

PARENTAL INVESTMENT IN HERRING GULLS: CLUTCH APPORTIONMENT AND CHICK SURVIVAL¹

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Abstract. Patterns of parental investment were studied in Herring Gulls (*Larus argentatus*) during the summer of 1984 at a colony on Kent Island, New Brunswick. Egg loss, egg mass, chick mass, and tarsometatarsus length of chicks at hatch were recorded for three- (C3) and two-egg clutches (C2). In C3 clutches C-eggs were significantly lighter than A- and B-eggs, and in C2 clutches B-eggs were significantly lighter than A-eggs. B-eggs in C3 clutches were significantly heavier than C2 B-eggs. Egg loss was greatest in C2 clutches. A- and B-chicks hatched significantly heavier, and survived significantly longer than C-chicks. In C2 broods A-chicks hatched significantly heavier than B-chicks, but both chicks had similar average survivorship probabilities/day (ASP/D). A- and B-chicks and C3 broods had significantly higher ASP/D compared to the C-chick. Only the A-chick in C3 broods exhibited a significant correlation between mass at hatching and survivorship. A significant correlation of tarsometatarsus length at hatch with survivorship was observed for C-chicks. These results suggest that parental investment patterns vary with clutch size and clutch mass.

Key words: Herring Gull; *Larus argentatus*; parental investment; clutch apportionment; egg mass; hatchling mass.

INTRODUCTION

Parental investment (PI) as defined by Trivers (1972) is, "... any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parents' ability to invest in other offspring." In birds, "other" offspring may be offspring from a future reproductive effort, or contemporaneous members of a clutch or brood. The cost to future offspring of current investment levels is difficult to quantify, and may be compounded by factors such as female age and/or breeding experience (Davis 1975, Coulson and Horobin 1976, Mills 1979, Thomas 1983, Nisbet et al. 1984), and date of laying (Parsons 1972, Mills 1979).

It may be assumed that factors which contribute to the effects of differential investment between seasons are constant within a clutch. Consequently the cost of increased investment in one egg or chick at the expense of another may be best examined by comparing relative parameters of investment within a clutch or brood.

Egg mass may vary within a clutch (see Clark and Wilson 1981 for a review). In larids, egg mass

generally decreases with laying order (e.g., Nisbet and Cohen 1975, Parsons 1975a, Hahn 1981). Several researchers have investigated factors affecting decreasing egg mass with laying order in larids (Parsons 1970, 1975a; Mills 1979; Thomas 1983; Quinn and Morris 1986). Although a depletion of resources available to females during egg laying may result in decreasing egg size, there is also evidence indicating that females may control egg size regardless of the amount of nutrients available. Firstly, female Herring Gulls (*Larus argentatus*) can lay more than three eggs (Parsons 1975b). Also, Parsons (1976) experimentally induced female Herring Gulls to lay larger C-eggs (third laid) by removing the A-egg (first laid) when it was laid. Parsons (1972) concluded that the proximal cause of the smaller C-egg is the onset of incubation which reduces albumin secretion.

Since egg size may be controlled by the female and chick survival is positively correlated with egg size (Parsons 1970, Nisbet 1973, Lundberg and Väisänen 1979), it may be hypothesized that if adequate resources are available, a female will invest proportionately more in her eggs, especially the C-egg. The purpose of this study was to examine parental investment patterns within clutches of three and two eggs by comparing egg and chick masses as a function of clutch size and clutch mass, and their subsequent effects on egg and chick survivorship.

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TABLE 1. Mean fresh egg masses ($g \pm SE$) of eggs in three-egg ($n = 138$) and two-egg clutches ($n = 160$). Means, within a clutch size, followed by a similar letter are not statistically different.

Clutch size	Egg		
	A	B	C
3	90.82 \pm 0.60 ^A	89.33 \pm 0.51 ^A	81.32 \pm 0.57 ^B
2	88.13 \pm 0.55 ^A	83.23 \pm 0.50 ^B	

METHODS AND MATERIALS

The study was conducted on Kent Island, Bay of Fundy, New Brunswick, Canada (44°35'N 66°45'W). The Herring Gull colony (ca. 2,000 pairs, Hébert 1985) was situated at the southern end of the island (see Paynter 1949), and was searched daily for nests from 7 May through 18 June, and on 20 and 22 June. Nests initiated in the study area were marked with numbered and/or lettered wooden stakes. As the colony was visited daily it was possible to determine the identity of eggs within the laying sequence. Each egg was marked either A, B, or C on the blunt end using a nontoxic felt marker. Fresh eggs were weighed to the nearest 0.5 g or 1.0 g using a 100-g or a 300-g Pesola spring scale, respectively. Mean fresh egg masses in two- and three-egg clutches were compared within and between groups using *t*-tests. When sample sizes were severely disparate or variances were unequal comparisons were made using a Mann-Whitney *U*-test (Zar 1984).

