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**EGG- AND CLUTCH-SIZE VARIATION, AND CHICK  
GROWTH IN LESSER BLACK-BACKED GULLS  
LARUS FUSCUS: ADAPTATION OR CONSTRAINT?**

**BY**

**DAVID ANDREW LAWSON.**

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M.Sc. Advanced Course in Ecology.

(i)



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## SUMMARY.

- (1). The first part of this study investigated separately the effects of both position in the nest (i.e. laying order) and clutch size upon egg volume, incubation period and hatching success of eggs from a total of 89 nests of the Lesser-black Backed Gull, *Larus fuscus* L., breeding on Walney Island, U.K.
- (2). Significant decreases in egg volume were found to occur from a- to b-, b- to c-, and a- to c-eggs in 3-egg clutches, but not between volumes of a-eggs from clutches containing 1, 2 or 3 eggs.
- (3). Egg incubation periods, with respect to laying order, also differed significantly from each other in 3-egg clutches, such that the time between laying and hatching decreased from a-, through b-, to c-eggs.
- (4). A lower proportion of c-eggs hatched successfully, in relation to a- and b- eggs also from 3-egg clutches. Moreover, single a-eggs hatched successfully less often than those within 2- and 3-egg clutches.
- (5). Following hatching of eggs, the second part of the study investigated chick growth, in relation to position in the brood, brood size, and clutch size.
- (6). Within 3-chick broods, a-, b- and c-chicks showed the same pattern of growth.
- (7). Among 2-chick broods, no difference was found in growth parameters of broods from nests which had originally contained clutches of 2, and those which had originally contained clutches of 3 eggs.
- (8). Mean chick growth within a brood was no different among nests containing 1, 2 or 3 nestlings.
- (9). These results are discussed in terms of the current debate concerning whether egg-sizes and clutch sizes in birds are adaptive or constrained.

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Many thanks to the Cumbria Wildlife Trust, and in particular to Bill Makin (warden of South Walney Nature Reserve) for permission to work upon the gull colony. Thanks also to Dr. K. C. Hamer for his guidance throughout the fieldwork and writing-up periods of this study.

## CHAPTER 1: INTRODUCTION.

The Laridae is a cosmopolitan family containing approximately 90 species of small to large charadriiform seabirds worldwide, constituting between 11 and 17 genera. This includes the 38-45 species of gulls (subfamily Larinae) and 32 species of terns (Sterninae). Members of the family tend to possess coloration which is largely black and/or white, and are migratory. In terms of breeding, species are monomagous, and being gregarious, nest colonially either on the ground, in cliffs, or in trees. Natural food sources include a variety of aquatic animals (fish, crustaceans, molluscs, etc.) and carrion.

For many larid species, it is typical for breeding females to lay a modal clutch size of three eggs. Furthermore, within such a clutch, eggs often display a general trend for decreasing mass and volume with laying order (e.g. Nisbet and Cohen 1975, Parsons 1975a, Hahn 1981). In particular, such decreases are most apparent with respect to the third-laid, or "c-egg" within the clutch. For example, in a study of Herring Gull (*Larus argentatus*) clutches, whilst the second-laid b-egg was rarely more than 2% smaller than the first laid a-egg, the last-to-arrive c-egg was on average 11% smaller than the latter (Parsons 1972). For the Lesser-Black-backed Gull (*Larus fuscus*), which also lays a modal clutch size of three eggs (Bolton 1991), this difference has been recorded as 9.4% (Paludan 1951), for the Laughing Gull (*Larus atricilla*) as 7.0% (Preston & Preston 1953), and, for the Black-legged Kittiwake (*Rissa tridactyla*) as 7.3% (Coulson 1963). Similar size discrepancies with respect to the c-egg have also been recorded more recently in, for example, the Glaucous-Winged Gull (Reid 1987), Western Gull *Larus occidentalis* (Pierotti & Bellrose 1986, Sydeman & Emslie 1992), and Common Terns *Sterna hirundo* (Bollinger 1994). However, it is not known whether these within-clutch differences are invariable attributes of each species, or are effected by other factors such as female nutrient status (the use of supplementary feeding experiments having yielded disparate results: see Bolton, Houston & Monaghan 1992).

