-4 days post brood completion for peak control and peak experimental broods.
Figure 4. The relationship between egg volume and chick mass at hatch in 1988 peak study broods.
E. Feeding Rates

In 1987 and 1988, feeding rates were determined by observing the number of feeds obtained by each chick in the brood. A chick was recorded as having fed if it obtained any part of the bolus delivered by the parent. Pooling of first and second chicks was possible as there were no significant differences in the number of feeds received by first and second chicks in broods in which they were distinguishable (Mann-Whitney U-tests, p's>0.05). In 1987, first chicks received 0.29±0.20 feeds/hr (n=8) while second chicks received 0.26±0.18 feeds/hr (n=8). In 1988, first chicks received 0.28±0.11 feeds/hr (n=10) while second chicks received 0.25±0.11 feeds/hr (n=10).

To determine if third chicks were disadvantaged with respect to feeding, the number of feeds received by first and second chicks (pooled) were compared to the number of feeds received by third chicks when all three chicks were present in the nest (Table 3). There were no significant differences in the number of feeds received by chicks with respect to hatching order in broods fledging all three chicks (1987, Mann-Whitney U-test, p>0.05; 1988, statistical analysis inappropriate, n₁=2, n₂=4). Also, there were no significant differences in the number of feeds received by first and second chicks, and third chicks in broods where at least the third chick died (1987, Mann-Whitney U-test, p>0.05; 1988, Wilcoxon Signed Rank, p>0.05). In broods in which only the third chick died, there were no significant differences in the number of feeds received by first and second chicks, and third chicks when all three chicks were present (1987 and 1988, Mann-Whitney U-tests, p's>0.05). In 1988, feeding rates to first and second chicks (pooled) in peak control and peak experimental broods that lost at least the third chick (Mann-Whitney U-test, p>0.05) and in broods that lost only the third chick (Mann-Whitney U-test, p>0.05) were not significantly different.
Table 3. Mean feeds/hr (±1SD) to chicks in peak broods with respect to hatching order when all 3 chicks were present.

<table>
<thead>
<tr>
<th>Nest (Year)</th>
<th>1st and 2nd Chicks (Mean Feeds/Hr±1SD)</th>
<th>3rd Chicks (Mean Feeds/Hr±1SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fledging 3 Young</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1987 PC</td>
<td>0.36±.10 (n=10)</td>
<td>0.32±0.10 (n=5)</td>
</tr>
<tr>
<td>1988 PC</td>
<td>0.40±0.03 (n=4)</td>
<td>0.35±0.0 (n=2)</td>
</tr>
<tr>
<td>1988 PE</td>
<td>NA</td>
<td>NA</td>
</tr>
<tr>
<td>At least 3rd Chick Died</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1987 PC</td>
<td>0.24±0.19 (n=14)</td>
<td>0.20±0.20 (n=7)</td>
</tr>
<tr>
<td>1988 PC</td>
<td>0.24±0.10 (n=18)</td>
<td>0.18±0.11 (n=9)</td>
</tr>
<tr>
<td>1988 PE</td>
<td>0.16±0.12 (n=9)</td>
<td>NA</td>
</tr>
<tr>
<td>Only 3rd Chick Died</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1987 PC</td>
<td>0.30±0.19 (n=8)</td>
<td>0.20±0.17 (n=4)</td>
</tr>
<tr>
<td>1988 PC</td>
<td>0.21±0.11 (n=8)</td>
<td>0.10±0.07 (n=4)</td>
</tr>
<tr>
<td>1988 PE</td>
<td>0.35±0.07 (n=6)</td>
<td>0.0±0.0 (n=1)</td>
</tr>
</tbody>
</table>

1 Peak control broods
2 Peak experimental broods
Feeding rates to first and second chicks (pooled) in broods that fledged all three chicks were compared to broods that lost at least the third chick, and broods that lost only the third chick. In 1987 peak control broods, there were no significant differences (Mann-Whitney U-tests, p's>0.05). In 1988 peak control broods, again, differences were not significant (Mann-Whitney U-tests, p's>0.05). Feeding rates to third chicks in broods that fledged all three chicks and in broods that lost at least the third chick, and only the third chick, were also compared. In 1987 peak control broods and in 1988 peak control broods, these differences were not significant (Mann-Whitney U-tests, p's>0.05).

Table 4 presents the mean total number of feeds delivered to broods in 1987 and 1988 along with the mean number of feeds received by dying and surviving chicks. In 1987, there was no significant difference in the mean number of feeds received by third chicks that survived and those that died (Mann-Whitney U-test, p>0.05), while in 1988 this difference was significant (Mann-Whitney U-test, U'=31, n₁=4, n₂=8, p<0.05). There were no significant differences in the mean number of total feeds delivered per hour to broods fledging three chicks and those losing at least one chick in either study year (Mann-Whitney U-tests, p's>0.05). The total number of feeds delivered per hour when all three chicks were present, to broods in 1987 was compared to the number of feeds delivered to broods in 1988. There was no significant difference (Mann-Whitney U-test, p>0.05).

Statistical analysis was not possible in peak experimental broods due to small sample sizes. However, the number of feeds received by surviving chicks was compared to the number of feeds received by chicks that died or disappeared and the difference was significant (Mann-Whitney U-test, U'=68, n₁=12, n₂=6, p<0.05). Feed rates to peak control broods losing at least one chick and peak experimental broods losing at
Table 4. Mean feeds/hr (±1SD) to chicks or broods in peak control (1987, 1988) and peak experimental (1988) study groups.

<table>
<thead>
<tr>
<th>Chick or Broods</th>
<th></th>
<th>Peak Control 1987</th>
<th>Peak Control 1988</th>
<th>Peak Experimental 1988</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surviving 3rd Chicks</td>
<td>0.33±0.09</td>
<td>0.32±0.07</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>(n=6)</td>
<td>(n=4)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dying 3rd Chicks</td>
<td>0.21±0.18</td>
<td>0.15±0.08</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>(n=8)</td>
<td>(n=8)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Surviving Chicks ¹</td>
<td>NA</td>
<td>NA</td>
<td>0.29±0.11</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(n=12)</td>
<td></td>
</tr>
<tr>
<td>Dying Chicks ²</td>
<td>NA</td>
<td>NA</td>
<td>0.07±0.10</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(n=6)</td>
<td></td>
</tr>
<tr>
<td>Broods Fledging 3 Chicks</td>
<td>0.45±0.11</td>
<td>0.41±0.00</td>
<td>NA</td>
<td></td>
</tr>
<tr>
<td>(n=5)</td>
<td>(n=2)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Broods Losing At Least 1 Chick</td>
<td>0.37±0.24</td>
<td>0.28±0.10</td>
<td>0.27±0.16</td>
<td></td>
</tr>
<tr>
<td>(n=11)</td>
<td>(n=11)</td>
<td></td>
<td>(n=8)</td>
<td></td>
</tr>
<tr>
<td>All Study Broods</td>
<td>0.37±0.22</td>
<td>0.30±0.11</td>
<td>0.27±0.16</td>
<td></td>
</tr>
<tr>
<td>(n=13)</td>
<td>(n=13)</td>
<td></td>
<td>(n=8)</td>
<td></td>
</tr>
</tbody>
</table>

¹ in peak experimental broods all surviving chicks pooled due to small sample size

² in peak experimental broods all dying chicks pooled due to small sample size
least one chick revealed no significant difference (Mann-Whitney U-test, p>0.05). Also, there was no significant difference in the overall feed rates to peak control and peak experimental broods (Mann-Whitney U-test, p>0.05).