The relationship between egg mass and clutch mass was examined further, in three-egg clutches, by grouping clutches into three classes (light, medium, and heavy) based on total clutch mass. Sample sizes for the three groups were made as equal as possible while still keeping all clutches of a particular total mass within one group. The mean mass of A-, B-, and C-eggs was then calculated for each group.

Chicks at hatching were weighed to the nearest 0.5 g using a 100-g Pesola spring scale, or to the nearest 1.0 g with a 300-g Pesola spring scale. Tarsometatarsus (heel to tip of middle toe) lengths were measured to the nearest 0.5 mm using cal-

ipers or a steel ruler. Chicks were banded at hatching with colored plastic bands and color-marked with nontoxic felt markers. U.S. Fish and Wildlife Service aluminum bands were added later. Chick survivorship probabilities were estimated and analyzed using the Mayfield (1975) method. All statistical tests used a $P \leq 0.05$ level of significance.

RESULTS

The first egg was found on 18 May. Clutch initiation peaked on 4 June, and by 8 June 75.3% of all two- and three-egg clutches had been initiated ($n = 320$).

EGG MASSES

Mean fresh masses of A-eggs in two-egg clutches (C2) were significantly heavier than B-eggs ($n = 160$) ($t = 12.56$, $df = 159$, $P < 0.001$; Table 1). In three-egg clutches (C3) ($n = 138$) the mean egg mass of A- and B-eggs were significantly heavier than that of C-eggs (ANOVA, $F = 50.07$, $df = 3,410$, $P < 0.001$; A vs. C, SNK, $q = 16.9$, $P < 0.001$; B vs. C, SNK, $q = 14.3$, $P < 0.001$; Table 1). A-eggs in C2 and C3 clutches had a similar mean fresh egg mass, while B-eggs in three-egg clutches were significantly heavier than those in two-egg clutches ($t = 8.43$, $df = 296$, $P < 0.001$).

CLUTCH MASS

The difference in mass between A- and B-eggs was significantly greater in moderate weight clutches compared to light clutches ($U = 1,338$, $P < 0.05$; Table 2). Although not significant ($U =$

TABLE 2. Mean egg masses ($g \pm SE$) from light ($n = 40$), moderate ($n = 54$), and heavy ($n = 44$) clutches.

Clutch type	Mean clutch mass	Egg		
		A	B	C
Light	241.16 \pm 1.25	83.28 \pm 0.71	82.69 \pm 0.49	75.21 \pm 0.75
Moderate	262.41 \pm 0.66	91.52 \pm 0.45	89.21 \pm 0.38	81.49 \pm 0.50
Heavy	281.19 \pm 1.55	96.82 \pm 0.85	95.51 \pm 0.64	88.06 \pm 1.12

TABLE 3. Mean hatchling mass (g \pm SE) and mean tarsometatarsus length (mm \pm SE) at hatch for Herring Gull chicks in three- and two-chick broods.

Brood type	Chick	Hatch mass	<i>n</i>	Tarsometatarsus length	<i>n</i>
3-chick	A	63.32 \pm 1.32	14	60.96 \pm 0.76	13
	B	63.42 \pm 1.66	14	59.85 \pm 0.52	14
	C	57.00 \pm 2.08	14	57.00 \pm 1.19	11
2-chick	A	61.45 \pm 0.85	28	58.90 \pm 0.43	26
	B	57.59 \pm 0.80	28	57.90 \pm 0.67	26

1,415, $P < 0.10$) the difference in mass between A- and B-eggs was larger in moderate weight clutches compared with heavy clutches (Table 2). B-eggs were significantly heavier than C-eggs in the three classes of mean total clutch mass, but more so in moderately heavy clutches (Table 2). There was a significant difference in the proportion of B-eggs that were heavier than A-eggs between the three classes of clutch mass ($\chi^2 = 6.68$, $df = 2$, $P < 0.05$). B-eggs were more often heavier than A-eggs in light clutches compared to moderate clutches ($\chi^2 = 4.70$, $df = 1$, $P < 0.05$). There was also a trend for B-eggs to be heavier than A-eggs more often in heavy clutches compared to moderate weight clutches.