Some larid species also display marked variation between conspecifics in the number of eggs laid: whilst three-egg clutches may be the most common, and whilst

nests with a greater complement than this tend to be rare, there can be nevertheless, frequent examples of completed clutches which contain only two, or even one single egg. With respect to the adaptive significance of this variation, it is possible that a female matches her clutch size to parental ability to provide food for the resulting chicks (see Lack 1968, Ricklefs 1973). Also, because, proximately, egg production is related to the level of female pre-breeding body protein reserves (Houston *et al* 1983, Bolton *et al* 1992), this suggests that the latter provides a good indication of later ability to provision for offspring (this indication could possibly take into account not only female, but also male ability at food provisioning, because his courtship feeding of the female will contribute to her level of reserves).

The variability of clutch size may have important implications for studies examining the effects of position within the clutch. For example, taking a sample of nests, each of which contains either a 1-, 2- or 3-egg clutch, it is possible to obtain data for a-eggs from nests containing 1, 2, and 3 eggs, whilst for b-eggs the choice is limited to 2- and 3-egg clutches, and for c-eggs data can only be obtained from nests containing the full modal complement. However, in many studies where comparisons of egg size are made with respect to laying sequence, it is often not clearly stated whether the researchers limited themselves solely to three-egg clutches, or in fact used, for example, measurements from a-eggs in various clutch sizes combined. As previous work has found that, on average, females which lay smaller clutches also lay smaller eggs (Parsons 1976, Houston *et al* 1983), then clearly, such merging of data across different clutch sizes could potentially affect the integrity of the results.

Similarly to volume, within-clutch incubation periods of eggs have also been noted as decreasing with laying sequence. Indeed, this is thought to be related to egg size, so that the c-egg in particular displays the greatest reduction in this parameter (Parsons 1972, 1976), although a lesser decrease from a- to b-eggs has also been documented (Hebert & Barclay 1988). However, the possibility of clutch size also influencing incubation periods appears to have received little attention.

In contrast, there is known to exist a significant negative relationship between clutch size and the hatching success of eggs within a nest (Paynter 1949, Brown 1967, Parsons 1975b, Hebert & Barclay 1988), whilst laying sequence apparently has no effect (Parsons 1970, Bolton, Houston & Monaghan 1992).

This study, involving fieldwork conducted upon the Lesser Black-backed Gull (*L. fuscus*) on Walney Island, U.K, divides into two parts. The first of these investigates the effects of laying sequence and clutch size (in isolation from each other) upon various egg parameters: initially, within-clutch differences in egg size, incubation period and hatching success are examined with respect to laying order, whilst controlling for clutch size (so that, although a-, b-, and c-eggs from 3-egg clutches will be compared with each other, the effect of laying sequence upon eggs in 2-egg clutches will be analysed separately). Next - and contrastingly - whenever possible, the study also investigates between-clutch differences in these parameters, controlling for laying sequence (so that, for example, lone a-eggs representing a complete clutch are compared with a-eggs from clutches containing 2 and 3 eggs in total).

Following hatching of eggs, there is considerable debate concerning the nature of subsequent chick growth. Ricklefs (1973) asserted that the latter generally takes place at some physiological maximum rate, determined by for instance, the rate of cell division. In this scenario, chick growth is inflexible, and virtually unaffected by external factors such as the amount of food given to the young bird, except in cases of starvation. Therefore, variations between individuals should be small.

In contrast, a second possibility is that chicks are in fact flexible (up to some maximum rate) and display large variations in growth. This is supported by empirical data concerning intraspecific variation in growth in several species (Klaassen *et al* 1992, Kersten & Brenninkmeijer 1995), although few studies have examined the variation among members of individual broods.

Therefore, whilst examining chick growth with respect separately to position in the clutch, brood-size, and clutch-size, the second part of this study hopes to make a contribution to the above debate.