F. Chick Survival

Chick survival to 21 days with respect to hatching sequence was compared for three-chick study broods from 1987 and 1988 breeding seasons (Figure 5). In 1987, 12 of 14 first chicks, 13 of 14 second chicks, and 6 of 14 third chicks survived to fledge. Third chick survival was significantly different from that of first and second chicks (Cochrane Q Test, Q=12.28, df=2, p<0.05; pairwise comparisons; first vs. second: s=0.46, p>0.05; second vs. third: s=3.24, p<0.05; first vs. third: s=2.78, p<0.05). In 1988 peak control broods, 10 of 15 first chicks, 9 of 15 second chicks, and 3 of 15 third chicks survived to fledge. Third chick survival was significantly different from that of first chicks and slightly lower than that of second chicks (Cochrane Q Test, Q=7.82, df=2, p<0.05; pairwise comparisons, first vs. second; s=0.37, p>0.05, second vs. third; s=2.22, 0.10>p>0.05, first vs. third; s=2.59, p<0.05).

Between year comparisons revealed no significant differences in the survival rates of chicks to 21 days of age with respect to hatching order (Fisher Exact Probabilities, p's>0.05). However, in 1987, 32 of a total of 45 chicks survived to 21 days, while in 1988, 36 of a total of 87 chicks did so. This difference was significant (2x2 X2=10.50, df=1, p<0.05).

In peak experimental broods, 7 of 9 first chicks, 4 of 9 second chicks, and 2 of 9 third chicks survived to 21 days. There were no significant differences in the survival of chicks with respect to hatching sequence (Cochrane Q Test, Q=5.43, df=2, p>0.05). Also, there were no significant differences between peak control and peak experimental broods in terms of chick survival with respect to hatching order (Fisher
Figure 5: Chick survival to 21 days in 1987 peak control and 1988 peak control and experimental study broods.
* number of study broods included in individual chick analysis
^ PC-peak control, PE-peak experimental
Exact Probabilities, p's > 0.05). The overall survival rate of chicks in peak experimental broods (13 of 27 survived to 21 days) was not significantly different from that of peak control broods ($2 \times 2 \chi^2 = 0.38, df = 1, p > 0.05$).

G. Chick Age at Death/Disappearance

The ages of chicks at death (or disappearance) were compared between first and second chicks (pooled as they were often indistinguishable) and third chicks for study broods in 1987 and 1988 (Table 5). In peak control broods, there were no significant differences in the ages of chicks at death in either study year (Mann Whitney U-tests, 1987: $U' = 29.5, n_1 = 5, n_2 = 9, p > 0.05$; 1988: $U' = 250, n_1 = 19, n_2 = 24, p > 0.05$). Chicks in 1988 peak control broods tended to die or disappear at a younger age than chicks in 1987 peak control broods (first and second chicks (pooled); Mann-Whitney U-test, $U' = 99, n_1 = 5, n_2 = 24, p < 0.05$; third chicks, $U' = 126.0, n_1 = 9, n_2 = 19, p < 0.05$).

In peak experimental broods, the ages of first, second and third chicks at death were compared (first and second chicks were not pooled). Third hatched chicks died at a younger age than second chicks and at a significantly younger age than first hatched chicks (Kruskal-Wallis, $H_c = 9.22, df = 2, p < 0.05$, pairwise comparisons; first vs. second: $Q = 0.82, p > 0.05$; second vs. third: $Q = 2.31, 0.10 > p > 0.05$; first vs. third: $Q = 2.54, p < 0.05$).

Comparisons between peak control and peak experimental broods revealed no significant difference in the age of first and second chicks (pooled) at death (Mann-Whitney U-test, $U' = 106, n_1 = 7, n_2 = 24, p > 0.05$). Third chicks in peak experimental broods died at a significantly younger age than those in peak control broods (Mann-Whitney U-test, $U' = 120.5, n_1 = 8, n_2 = 19, p < 0.05$).

Table 6 presents the proportion of broods in which the first or second chick died first and in which the third chick died first. In 1987,
Table 5. Mean age (days) of chicks at death ($\bar{x} \pm 1$SD) with respect to hatching order for peak study broods from 1987 and 1988.

<table>
<thead>
<tr>
<th>Year of Study</th>
<th>Chick 1</th>
<th>Chick 2</th>
<th>Chick 3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1987</strong></td>
<td>11.00 ± 8.54</td>
<td>19.00</td>
<td>11.44 ± 7.17</td>
</tr>
<tr>
<td>Control</td>
<td>(n=3)</td>
<td>(n=1)</td>
<td>(n=9)</td>
</tr>
<tr>
<td></td>
<td>14.2 ± 7.46*</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(n=5)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>1988</strong></td>
<td>5.80 ± 4.15</td>
<td>6.50 ± 4.46</td>
<td>5.32 ± 3.67</td>
</tr>
<tr>
<td>Control</td>
<td>(n=5)</td>
<td>(n=6)</td>
<td>(n=19)</td>
</tr>
<tr>
<td></td>
<td>6.29 ± 4.57*</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(n=24)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Experimental</td>
<td>11.5 ± 1.73</td>
<td>6.8 ± 3.96</td>
<td>2.25 ± 1.67</td>
</tr>
<tr>
<td></td>
<td>(n=2)</td>
<td>(n=5)</td>
<td>(n=8)</td>
</tr>
<tr>
<td></td>
<td>8.14 ± 4.06*</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>(n=7)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* mean age at death when chicks 1 and 2 are pooled.
- refer to appendix 2 a,b,c.
Table 6. Proportion of broods (that lost at least one chick), in which the third chick died first, and in which the first or second chick died first.

<table>
<thead>
<tr>
<th>Study Group</th>
<th>Proportion of broods in which 3rd chicks died first (n)</th>
<th>Proportion of broods in which first or second chicks died first (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peak Control 1987</td>
<td>0.78 (7)</td>
<td>0.22 (2)</td>
</tr>
<tr>
<td>Peak Control 1988</td>
<td>0.71 (17)</td>
<td>0.29 (7)</td>
</tr>
<tr>
<td>Peak Experimental 1988</td>
<td>0.90 (9)</td>
<td>0.10 (1)</td>
</tr>
</tbody>
</table>
the third chick was the first to die or disappear in 7 of 9 broods that lost a chick. In 1988, the third chick was the first to die (another chick may have also died on the same day) in 17 of 24 broods that lost a chick. A greater number of broods lost the third chick first \((1 \times 2 \chi^2 = 4.17, \text{df} = 1, p < 0.05)\). In 9 of 10 peak experimental broods that lost a chick, the third chick died or disappeared first. Again, a greater number of broods lost the third chick first \((1 \times 2 \chi^2 = 6.4, \text{df} = 1, p < 0.05)\).

H. Effect of Sibling Death/Disappearance on Remaining Sibling Survival

In order to determine the effect of sibling mortality or disappearance from the natal brood on the survival of remaining siblings, the probability of survival of each chick in the brood was determined for broods in which another sibling died first (SDF) or in which another sibling did not die first (NSDF) (Figure 6). In 1987, the survivorship of first hatched chicks in nests where neither sibling died first was 75\% (6/8). This value increased to 85.7\% (6/7) in nests where another sibling died first (in 6 of 7 cases, the sibling that died first was the third chick). First chick survivorship did not increase significantly (Fisher Exact Probability, \(p > 0.05\)). The survivorship of second hatched chicks in nests where neither sibling died first was 85.7\% (6/7) which increased to 100\% (8/8) in nests where a sibling died first (in 6 of 8 cases, the sibling that died first was the third chick). The survivorship of second chicks did not increase significantly when a sibling died first (Fisher Exact Probability, \(p > 0.05\)). Third chick survivorship in broods where neither sibling died first was 43\% (6/14) which fell to 0\% (0/2) in broods where a sibling died first. Survivorship in each brood type was not significantly different (Fisher Exact Probability, \(p > 0.05\)).