EGG LOSS

In two-egg clutches, significantly more A- than B-eggs were lost (due primarily to intraspecific predation) within 5 days of laying ($\chi^2 = 5.62$, $df = 1$, $P < 0.025$). There was no difference in the proportion of A-, B-, or C-eggs that were lost in three-egg clutches ($\chi^2 = 2.33$, $df = 2$, $P > 0.25$). Egg loss was highest for A-eggs in both C2 (37/141) and C3 (12/94) clutches, but significantly higher in C2 clutches ($\chi^2 = 5.40$, $df = 1$, $P < 0.025$). There was no significant difference in the proportion of B-eggs lost between two- (20/141) and three-egg (8/94) clutches. Overall, egg loss within 5 days of laying was significantly greater in C2 compared to C3 clutches ($\chi^2 = 12.71$, $df = 2$, $P < 0.001$).

HATCHING SUCCESS AND HATCHLING MASS

Mean hatching success (no. eggs hatched/clutch) in two-egg nests (0.95 ± 0.09 ; $n = 102$) was just over half that of three-egg nests (1.73 ± 0.16 ; $n = 49$; $t = 4.84$, $df = 149$, $P < 0.001$). In C2 broods A-chicks hatched significantly heavier than B-chicks ($t = 19.63$, $df = 27$, $P < 0.001$), and also had significantly longer tarsometatarsi ($t = 3.26$, $df = 25$, $P < 0.005$; Table 3). In C3

broods A- and B-chicks hatched significantly heavier than C-chicks (A vs. C, $U = 145.5$, $P < 0.025$; B vs. C, $U = 146.5$, $P < 0.025$). C-chicks also had significantly shorter tarsometatarsi at hatch compared to A- ($U = 116.5$, $P < 0.005$) and B-chicks ($U = 119$, $P < 0.025$). Between groups, the respective A-chicks had similar masses at hatching. B-chicks in C2 broods hatched significantly lighter than their C3 counterparts ($U = 283.5$, $P < 0.005$; Table 3). Finally, with respect to tarsometatarsal lengths at hatch, all chicks were similar except the C2 B-chick which had significantly shorter tarsometatarsi than C3 B-chicks ($U = 254$, $P < 0.05$; Table 3).

CHICK SURVIVORSHIP

The average survivorship probability/day (ASP/D) for A- and B-chicks in C2 broods was the same (Table 4). In C3 broods there was a significant difference in the ASP/D of A-, B-, and C-chicks ($\chi^2 = 13.09$, $df = 2$, $P < 0.005$). C-chicks in C3 broods had a significantly lower ASP/D than A-chicks ($\chi^2 = 10.51$, $df = 1$) and B-chicks ($\chi^2 = 10.12$, $df = 1$). A-chicks from C2 and C3 broods had similar ASP/D (Table 4).

TABLE 4. Average survivorship probability/day (ASP/D) up to 5 days posthatch for Herring Gull chicks in three- and two-chick broods.

	Chick	3-chick brood (<i>n</i> = 15)	2-chick brood (<i>n</i> = 28)
Total no. of days	A	68	108
	B	65	83
	C	33	
No. of chicks disappearing	A	5	12
	B	5	15
	C	12	
ASP/D	A	0.92	0.88
	B	0.92	0.81
	C	0.63	

Note: ASP/D values were calculated using Mayfield's (1975) method and were compared using the total estimated survival and mortality values, which are a function of the ASP/D values.

TABLE 5. Spearman's rank correlations between egg mass (EMS), hatch mass (HMS), tarsometatarsus length at hatch (TAR), and the number of days posthatch (up to 40 days) a chick survived (DAYS) for Herring Gull chicks in three- and two-chick broods. Numbers in parentheses are sample sizes. Coefficients not shown are not significant ($P > 0.05$).