## CHAPTER 2: MATERIALS AND METHODS.

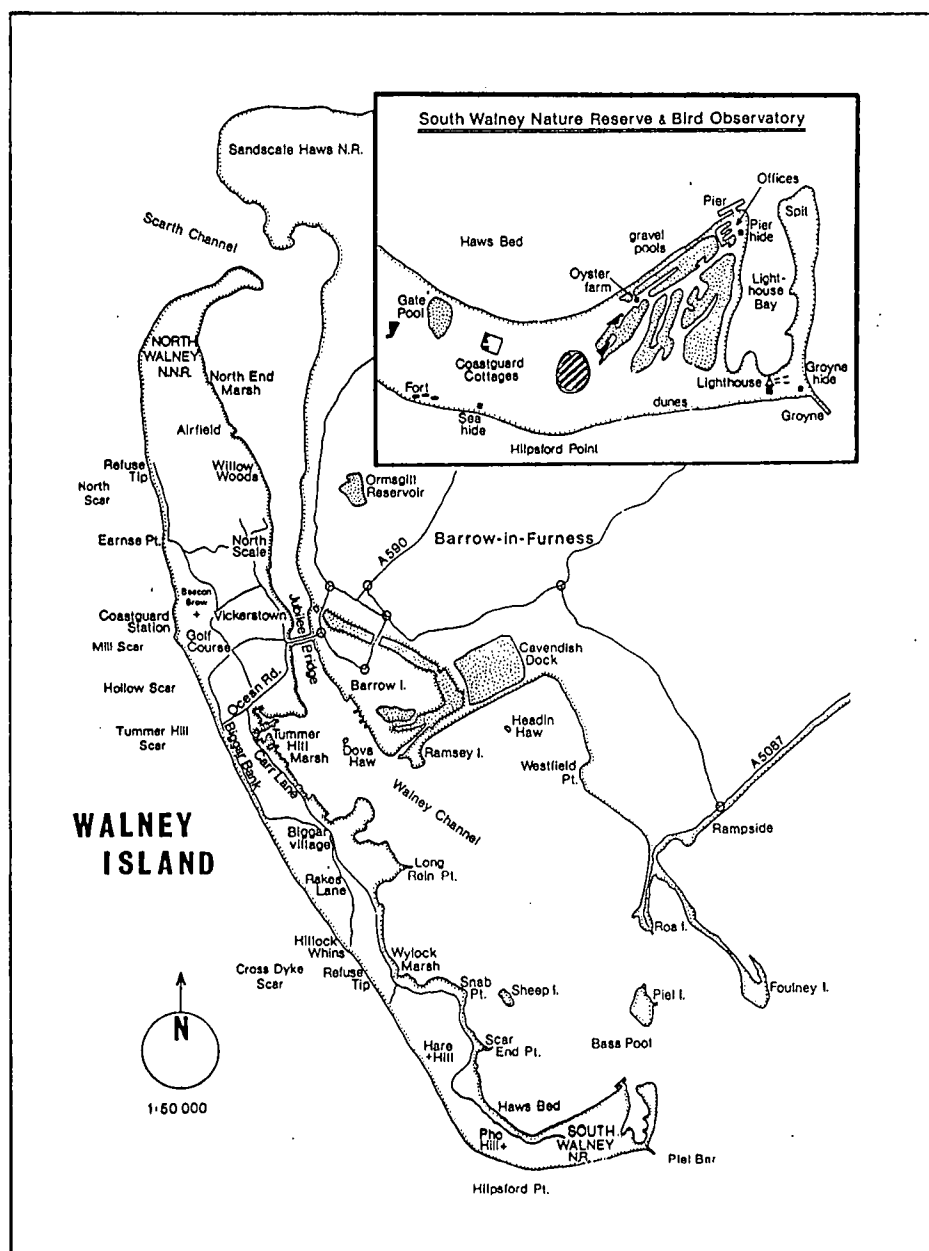
### Section One: Study site description.

Walney Island, Cumbria, U.K. is situated at the northwest corner of Morecambe Bay, and lies adjacent to the southwestern extremity of the mainland Furness Peninsula. Upon this low lying island there exist two nature reserves, both owned and managed by the Cumbria Wildlife Trust, but occupying areas located at opposite ends of the landmass.