In 1988 peak control broods, the survivorship of first chicks in broods where neither sibling died first was 25\% (2/8) which increased significantly to 82.4\% (14/17) in broods where another sibling died first.
Figure 6. Survivorship of chicks in broods where another sibling died first (SDF) and in broods where another sibling did not die first (NSDF).
(Fisher Exact Probability, p=0.01; in 11 of 17 case the sibling that died first was the third chick). The survivorship of second chicks in broods where neither sibling died first was 28.6% (2/7) which increased to 69% (9/13) in broods where another sibling died first (in 9 of 13 cases, the third chick died first). Second chick survivorship did not increase significantly (Fisher Exact Probability, p>0.05). Third chick survivorship in broods where neither sibling died first was 11.8% (2/17) which increased to 22.2% (2/9) in broods where another sibling died first. Third chick survivorship did not increase significantly (Fisher Exact Probability, p>0.05).

In 1988 peak experimental broods, there were no broods in which a sibling did not die before the fate of the first chick was realized. However, in broods where a sibling died first, 78% (7/9) of first hatched chicks survived to 21 days. The survivorship of second chicks in broods where another sibling did not die first was 0% (0/2) which increased to 57% (4/7) in broods where a sibling died first (in all cases, the third chick died first). The increase in survivorship was not significant (Fisher Exact Probability, p>0.05). The survivorship of third chicks in broods where another sibling did not die first was 12.5% (1/8) which increased to 100% (1/1) in broods where a sibling did die first. Survivorship did not increase significantly (Fisher Exact Probability, p>0.05).

2. Chick Movements from Natal Territory

The characteristics of adoptions that occurred in 1987 and 1988 are in Table 7. In 1987, nine chicks were observed in territories other than their natal territories, six (67%) of which were considered to have been adopted as they remained in a foreign territory for ≥2 days. The remaining three chicks were in foreign territories for <2 days and were referred to as "runners" (see Morris et al. 1989). Of 16 study broods with colour banded chicks, 3 (18.8%) adopted a chick, while 3 of a total of 48 (6.25%)
Table 7. Adoptions in 1987 and 1988 peak breeding season.

<table>
<thead>
<tr>
<th>Adoption Number (Year)</th>
<th>No. and age (days) of Chicks in Foreign Brood at time of adoption</th>
<th>Days in Foreign Brood</th>
<th>Hatch Order Adoptee</th>
<th>Feeds/hr at Recip. Nest Before Adoption</th>
<th>Feeds/hr at Recip. Nest After Adoption</th>
<th>No. Chicks Fledged (year)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Parent’s Own Adopted</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Parent’s Own Adopted</td>
</tr>
<tr>
<td>1 (1987)</td>
<td>3 (6d) 1 (Old*)</td>
<td>24d</td>
<td>NA</td>
<td>0.5</td>
<td>0.59</td>
<td>3 1</td>
</tr>
<tr>
<td>2 (1987)</td>
<td>3 (4d) 1 (5d)</td>
<td>25d</td>
<td>1st</td>
<td>NA</td>
<td>0.55</td>
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<tr>
<td>3 (1987)</td>
<td>3 (16d) 2 (17d, NA)</td>
<td>12d</td>
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<td>4 (1987)</td>
<td>3 (15d) 1 (NA)</td>
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<td>6 (1987)</td>
<td>NA 1 (5d)</td>
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<td>3.0±0.0 (8.3±5.9)</td>
<td>19.3±7.4</td>
<td>0.51±0.007</td>
<td>0.51±0.08</td>
<td>3.0±0.0 (8.3±5.9)</td>
<td>19.3±7.4</td>
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| 7 (1988)               | 1 (7d) 1 (7.5d)                                              | 16d                  | 3rd                 | NA                                     | 0.41                                   | 1 1                      |
| 8 (1988)               | 3 (4.5d) 1 (9d)                                              | 5d                   | 2nd                 | NA                                     | NA                                     | 1 0                      |
| 9 (1988)               | 1 (2d) 1 (12d)                                               | 13d                  | 3rd                 | NA                                     | NA                                     | 0 1                      |
| 10 (1988)              | 1 (Youn.*) 1 (8.5d)                                          | 5d                   | 2nd                 | NA                                     | NA                                     | 1 0                      |
| 11 (1988)              | 1 (11.5d) 1 (NA)                                            | 3d                   | NA                  | NA                                     | NA                                     | 1 0                      |
| 12 (1988)              | 1 (17.5d) 1 (Youn.*)                                         | 5d                   | NA                  | 0.07                                   | 0.07                                   | 1 0                      |

|                        |                                                               |                      |                     |                                         |                                         |                          |
|                        | 1.3±0.76 (9.3±1.9)                                           | 7.8±5.3              | 0.24±0.24           |                                         |                                        |                          |

* Precise age of chicks unknown, however, known to be younger (Youn.) or older (Old).
colour banded chicks abandoned their natal territory. The mean age of chicks that abandoned their natal territory and were subsequently adopted was 8.25±5.85 days (n=4). All chicks were adopted into broods with younger resident chicks. Adopting broods had a mean size of 3.00±0.0 (n=4) chicks prior to adoption and the mean age of the eldest chick in adopting broods was 10.25±6.13 days (n=4). Of the nine chicks that abandoned their natal territories, seven (78%) survived to fledging.

The number of feeds delivered in adopting broods prior to adoption was compared to that after adoption had taken place. Before adoption, 0.51±0.007 feeds were delivered per hour (n=2) while after adoption 0.51±0.08 feeds were delivered per hour (n=4). Due to small sample size, statistical analysis was inappropriate.

In 1988, 9 chicks were observed in territories other than their natal territories, six of which remained in the foreign territories for ≥2 days. The remaining three chicks remained in foreign territories for <2 days and were considered runners. Of 49 peak study broods, 2 (4.08%) adopted a chick. Of 147 colour banded chicks in the study area, 5 (3.4%) abandoned their natal territories. One chick from a peak experimental brood was adopted which represents 3.33% of peak experimental chicks. One of ten experimental broods had a chick adopted which represents 10% of the broods. The mean age of chicks that abandoned their natal territory and were subsequently adopted was 9.25±1.94 days(n=4). Of five cases where the relative ages of adopted chicks and resident chicks were known, there was one case where the adopted chick was younger than the resident chicks. The mean number of chicks present in the recipient brood at the time of adoption was 1.29±0.76 (n=6). The mean age of the eldest chick in the recipient broods was 8.5±6.13 days (n=4). Of a total of nine chicks that abandoned their natal territory, only two (22.2%) survived to 21 days of age. Feeding data prior to and after adoption was not available for comparison for 1988 adoptions.
Comparative chick survival data are presented in Table 8. In order to determine the costs of adoption to foster parents, the survival of chicks in non-adopting broods was compared to that of resident chicks in broods that did adopt. In 1987 broods that did not adopt a chick, 27 of a total of 39 chicks survived to fledge, while in broods that did adopt, 6 of a total of nine resident chicks survived to fledge. This difference was not significant (Fisher Exact Probability, p>0.05). In 1988 broods that did not adopt a chick, 22 of a total of 45 chicks survived to fledge while in broods that did adopt a chick, 5 of 8 resident chicks survived to 21 days. This difference was not significant (Fisher Exact Probability, p>0.05).