Brood type	Chick	EMS vs. HMS	HMS vs. TAR	HMS vs. DAYS	TAR vs. DAYS
3-chick	A	0.72 (14)		0.57 (15)	
	B	0.81 (13)	0.74 (14)		
	C	0.88 (12)	0.64 (11)		0.58 (11)
2-chick	A	0.55 (28)			
	B	0.81 (27)	0.63 (25)		

B-chicks from C3 broods had a higher ASP/D than did those from C2 broods, and this difference approached significance ($\chi^2 = 3.55$, $df = 1$, $P < 0.10$).

Hatchling mass was positively correlated to egg mass for all eggs in C2 and C3 clutches (Table 5). Tarsometatarsus lengths at hatch were also correlated with hatchling mass, but only significantly so for B-chicks in C2 broods, and B- and C-chicks in C3 broods. Survivorship was positively correlated with hatchling mass for A-chicks in C3 broods, and nearly so for C-chicks in C3 broods ($P = 0.065$). Finally, survivorship of the C-chick was positively correlated with tarsometatarsal length at hatch (Table 5).

Fledging success was low in both groups, and statistical analysis was not attempted. However, C2 broods had a lower mean fledging success (0.21 ± 0.09 chicks/nest) compared to C3 (0.33 ± 0.21 chicks/nest) broods.

DISCUSSION

Parental investment can be broken down into several distinct and related components. In this study we examined clutch size, apportionment of clutch mass, egg mass, and their effects on egg and chick survivorship.

Chick survivorship is correlated with egg size in a number of species (e.g., Parsons 1970, Nisbet 1973, Lundberg and Väisänen 1979, O'Connor 1979). If offspring fitness rather than the number of offspring has been optimized by natural selection (Brockelman 1975) we hypothesize that,

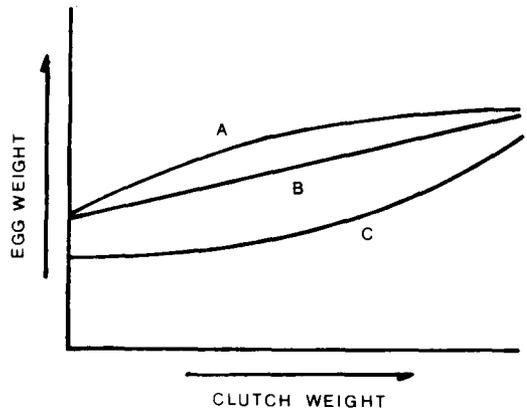


FIGURE 1. Model approximating the pattern of clutch apportionment for eggs in three-egg clutches.

given a set clutch size, a female should maximize her investment in each egg. That is, the more energy a female has available for egg production, the more she should invest in each egg, so that survival of progeny is increased. In this study we did find an increase in egg mass with an increase in clutch mass, but the apportionment of the extra energy varied according to the position of the egg in the laying order and clutch mass.

The difference in mass we observed for A-, B-, and C-eggs in light, moderate, and heavy clutches can be used to produce a model of clutch apportionment for Herring Gulls laying three-egg clutches (Fig. 1). In light clutches, Herring Gulls invest similar amounts of energy in the A- and B-egg, at a cost to the C-egg. Investing more in the A- or B-egg would presumably reduce the amount of energy remaining for the C-egg, possibly below the level required to produce a viable C-egg (Parsons 1975a).

In clutches of moderate weight, the B-egg is at a disadvantage because of the proportionately greater increase in the mass of the A-egg. The B-egg may, however, benefit by having a shorter incubation period. This could minimize the size and hatching discrepancy between the A- and B-chick, and thus put the B-chick in a more favorable position should the A-chick be lost.

In heavy clutches, female Herring Gulls again apportion similar amounts of energy into the A- and B-eggs, but increase the proportion devoted to the C-egg. Increasing the apportionment to already heavy A-eggs may not significantly increase the fitness of the A-chick (Smith and Fretwell 1974), and may significantly reduce the fitness of the C-chick, and possibly the B-chick.

Likewise the B-egg has an advantage over the C-egg (both in mass and hatching date), regardless of clutch mass. Hence a female Herring Gull may benefit more by investing proportionately more in the C-egg rather than the B-egg. Such a strategy would increase the C-chick's probability of survival, while maintaining the B-chick advantage (as a result of hatching heavier and before the C-chick).