The South Walney Nature Reserve is inhabited (in fact dominated) by a very large, easily accessible (and, indeed, much studied), mixed breeding colony of *L. fuscus* and *L. argentatus*, within which all fieldwork was conducted, between the dates of 9th. May and 21st. July 1995.

Although some pairs of gulls could be seen nesting upon the east-facing shingle beaches, the current study focused upon nests of *L.fuscus* within the main body of the colony. This was located further back from the immediate coastline, occupying land with topography similar to that of a dune system, and a surface cover consisting primarily of a patchwork containing bare sandy soil, short grassy turf, dense clumps of Nettle (*Urtica dioica* L.) and stands of Bracken (*Pteridium aquilinum* L.), together with abundant examples of Ragwort (*Senecio jacobea* L.). Specifically, fieldwork was conducted within a relatively small area designated by the reserve warden (see overleaf: Figure 1).

**Figure 1.** Map of Walney Island (inset: South Walney Nature Reserve, with extent of study site marked approximately by red hatching).



## **Section Two: Fieldwork techniques & data acquisition.**

At the beginning of the study period, the first visit to the colony revealed that breeding pairs of *L. fuscus* were at various stages of nesting, and whilst nests with no eggs present could still be located, more commonly the adults were already in possession of 1-, 2-, and frequently 3-egg clutches. Combined with the fact that the number of nests available for study was limited by the extent of the designated area, it was, therefore, not possible to restrict the study only to following the fate of clutches which had yet to be laid, or which had only one egg already present (and with which the laying order of the subsequent eggs could be directly established). Therefore, nests already containing clutches of 2 and 3 eggs were also included in the research.

With this in mind, overall a total of 89 nests, as selected for study, encompassed the above-mentioned range of clutch sizes. Each nest was marked using a numbered, 3-foot tall garden cane, painted white at the tip to increase visibility. This was pressed firmly into the sandy substrate, at a distance of approximately eighteen inches to the north of the nest.

Following the marking of the nest itself, each egg already present was in turn removed from the nest, and with the aid of a pair of calipers, both its length (diameter from pole to pole on the long axis) and breadth (greatest diameter at right angles to the long axis) were measured and recorded to the nearest 0.1mm. Egg volume was later calculated from the following equation (Harris 1964):

$$\text{Egg volume (cm}^3\text{)} = 0.000476 \times \text{length (mm)} \times \text{width}^2 \text{(mm)}.$$

Before replacement into the nest, using an indelible pen, the nest number was also written upon the egg itself (so that, if eggs were removed, or even taken into neighbouring study clutches, this would have been apparent). More importantly, however, each egg was also given a letter to identify it within the clutch. For nests with only one egg present, this egg was given the letter A to signify it was the first to be laid. However, for eggs already in clutches of more than one at the first visit to the nest, laying order is unknown. Such eggs were therefore labelled X and Y (2 eggs present), or X, Y and Z (3 eggs present), which was intended to imply nothing about

their respective positions within the laying order of the clutch, but simply allowed one to be distinguished from the other. (Many such eggs were nevertheless assigned an order within the laying sequence following hatching: where laying orders were unambiguous, results indicated that in no single clutch did a c-egg hatch before the b-egg, nor the latter before the a-egg. Therefore, similarly to Bolton (1991), where eggs hatched asynchronously with respect to nest visits, laying order was implied for previously uncategorized eggs, using the assumption that the first to hatch was also the first to be laid, and so on).

Subsequent visits to marked nests during the period of egg laying were conducted at intervals of between two and three days. Because two new eggs were rarely laid into any one such nest between checks, this meant that, for unstarted and incomplete study clutches it was possible to determine the order of eggs laid after the initial marking of the nest. Therefore, on such repeat visits, a newly arrived egg - if present - was subjected to exactly the same procedure as described above, except that its position in the clutch was beyond doubt, and it was therefore labelled simply either A, B, or C, according to whether it was the first, second or third to be laid.