In order to determine potential survival benefits to adopted chicks, their survival rates were compared to those of their siblings that remained in their natal territories. In 1987, six of six (100%) adopted chicks survived to 21 days while of 2 siblings of known fate, 2 (100%) survived to 21 days. There was no significant difference (Fisher Exact Probability, p>0.05). In 1988, two (33.3%) of six adopted chicks survived to 21 days, while one (16.7%) of their natal brood mates that remained in the natal territory survived to fledge. This difference was not significant (Fisher Exact Probability, p>0.05).
Table 8. Comparative survival data of resident chicks, adopted chicks, and siblings of adopted chicks in peak study broods in 1987 and 1988.

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<td>Resident Chicks in Adopting Broods</td>
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<td>Siblings of Adopted Chicks that did not Abandon Natal Territory</td>
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Proportion of chicks surviving and dying (n)
Discussion:

There has been considerable speculation as to the adaptive significance of intra-clutch egg size variation, asynchronous hatching, and the associated increased mortality rate among later hatching offspring (Parsons 1970, 1975, Davis 1975, Mock 1984, Slagsvold et al. 1984). Various hypotheses have been proposed to explain such characteristics. The Sibling Rivalry Reduction hypothesis suggests that the establishment of competitive asymmetries among chicks in the brood reduce wasteful sibling competition for resources (Hahn 1981, Braun and Hunt 1983, Slagsvold et al. 1984). The Insurance hypothesis views the smaller last egg of the Common Grackle (Quiscalus quiscula) as insurance against the loss of previous eggs or older siblings (Howe 1978), while the Peak Load Reduction hypothesis suggests that asynchronous hatch intervals spread out the periods of peak food demand in passerine broods (Hussel 1972, Bryant 1978). Further interpretations suggest that asynchronous hatch intervals speed up the time to fledging of the first chick, reducing the likelihood of losing the entire brood to a predator (Tyrvainen 1969). Often, however, the above hypotheses fail to explain the increased mortality among later hatching offspring and/or fail to incorporate the significance of intra-clutch egg size differences.

The most widely accepted hypothesis is the Brood Reduction hypothesis which suggests that the pattern of mortality associated with asynchronous hatching and decreased egg size with laying order increase parental reproductive output by reducing the chance of total reproductive failure in a year when parents are unable to provide sufficiently for the entire brood (Lack 1947, 1968). The Brood Reduction hypothesis is a cogent one as it is based on a simple mechanism of competitive asymmetries among chicks to create a feeding hierarchy that allows
parents to increase their inclusive fitness by regulating the pattern of mortality among their offspring (Hahn 1981).

1. Brood Reduction in Ring-billed Gulls:

A. Intra-clutch egg size and hatch interval variation

Parental control may be mediated through the differential provisioning of eggs within the clutch (Parsons 1970) and incubation patterns that favour early hatching offspring at the expense of the youngest sibling (Nisbet 1973, Parsons 1975). In both 1987 and 1988 peak study clutches, third laid eggs were consistently smaller in volume than both first and second laid eggs in the clutch. The pattern of intra-clutch egg size variation was similar for both study years despite the finding that eggs laid in 1987 were larger than those laid in 1988. These findings correspond with the observation that in many gull species, third laid eggs are typically smaller in length and breadth than previously laid eggs (Parsons 1976, Nisbet 1978, Ricklefs et al. 1978, Hahn 1981, Pierotti 1982b, Braun and Hunt 1983). Although egg size varied between study years, the third egg was consistently the smallest in the clutch, indicating that the pattern of egg size variation is not solely due to the depletion of energy reserves in the laying female (Parsons 1976).

Intra-clutch hatch intervals of the Ring-billed gull lengthen as the breeding season progresses. Eggs laid during the peak nesting period hatch relatively synchronously compared to clutches laid later in the breeding season (Chardine and Morris 1983). In 1987 and 1988, mean hatch intervals of peak clutches were greater than one day and the mean hatch interval from the second egg to the third egg was double that from the first egg to the second egg. Thus, despite relatively short hatch intervals, the hatch of the third egg was delayed from that of first and second eggs.
Slagsvold et al. (1984) suggested that intra-clutch egg size variation is of ultimate adaptive value in that it represents a mechanism by which parents are able to adjust the magnitude of their reproductive effort relative to environmental conditions as well as their own breeding condition. The adaptive value of egg size variation within the clutch is closely linked to the hatching pattern of the eggs. As the hatching pattern is directly related to parental behaviour, it may be viewed as an example of extended phenotype which presumably functions to enhance parental efficiency and thereby their lifetime fitness (Mock and Ploger 1987). Quinn and Morris (1986) suggested that the intra-clutch hatch intervals and the pattern of resource apportionment to eggs within a clutch may be tuned to a post hatching environment that is both competitive and asymmetrical, benefiting early hatched and penalizing last hatched young.

The hatch intervals and egg size differences observed in peak 1987 and 1988 clutches produced third chicks at an immediate size and age disadvantage. By establishing initial competitive asymmetries among chicks in the brood, parents facilitate efficient brood reduction if conditions are such, during the post hatch period, that the entire brood can not be raised successfully. Several researchers have interpreted the laying of a smaller last egg, along with asynchronous hatch intervals, in this manner (Howe 1978, Ricklefs et al. 1978, O'Connor 1979, Clark and Wilson 1981, Slagsvold et al. 1984).

B. Third Chick Disadvantage

According to the Brood Reduction Theory, intra-clutch egg size differences along with the delayed hatching of the last laid egg are adaptive in that they establish size disparities among chicks in the brood. In 1988, chicks were weighed at hatch. There was a significant relationship between mass of chicks at hatch and egg volume; smaller
eggs produced chicks of lower mass than larger eggs. Initial size differences were apparent between the mass of first and third chicks while differences between the mass of second and third chicks were less apparent. These findings indicate that the initial egg size differences observed in peak study broods, produced initial size disparities among chicks at hatch, corresponding with predictions associated with the Brood Reduction Hypothesis.

My findings correspond with those of Howe (1976) in that there was a direct correlation between fresh egg weight and hatchling mass. Pierotti and Bellrose (1986) and Hebert and Barclay (1986) found that third hatched chicks in the Western Gull and the Herring Gull were smaller at hatch than nest mates and attributed this finding to initial egg size differences and asynchronous hatch intervals.

In 1988 all live chicks were reweighed within the period from 0-4 days post brood completion. Mass differences were apparent between first and third chicks as well as second and third chicks: third chicks were significantly smaller than previously hatched siblings. The mass disadvantage of second and third chicks at hatch had increased significantly by 0-4 days post brood completion. These findings indicate that the initial size disparities among chicks at hatch became exaggerated early in the nestling stage. Therefore, although egg size differences alone established size disparities among chicks, the delayed hatching of the third egg further exaggerated these size disparities such that, within the early post brood completion period, the size disadvantage of both second and third hatched chicks had increased. Therefore, intra-clutch egg size differences, combined with hatch intervals of Ring-billed gull peak clutches established and maintained size disparities among chicks in the brood, at least up to four days post brood completion.
These findings correspond with observations that third hatched chicks, disadvantaged by hatch asynchrony and intra-clutch egg size differences, grew more slowly than their siblings (Pierotti and Bellrose 1986). Fujioka (1985) found larger differences in body size among Cattle Egret (Bubulcus ibis) siblings were produced by hatch asynchrony and were maintained or increased during the early phase of chick growth. In Common Terns (Langham 1972) and Western Gulls (L. occidentalis; Pierotti and Bellrose 1986), the mass difference of the third chick was marked in the first week, attributed to slower growth rates within this period.