As with other studies (Parsons 1970, Davis 1975, Thomas 1983), we found a positive correlation between hatch mass and chick survivorship, but only significantly so for A-chicks in three-chick broods, and nearly so for C-chicks ($P = 0.065$). A significant correlation between hatch mass and survivorship for B-chicks may be obscured by the effects of asynchronous hatching and was possibly confounded, in this study, by an extended period of fog which occurred during peak hatching (Hébert 1987). Furthermore, since B-chick hatchling masses were similar to those of A-chicks it is possible that survivorship in the B-chick depends more on the presence of the A-chick rather than hatchling mass (Graves et al. 1984).

Heavier chicks hatch from heavier eggs, and hence have more stored energy (Parsons 1970, Ricklefs et al. 1978), which results in an increased probability of survival (Parsons 1970, Nisbet 1978, this study). That the "extra" mass of the A-egg indicates an increase in mass of the A-chick, and not its size per se, is evidenced by the fact that neither its egg or hatchling mass were correlated to tarsometatarsal length at hatch. The extra reserve is important during the transition period when the parents switch from incubating to brooding (Kadlec and Drury 1968; Parsons 1970, 1972).

Tarsometatarsus lengths at hatch for the B- and C-chicks were correlated to hatch weight, and thus may indicate a chick counterstrategy (Trivers 1974) to the parental strategies of asynchronous hatching and/or inferior size. Our observations of a significant correlation between tarsometatarsus length at hatch and survivorship of the C-chick, as well as a trend in the same direction for the B-chick support this suggestion. The mechanism(s) involved during embryonic development in channelling energy to produce longer legs is, to our knowledge, unknown. However, Parsons (1970) and Ricklefs et al. (1978) have observed that the C-chick is able to conserve more lipids during development compared

to the A- or B-chick. Hence, it may be possible that longer tarsometatarsi at hatch is a chick strategy and not a parental manipulation. The need for nutrient reserves in the C-chick, although important, may not be at a premium as in the A- and possibly the B-chick. However, well-developed tarsometatarsi may have an adaptive significance, since at about the time the C-egg hatches, the parents are feeding the chicks away from the nest (Graves et al. 1984, pers. observ.), putting the C-chick at yet a further disadvantage. This disadvantage would be reduced if C-chicks hatched with longer tarsometatarsi, and could thus locomote more readily.

That PI varies between Herring Gull pairs is easily observed in the variation of clutch size, and their respective hatching success rates. In this species considerable evidence suggests that parents with three-egg clutches are, on average, more successful than those with two-egg clutches (e.g., Harris 1964, Kadlec and Drury 1968, Parsons 1975b, this study). In this study egg loss (due to predation), within 5 days of laying, was greater in two-egg clutches compared to three-egg clutches. This is due to the fact that pairs with two-egg clutches are generally less attentive than pairs with three-egg clutches (Beers 1961, Brown 1967). As a result of the higher rate of egg loss, hatching success was also lower for Herring Gull pairs with two-egg clutches.

Clutch apportionment patterns in two-egg clutches were similar to that in three-egg clutches. However, unlike three-egg clutches, the mass at hatching of A-chicks in two-egg clutches did not correlate significantly with survivorship. Smaller clutches are, in general, laid by younger less experienced birds, as evidenced by the higher proportion of egg loss and the lower hatching and fledging success observed in this and other studies (e.g., Coulson and White 1958, Coulson and Horobin 1976). Thus it may be argued that younger birds which lay large eggs are not able to profit consistently from this increased investment. Also, the effectiveness with which young birds make the transition from incubation to brooding may vary to such an extent as to mask any benefits that might result from laying heavier eggs.

As with B-chicks from three-chick broods, an increase in the hatching mass of B-chicks in two-chick broods did not affect survivorship. Also, tarsometatarsus length at hatch was positively correlated with hatchling mass, but not to sur-

vival. Presumably the same arguments put forth for B-chicks in three-chick broods are also in effect here for B-chicks in two-chick broods.

In summary, the results of this study indicate that female Herring Gulls may vary proportionate investment levels within a clutch according to clutch mass and size, and the position of the egg in the laying sequence. Chick strategies, with respect to energy reserves and tarsometatarsal length at hatch, may serve to reduce the effects of inefficient brooding and parental manipulation in terms of egg size and hatching asynchrony respectively.

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