The exact time at which an egg was laid is of course unknown. However, for eggs not already present at the time when a nest was first marked, it was decided to estimate a laying date (to the nearest half-day) by taking it to be the mid point between the date of the first visit when the egg was present, and the date of the previous visit when it was not.

Also, each time a clutch was visited, any previously marked egg that had now disappeared from the nest was recorded as having done so. Similarly, records were made of eggs that were still present, but which were broken or otherwise obviously damaged.

Hatchlings began to appear in study nests from the 28th. May onwards. Similarly to egg laying, in each case it is not known exactly when a chick hatched, but only which two visits it took place between. Therefore, hatch date was estimated (also to the nearest half day) in the same manner as laying date. For example, if a chick was present on day 34, and not on day 30, then hatch date would be day 32. However, upon previously visiting a nest, if an egg was found to be pipping, this was entered into the record for that particular visit. It is therefore possible to refine the

estimate for hatch date in the cases of such eggs, relative to those for whom signs of hatching were not observed. For instance, if, in the above example the egg was recorded as pipping on day 30, then the estimated hatch date would be brought forward from day 32 (which is what a still intact - and therefore less advanced - egg would be assigned) to day 31. At this point, for every egg where it proved possible to estimate both laying and hatching dates, an approximate incubation period could therefore be obtained.

With respect to the chicks themselves, when an individual was encountered within a study nest for the first time, a number of standard measurements were taken. Initially, the young bird was placed into a draw-corded bag, and weighed (to the nearest 5 grams) using a Salter 1 Kg. sprung scale. It was desirable to take this measurement first, as some chicks often regurgitate considerable amounts of food after being handled for a period of time, and if they did this before weighing, whilst others did it only afterwards (or not at all), then this would generate greater variability in the data.

Secondly, using the same calipers employed previously for determining egg lengths and breadths, measurements (to the nearest mm) of bill and tarsus length were taken. Specifically, the bill was measured as the length of the upper mandible in a straight line (chord of the culmen) from its tip to the edge of the feathering at the base of the skull, whilst the tarsus was taken as the length from the angle (posterior) of the intertarsal joint to the base of the last complete scale (anterior) before the divergence of the toes (see Thomson 1964).

Finally, before being replaced into the nest, the chick was tagged by placing a small piece of white electricians insulating tape around the right leg, above the ankle. The tape was cut so that it possessed two fold over "tabs". After placing it around the leg, the two ends of the tape had their sticky sides facing each other, and hence, when pressed together they bonded strongly. The two tabs then folded over this bond to further enhance security. After checking the tag was not too tightly fastened about the leg, it was labelled with indelible ink to give the chick an identifying code. As with eggs, this code consisted of the nest number, together with the appropriate letter to signify which egg the chick hatched from.

However, in many instances, the entire complement of 2- and 3-egg clutches hatched within a single interval between nest visits, so that it was not possible to determine absolutely which chick hatched from which egg. Sometimes the newest arrival would still be sitting within the remains of its labelled egg, and could hence be identified. Furthermore, if, in such a situation, a total of only two chicks hatched between visits, this meant that the older one present could (by a process of elimination) also therefore be identified. Nevertheless, discovering hatchlings whilst still surrounded by their own eggshell proved uncommon, and in many other cases, an alternative approach to categorize chicks had to be adopted: Bolton, Houston and Monaghan (1992) found that larger eggs gave rise to nestlings which were on average both heavier and skeletally larger. Of these two parameters, it seems likely that chick weight would be the more variable, as at this early stage of development, the young birds are so small that the consumption of a meal brought back by a parent can cause a considerable relative increase in body weight.

Therefore, using tarsus lengths as a measure of relative skeletal size, it was possible to imply that, in cases where egg volumes decreased with laying order, the largest chick in the nest came from the a-egg, the next largest from the b-egg, and so on, with the effect of egg size being compounded by that of hatch order. However, if, for example, the b-egg in the clutch was actually larger than the a-egg, then this would tend to counter any advantage that the a-chick would accrue from hatching first, so that the two chicks might be of similar size when the nest is visited. Therefore, in cases where egg volumes did not decrease with laying sequence, the associated chicks remained unclassified. As with eggs, every such unidentified chick was given a labelled tag that stated which nest it came from, and which allowed siblings to be distinguished from each other, but which did not make any inference about which egg a particular hatchling emerged from.