Mock and Ploger (1987) suggested that despite disagreement as to the adaptive function of decreased egg size with laying order and asynchronous hatching, it is clear that these characteristics effectively establish early competitive asymmetries among chicks within the brood.

According to the Brood Reduction Hypothesis, third chicks are predicted to be at a disadvantage with respect to feeding due to their inability to compete with larger and older siblings. Slagsvold et al. (1984) and Hebert and Barclay (1986) suggested that the sibling feeding hierarchy renders the smallest and weakest chick unable to compete with siblings for food and therefore reduces wasteful competition for parental resources. In my study, there were no significant differences in feeding rates to first, second and third chicks from peak broods in either study year. However, in 1988, third chicks that died received significantly fewer feeds than those that survived. Furthermore, although differences were not significant, third chicks received fewer feeds per hour than older siblings. Although these results suggest that the competitive asymmetries established among chicks in peak broods did not lead to the expected sibling feeding hierarchy, decreased feeding rates to third hatched chicks may have contributed to their demise. The finding that, although differences were not significant, in 1987 and 1988, broods that
fledged three chicks were fed at consistently higher rates than broods that lost a chick, provides further evidence that food deprivation may have contributed to the demise of the chicks.

It is difficult to obtain accurate quantitative feeding data for species such as Ring-billed gulls. Ring-billed gulls feed by regurgitating a bolus of food into the nest cup and do not directly feed the chicks themselves. I was able only to determine if a chick received any part of a feed and was not able to quantify how much of a feed was obtained. This may have had a significant effect on the results; older siblings may have prevented smaller chicks from receiving equal shares of the bolus. Accordingly, the amount of food obtained by third chicks may have been overestimated. Despite my results that suggest a sibling feeding hierarchy was not established, as difficulties in obtaining accurate feeding data may have obscured actual feeding differences among chicks in the brood, the potential existence of a sibling feeding hierarchy cannot be ruled out. Ring-billed gulls are therefore not an ideal species for studies related to feeding rates.

The survival chances of any particular chick is related to the size of the egg from which it hatched (Moss et al. 1981, Birkhead and Nettleship 1982). According to the Brood Reduction Hypothesis, third chicks are predicted to suffer increased mortality rates compared to larger and older siblings due to an inability to compete for parental resources. In both 1987 and 1988 three-chick study broods, third chick survival was reduced compared to first and second hatched chicks in the brood, while first and second hatched chicks experienced relatively equal probabilities of survival. These findings indicate that third hatched chicks experienced increased mortality rates compared to previously hatched siblings. Egg size differences and the delayed hatching of the third egg produced size disparities among chicks in the brood which led to a decreased probability
of survival among the smallest and youngest siblings. These findings correspond with those of Pierotti and Bellrose (1986) and Hebert and Barclay (1986) in that there was a third chick disadvantage with respect to survival.

C. Adaptive Significance of Brood Reduction

Mock and Parker (1987) suggested that parents initially create more nestlings than they are capable of rearing under poor or average conditions. Howe (1978) suggested that brood reduction represents a parental strategy allowing the production of an extra egg as insurance against the infertility of a previously laid egg or the death of an older sibling in poor or average years, while allowing for the possibility of an extra unit of reproductive fitness if conditions are such that the entire brood can be reared successfully. The brood reduction strategy enables parents to maximize their reproductive success in the face of resource unpredictability (Mock and Parker 1986).

In my study there was evidence that 1987 was a more favourable year than 1988. Differences in several reproductive parameters suggest that conditions may have varied between study years. Mills (1979) showed that the most efficient foragers produced the largest eggs while Winkler and Walters (1983) found that egg size increased when food was abundant in larids. In 1987, second and third laid eggs were larger than those laid in 1988. These results indicate, that at least during the period of egg formation, resource availability was higher in 1987 than in 1988. The finding that, in 1988 peak clutches, the second egg was significantly smaller than the first egg, while no such difference was apparent in 1987 clutches, provides further evidence for differences in resource availability. As patterns of egg size variation may in part be related to the magnitude of energy reserves available to females for reproduction
(Pierotti 1982, Houston et al. 1983), these findings suggest that conditions prior to egg laying were more favourable in 1987 than in 1988.

Differences in conditions prevalent during the post hatching period were also apparent. Food availability can greatly affect the survival of gull chicks. Graves et al. (1984) found that fledging success of Herring gulls increased significantly when food supplements were provided. Langham (1972) suggested that chicks are more likely to succumb to starvation during the period just after hatching, when only one parent is free to forage. Parents in 1987 fledged a significantly greater proportion of their chicks than did parents in 1988. Also, chicks in 1988 died at a significantly younger age than those in 1987. Although differences in feeding rates to 1987 and 1988 broods were not significant, broods in 1988 consistently received fewer feeds per hour than those in 1987. The finding that there was no difference in feeding rates to surviving and dying third chicks in 1987 suggests that food did not contribute to the demise of chicks in 1987 to the same extent as in 1988. These findings indicate differences in food availability during the post hatch period, between 1987 and 1988 study years. Chicks in 1988 may have succumbed earlier to food stress than chicks in 1987 while a greater proportion of chicks in 1987 may have fledged due to increased food availability or increased parental attendance at the nest.

According to the Brood Reduction Hypothesis, if conditions are such that the entire brood is at risk, then brood size can be reduced through the elimination of the youngest nestling, thereby increasing the probability of survival of older siblings (Ricklefs 1965, Howe 1976, Hebert and Barclay 1986). If however, conditions are favourable, the strategy of producing more nestlings than parents are able to support, may produce an extra unit of reproductive fitness (Mock and Parker 1986). Mock and Parker (1986) suggested that the reproductive value of each
offspring can be partitioned into two components. The fraction of survivorship that is not contingent on the fate of siblings is referred to as 'extra reproductive value'. That fraction that depends critically on the fates of siblings is referred to as 'insurance reproductive value'. In 1987, survivorship of the third chicks was less contingent on the fate of siblings than it was in 1988. The death or disappearance of the third chick from peak broods in 1987 had little effect on the survivorship of the remaining siblings, while in 1988, the death or disappearance of the third chick from the brood greatly improved the probability of survival of the first chick and doubled that of the second chick. These findings correspond with the brood reduction hypothesis in that, in a good year, such as 1987, the smaller third egg represented 'extra reproductive value' to the parents and had little 'insurance value'. Conditions were such that parents were able to rear successfully the entire brood at a greater frequency than in 1988. In 1988, however, conditions were apparently less favourable, and third chicks represented to a great extent, insurance reproductive value. Parents in 1988 were not able to raise successfully the entire brood, therefore, by eliminating the third chick through efficient brood reduction, parents were able to increase significantly the probability of survival of older chicks. The brood reduction strategy enabled parents to exploit good conditions while maintaining relatively high reproductive success under poor conditions. Such a strategy may account for, at least in part, the relative success of Ring-billed gulls. Under good conditions, populations can be irruptive, while under poor conditions relatively high reproductive success is maintained. By creating competitive asymmetries among chicks in the brood, parents were able to maximize their reproductive success in the face of resource unpredictability.
D. Peak Experimental Broods

Peak experimental broods were manipulated to hatch at intervals double those of control broods. The manipulation procedure produced broods with chicks of relatively equal mass at hatch as eggs placed into experimental clutches were of relatively equal size. However, within the first four days post brood completion, the mass of the third chick was significantly lower than that of the first chick. A comparison between chick mass at 0-4 days post brood completion, between peak control and peak experimental broods, revealed a significant difference between the mass of first hatched chicks. First chicks in peak experimental broods were larger than those in control broods. Also, the mass disadvantage of both second and third hatched chicks increased significantly by 0-4 days post brood completion and was greater than that of chicks in peak control broods. Even in the absence of initial size disparities, asynchronous hatch intervals led to a significant mass disadvantage for third hatched chicks at 0-4 days post brood completion; first hatched chicks in experimental broods grew at a faster rate than those in control broods, at an apparent cost to second and third hatched chicks.

These observations from Ring-billed gulls correspond with those of Mock and Ploger (1987) in that the exaggerated hatch intervals led to a significant increase in the amount of food ingested by the first hatched chicks. This first chick feeding advantage led to an increase in the feeding disadvantage of subordinate chicks in the brood, as evidenced by the significantly greater mass disadvantage of second and third chicks in experimental broods as opposed to control broods. Consequently, the competitive advantage of dominant siblings increased significantly with increased hatch asynchrony.

Feeding rates in peak experimental broods were often difficult to analyze due to small sample sizes. However, there was a significant
difference in the number of feeds received by surviving and dying chicks. Furthermore, third chicks in peak experimental broods died at a significantly younger age than first and second hatched chicks. These findings indicate that the imposed asynchronous hatch interval exposed third chicks to food stress earlier in the nestling period than in control broods. Despite the lack of evidence of a sibling feeding hierarchy, food may have been a significant factor affecting the probability of survival of chicks in peak experimental broods.

The extended hatch interval also led to a change in the pattern of survival among chicks in the brood. Chick mortality rates were relatively equal for all chicks in the brood, in that third chick mortality rates were not greater than those of first and second hatched chicks. Also, there was no difference in the proportion of chicks fledged in peak control and peak experimental broods. Exaggerated hatch intervals did not lead to increased parental reproductive success. In my study, although there were no differences in chick survival between control and experimental broods, chicks in peak experimental broods may have been more susceptible to post-fledging mortality. Second and third chicks that survived may have fledged at a lighter mass than control chicks corresponding to the increased mass disadvantage observed early in the post hatch period. Also, the greater asynchrony would render smaller chicks more vulnerable to predation for longer periods of time (Mock and Ploger 1987).

The findings of my study correspond with those of Mock and Ploger (1987) in that increased hatch intervals did not increase chick survival to any extent greater than natural intervals. Mock and Ploger (1987) found that double hatch intervals reduced parental efficiency and concluded that parents may control intra-clutch hatch intervals in order to maximize efficiency and their lifetime inclusive fitness. Howe (1976) found that fledging weights had a significant effect on post fledging survival. Mock
and Ploger (1987) found that the magnitude of the competitive advantage of dominant siblings and the feeding disadvantage of subordinate chicks increased with increased hatch asynchrony. Parental efficiency decreased with double hatch intervals.

2. Adoption and Alloparental Care:

The brood reduction strategy allows parents to increase their inclusive fitness by regulating the pattern of mortality among their offspring (Hahn 1981). However, parental control over offspring survival may be dependent to some extent on the rate of development of chick mobility; once chicks become mobile parental control decreases. Therefore, offspring receiving inadequate parental care in their natal brood, due either to the brood reduction strategy or the loss of a parent, may have the behavioural option of seeking parental care elsewhere (Pierotti and Murphy 1987, Morris 1988). According to the theory of adoption as an intergenerational conflict, chicks are expected to abandoned their natal territory when their probability of survival in the natal brood is low. By becoming adopted, chicks are able to increase their probability of survival. As third chicks are more likely to be at a disadvantage due to the establishment of competitive asymmetries among chicks in the brood, they are predicted to abandon their natal territories at a greater frequency than first or second hatched chicks. Chicks that abandon their natal territory are predicted to move to nests where they are at least as old as the oldest chicks in the foreign brood. The theory of intergenerational conflict is based on the idea that there are opposing selective forces acting on foster parents and offspring. Therefore, adoption should represent a cost to foster parents reproductive fitness while benefiting adopted chicks. The relative strengths of the opposing
selective forces will determine the outcome of the intergenerational conflict (Pierotti and Murphy 1987).

Despite the ability of Ring-billed gulls to recognize their young within several days after hatch (Evans 1970), adoptions are still observed. Chicks seeking adoption are predicted to be at a disadvantage with respect to their ability to obtain food or by the loss of a parent. In my study, this prediction could not be addressed directly since chicks were known to have abandoned their natal territory only when when they were observed in another brood. It was not possible to determine the stimulus for the abandonment of the natal territory, and as parents were not marked, it was not possible to determine if a parent had been lost. Furthermore, small sample sizes made the comparison of feeding rates prior to and subsequent to adoption inappropriate. I was able to compare the proportion of chicks abandoning their natal territory in a good year as opposed to a poor year. Pierotti and Bellrose (1987), suggested that a greater proportion of chicks are expected to abandon their natal territory in a poor food year as more chicks would be disadvantaged by the brood reduction strategy. In 1987, which was apparently a more favourable year, 6.25% (n=3) of colour banded chicks abandoned their natal territory, while 3.4% (n=5) did so in 1988, which was apparently a less favourable year. This finding does not correspond with the prediction. However, 1988 results may have been an underestimate since a larger proportion of colour banded chicks in 1988 dissappeared, and their fate remained unknown. Many of these chicks may have been killed while attempting to leave their natal territory or may have been adopted into broods that were not visible from the observation blind. My results, however, do not correspond with observations that gull chicks that abandoned their natal territory were fed at low rates or were subject to starvation and attacks by other adults.

According to the theory of adoption as an intergenerational conflict, adoption is considered to be adaptive from the chicks perspective. Chicks that abandon their natal territory are predicted to have a low probability of survival which is greatly improved by becoming adopted. In 1987, of the 67% that were adopted, 100% survived to fledge while in 1988, of the 67% adopted only 33% survived to fledge. As chicks that became adopted had abandoned their natal territory, it was not possible to determine their probability of survival had remained in their natal territory. I was able only to compare the survival of chicks that became adopted to that of their siblings that remained in the natal territory. There was no apparent difference. However, this comparison is inadequate, as the survival probability of siblings in the natal territory may have been greatly improved when one of the siblings abandoned the territory. If it is assumed that chicks that abandoned their natal territory had a very low probability of survival, then the observed survival probabilities for adopted chicks may represent a significant increase. However, I was unable to obtain direct evidence that survival probability increased once a chick had become adopted.

A further prediction suggests that in species where brood reduction occurs, third hatched chicks should be the most likely to abandon their natal territory. As the third hatched chick is at a greater disadvantage due to smaller size and an inability to compete with older siblings, it should be most likely to leave the natal brood (Parsons 1975, Hahn 1981, Pierotti 1982b). Furthermore, by abandoning their natal territory, third chicks may be able to increase their inclusive fitness by improving the probability that their siblings will survive. In 1987, none of the chicks that abandoned their natal territory were third hatched chicks, while in
1988, two of four chicks of known hatch order, were third hatched chicks. Pierotti and Murphy (1987) found that there was a difference in the likelihood of chick desertion of the natal territory related to hatching sequence; third chicks deserted most often. In my study, such a trend was not observed. However, in 1987, 50% (n=3) of chicks that were adopted were of unknown hatch order. In 1988, 33% of adopted chicks were of unknown hatch order. Hatch order could only be determined if the adopted chick was colour banded. The difficulty in determining the hatch order of adopted chicks may have obscured trends that may have been present in the data.

An additional prediction suggests chicks that abandon their natal territory should move to nests where they are at least as large as the largest chick in the brood (Pierotti and Bellrose 1987). Adoptions observed in both 1987 and 1988, took place in broods were the adopted chick was at least as old as the oldest chick in the brood, in all but one case. Therefore, chicks appeared to be moving to broods where they were at least as large as the largest chick in the brood. By doing so adopted chicks were able to compete effectively with their foster siblings for food and thereby improve their probability of survival in the foster brood. In six of eight cases where the adopted chick was at least as old as the oldest chick in the foster brood, the adopted chick survived to fledge. In the one case where the adopted chick was known to be younger than the foster siblings, the adopted chick died. Chicks that moved to nests where they were the oldest may have been more likely to survive than those that moved to nests where they were younger than foster siblings.

According to the intergenerational conflict theory, selection acting on parents should favour those able to recognize their own offspring and reject unrelated offspring, thereby avoiding the evolutionary blunder of investing in another's offspring (Holley 1984) as adoption may represent a
considerable cost to foster parents in terms of lost time and energy that
does not contribute to inclusive fitness (Dawkins 1976, Waltz 1981,
exists, then adoption should represent a cost to foster parents and
therefore, foster parents should attempt to prevent adoption. In both
1987 and 1988, 33% of chicks that abandoned their natal territories were
not adopted. In 1987, two chicks that were not adopted dissappeared from
the study area while one returned to fledge in its natal territory. In 1988,
all chicks that were not adopted died or dissappeared. On many occasions
parents were observed vigorously attacking chicks that had wandered into
their territories, often to the point of death. There appeared to be
considerable risk involved in abandoning the natal territory as there was a
33% chance of being rejected and possibly killed by unrelated adults. Mock
(1984) and Pierotti and Murphy (1987) found that 20% of wandering
chicks were killed and suggested that parents do not adopt
indiscriminately and do attempt to prevent adoption by attacking foreign
chicks near their territory.

A related prediction suggests that parents should resist adoption
more vigorously in poor years when costs are expected to be higher.
Indirect evidence of costs to foster parents was obtained by comparing
the frequencies of adoption in a good year to that of a poor year. Pierotti
and Bellrose (1987) suggested that parents should resist adopting a chick
more vigorously in a poor year as opposed to a good year as the relative
costs would be higher. In 1987 and 1988, 18.8% and 4.1% of peak study
broods adopted a chick, respectively. This result indicates that parents in
a poor year may have been less willing to adopt than those in a good year
as costs were much higher. There may indeed be costs associated with
adoption especially in a poor or average year.
One of the principle causes of mortality among chicks of gull species is attacks or cannibalism by conspecific or congeneric gulls (Hunt and Hunt 1976, Pierotti 1980, 1982a, Fetterolf 1983). Killing behaviour by adult gulls has been attributed to misplaced territorial aggression (Hunt and McLoon 1975, Hunt and Hunt 1976) or an attempt to reduce the fitness of competitors (Davis and Dunn 1976, Pierotti 1980, 1982a). Such killing behaviour has also been attributed to attempts by adults to prevent adoption of unrelated offspring (Mock 1984, Parsons 1971, Hunt and McLoon 1975, Graves and Whiten 1980).

Costs to foster parents, as predicted by the intergenerational conflict hypothesis, were not apparent in either study year. Foster parents may experience reduced survival rates among their own offspring, a need to increase food delivery rates, or decreased growth rates in resident chicks (Nisbet and Drury 1972). In 1987 and 1988, the proportion of chicks fledged by adults that adopted a chick was comparable to adults that did not adopt. However, of six broods that fledged an adopted chick, five lost at least one resident chick. Also, foster parents did not appear to increase food delivery rates although statistical analysis was not possible. These results did not provide direct evidence of any costs to foster parents in terms of increased food delivery rates or decreased survival among their own offspring to 21 days of age.

Although the findings of my study provide no evidence of a cost of adoption to foster parents, it does not preclude the possibility of an intergenerational conflict. Costs to foster parents may be represented in other ways that were not measureable in this study. Chicks in enlarged broods may experience reduced post fledging survival due to lowered growth rates and fledging weights (Nisbet and Drury 1972, Harris and Rothery 1985). Costs associated with the propagation of competing genotypes are inherent in adoption, however, the significance of these
costs is unknown (Graves and Whiten 1980). Also, the effects of adoption on the lifetime fitness of foster parents have not been quantified. Potential costs include reduced future fecundity due to depleted energy reserves in the foster parents. Although immediate costs to foster parents were not apparent in my study, future cost incurred during the post-fledging period and in future breeding seasons may be significant and can not be dismissed until quantitative data are obtained.

Hebert (1988) suggested that costs to foster parents may be minimal if environmental conditions are optimal or the brood was accidentally reduced. Pierotti and Bellrose (1987) suggested that the cost of adoption to foster parents may be relatively small compared with the potential cost of mistakenly driving off its own offspring. If chicks are able to foil the parents ability to distinguish its offspring from unrelated offspring on its territory, then foster parents may incur a higher cost by mistakenly rejecting its own largest offspring.

The results of my study provide some support for the intergenerational conflict hypothesis. However, such support is weakened by small sample sizes and difficulties in obtaining quantitative data. Alternative hypotheses, however, are often less satisfactory. Often adoption is explained in terms of benefits acquired by foster parents, through gained experience or predation dilution. In my study, these potential benefits were not measured directly, however, experience was unlikely to benefit parents that already had chicks in the brood at the time adoption occurred. Predation dilution may represent a benefit to foster parents however, it is unlikely that this benefit would outweigh the cost of raising an unrelated offspring (Hebert 1988). Chicks that were adopted in 1987 and 1988 remained in the foreign brood until fledging and most likely also received post-fledging care. Chicks remained in foreign broods long past the period of high predation risk suggesting that although there
may be benefits associated with adoption, in terms of predation dilution, they are most likely incidental (Hebert 1988).

Kin selection and Reciprocal altruism have often been proposed to explain the occurrence of adoption in gull species. However, adult mortality rates, immigration, emigration, and differential philopatry among the sexes make these explanations unlikely (Chabrzyk and Coulson 1986). Observations of intense fighting and spiteful behaviour between neighboring adults (Tinbergen 1960, Hunt and McLoon 1975, Davis and Dunn 1976, Pierotti 1980, 1981, 1982 a,b) indicates that they are not likely related, or trading altruistic acts, render these explanations relatively unsatisfactory.

Group selection explanations are often unsatisfactory since immigration rates into most Ring-billed gull colonies (see Blokpoel and Haymes 1979, Blokpoel and Courtney 1982) are too high to be compatible with the maintenance of an altruistic allele.

It has also been suggested that adoption occurs as a result of errors in recognition or represents a maladaptation to current high nest densities. Tinbergen (1960) suggested that errors in recognition are most likely to occur when offspring are small and the ability of parents to recognize offspring are not fully developed. In my study, however, adoptions occurred in broods where chicks were up to 17 days old, when errors in recognition were extremely unlikely. Also, in 1987, 18.8% of peak study broods adopted a chick. This frequency is relatively high and not adequately explained by reproductive error or maladaptation.

Summary and Conclusions:

Many attempts have been made to explain the life history traits of gulls as the outcome of a single selective pressure. Observations that Ring-billed gulls are 1) long lived species, 2) allocate resources to
reproduction in such a way that future reproductive success is maximized, 3) show extensive parental care and 4) show delayed reproduction suggest that they are under intense K-selection.

However, Ring-billed gull populations have been increasing dramatically in the Great Lakes area since the early 1960's when availability of suitable breeding habitat and food resources increased (Blokpoel and Tessier 1986). The Great Lakes population of Ring-billed gulls has been increasing by approximately 19.1% annually, apparently growing from a small number of gulls that reinvaded the Great Lakes ecosystem after 1925 and established themselves at scattered localities throughout the Great Lakes (Ludwig 1943). The first notable successes occurred on Lakes Ontario and Erie. By 1960, these populations had expanded to Lakes Huron and Michigan. In 1945, there were approximately 60 pairs of Ring-billed gulls breeding on Lake Erie and by 1967 this number had increased to approximately 6300 breeding pairs (Ludwig 1974). Currently, the Lake Erie population is estimated at approximately 71,000 breeding pairs as of 1984 (Blokpoel and Tessier 1986). The colony in which my study took place has also undergone rapid growth. In 1976, approximately 214 pairs of Ring-billed gulls nested on the Port Colborne breakwater complex. This population remained relatively stable until 1978. By 1980, the population had doubled and by 1984 had reached 1,130 pairs (Blokpoel and Tessier 1986).

This population explosion suggests that conditions in the Great Lakes area have been so favourable that Ring-billed gulls simply cannot fail reproductively and therefore selection pressures acting on parental care quality and parental investment strategies are much less intense. The typical clutch size of Ring-billed gulls is three, suggesting that Ring-billed gulls may represent a relatively r-selected seabird when compared to tropical larids that typically lay only one egg per clutch. On the
selection continuum from R to K, Ring-bill gulls on the Great Lakes may be closer to the r end of the continuum than stable populations would be. Ludwig (1974) suggested that the long life-span and larger typical clutch size of Ring-billed gulls allows the species to be irruptive when conditions are favourable. Dramatic fluctuations in water levels in the Great Lakes constantly alter the amounts of available nesting habitat and prevent Ring-billed gulls from establishing the year to year stability of, and fidelity to, specific breeding grounds (Ludwig 1974). This information suggests that Ring-billed gulls do indeed breed in an unpredictable environment.

Despite recent evidence of strong expansion of Ring-billed gull populations in the Great Lakes area, my data along with that of others show that there remains a selection regime for brood reduction despite the apparent shift from strong k-selection to increased r-selection on the r-k selection continuum.

My data show that the observed intra-clutch egg size differences and hatch intervals established size disparities among chicks in the brood such that parents were able to control the pattern of mortality among their chicks. In a favourable year, parents were more likely to obtain an extra unit of reproductive fitness by successfully rearing the entire 3-chick brook. In a less favourable year, parents were able to increase the probability of survival of larger and older chicks by eliminating the third chick in the brood. Therefore, parents were able to maximize their reproductive success in the face of resource unpredictability.

It is often claimed that starvation is not an important factor with respect to chick mortality in an opportunistic species such as the Ring-billed gull. Ring-billed gulls are known to be highly opportunistic feeders, obtaining food at a variety of foraging areas, including waste dumps and freshly plowed fields. Therefore, in such an opportunistic species, it is
unlikely that food is a limiting factor. However, foraging efficiency can be affected greatly by environmental conditions such as adverse weather or extreme heat especially in the early post hatch period when only one parent is free to forage and chicks have not yet developed the ability to thermoregulate. Blokpoel and Tessier (1986) observed a significant increase in mortality among older Ring-billed gull chicks during a heat wave in 1983. This increase in mortality was attributed to the warming of surface waters which drove fish to deeper strata, beyond the foraging depths of Ring-billed gulls. It is probable that although food itself is not limited, the ability of Ring-billed gulls to forage efficiently may be reduced greatly by adverse environmental conditions.

Adoption in Ring-billed Gulls:

Adoption is often explained in terms of benefits acquired by foster parents. My study, however, provided no evidence of benefits, direct or indirect, to foster parents. Therefore, this theory does not adequately explain the occurrence of adoption in Ring-billed gulls. Explanations based on kin selection or reciprocal altruism are equally unsatisfactory based on observations of aggression and spiteful behaviour between neighboring Ring-billed gulls. Group selection explanations are generally unacceptable since immigration rates are often too high to maintain an altruistic allele in the population.

Therefore, the results of this study lead to 2 possible conclusions; 1) adoption occurs as a result of reproductive error or maladaptation and represents little or no cost to foster parents such that selection does not act against those that adopt or 2) adoption represents an intergenerational conflict with primary benefits received by chicks who seek adoption.
The results of my study suggest that there is indeed a pattern with respect to nests in which foreign chicks are found. They are consistently as large as the largest chick in the brood. My data also suggest that there may be a cost associated with adoption since many of the broods that adopted a chick lost at least one resident. These results, however, were not statistically significant and therefore, did not provide direct evidence of cost to foster parents. Benefits to chicks that were adopted may exist, however, in this study, this is based on the assumption that chicks had virtually no chance of survival in their natal brood.

The recurrent problem with adoption studies is limited sample size. Researchers are limited to observing adoptions that occur naturally in a restricted observation area. Also, the need to minimize investigator disturbance in the study area limits the parameters and characteristics that can be measured.

The results of my study are relatively ambiguous as to whether 1) adoption is adaptive from a chick perspective and selection favours disadvantaged chicks that seek adoption, 2) adoption represents a cost to foster parents and therefore selection acts against parents that adopt, or 3) adoption occurs due to high nest density and is under no selective pressure from either a chick or foster parents perspective.

Adoptions are usually relegated to the category of reproductive error. However, rather than resort to this unsatisfactory non-explanation, the results suggest that further research, into the area of cost and benefits to foster parents and adopted chicks respectively, is warranted.


Appendix 1. Intra-clutch hatch intervals (days) of 1988 peak control clutches. Sample sizes vary as the number of clutches for which the hatch interval from egg 1-2, egg 2-3 and egg 1-3, were recorded with maximum accuracy, differed. Hatch intervals recorded with maximum accuracy only were included in the data analysis.
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Appendix 2a. Ages of chicks at death or disappearance with respect to hatching order in 1987 peak control broods. Values with * represent those values used in the calculation of the mean age first hatched chicks. Values with + represent those used in the calculation of the mean age of second chicks at death. All remaining "Chick 1 + 2" values represent first or second chicks that were indistinguishable.
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Appendix 2b. Ages of chicks at death or disappearance with respect to hatching order in 1988 peak control broods. Values with * represent those values used in the calculation of the mean age of first hatched chicks. Values with + represent those used in the calculation of the mean age of second chicks at death. All remaining "Chick 1 + 2" values represent first or second chicks that were indistinguishable.
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Appendix 2c. Ages of chicks at death or disappearance with respect to hatching order in 1988 peak experimental broods. All first and second chicks were distinguishable.
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