Following tagging, visits were made to nests so that each chick was subjected to the measurement of weight, and of bill and tarsus length, at intervals of not greater than five days. During such a visit, any fatalities or disappearances of marked chicks were also entered into the record for that day. However, in many instances, after the initial couple of visits to the nest, subsequently the young birds could not be found, and indeed were never recovered either dead or alive even by the end of the study

period. In other cases, chicks could be located on some visits, but not on others, so that only a patchy record of growth could be obtained. At the completion of fieldwork, it was therefore decided to base analyses of growth upon simply the final set of measurements taken for each chick within a nest, at a time when the complete brood was known still to be alive.

## CHAPTER 3: RESULTS.

### Section One: Egg-based data.

#### (i). Egg volumes.

Firstly, egg volume data, grouped into samples with respect to both clutch size and laying order, were checked for normality. Kolmogorov-Smirnov one-sample tests indicated that all data conformed to the normal distribution (z-values ranged between a maximum of 0.14 and a minimum of 0.04;  $P > 0.05$  in all cases).

Table 1 displays the mean values obtained for egg volumes. Samples are again grouped according to clutch size, and also position of each egg within the clutch, to allow both between- and within-clutch comparisons, respectively.

**Table 1.** Mean egg volumes ( $\pm$  S.E.), calculated with respect to clutch size, and laying order within each clutch.

Clutch size.	Egg order.	Sample size ( <i>n</i> ).	Mean volume (cm <sup>3</sup> ).
1 egg	A	(12)	68.18 $\pm$ 1.50
2 eggs	A	(20)	71.65 $\pm$ 1.46
	B	(20)	65.94 $\pm$ 1.36
3 eggs	A	(37)	70.97 $\pm$ 0.95
	B	(36)	68.24 $\pm$ 1.14
	C	(42)	64.25 $\pm$ 0.88

Initially, data were analysed using a 2-way ANOVA, examining the effects of laying order and clutch size upon egg volume. However, it was not possible to examine higher order interactions: for example, it was impossible to have a c-egg from a 2-egg clutch, or a b-egg from a 1-egg clutch.

Nevertheless, the analysis indicated that there were significant differences in mean egg volumes with respect to laying order ( $F = 15.8$ ;  $n = 167$ ;  $P < 0.001$ ). For 3-egg clutches, to identify exactly where differences lay, this analysis was followed by a range test: using Tukey's H.S.D., significant differences were found to occur between a- and b-, b- and c-, and a- and c-eggs (in each pair-wise comparison, the latter being smaller by 3.84 %, 5.85 % and 9.47 % respectively), hence confirming the existence of an overall trend in 3-egg clutches for decreasing egg volume with position in the clutch (i.e. from a- through b- to c-).

Contrastingly, the 2- way ANOVA also indicated that no significant differences existed in mean egg volumes with respect to clutch size ( $F = 1.44$ ;  $n = 167$ ;  $P = 0.2$ ). This was confirmed by investigating the effects of clutch size solely upon the volume of a-eggs (because only a-eggs - by definition - can be present in each of the 1-, 2-, and 3-egg clutches): the analysis indicated that there existed no significant differences in a-egg volumes between 1-, 2- and 3-egg clutches (1-way ANOVA;  $F = 1.38$ ;  $n = 69$ ;  $P = 0.26$ ).

## **(ii). Incubation periods.**

These were analysed using the data from 3-egg clutches, hence controlling for clutch size. To begin with, egg incubation data, grouped into samples with respect to laying order, were checked for normality. Kolmogorov-Smirnov one-sample tests indicated that all data again conformed to the normal distribution (z-values ranged between a maximum of 0.26 and a minimum of 0.09; all were  $P > 0.05$ ).

Table 2 displays the mean values obtained for egg incubation periods. Samples are grouped according to the position of each egg within the clutch. Mean egg incubation period decreased with respect to laying order, the difference between the c-egg, and the other two (a- and b-) which preceded its arrival in the nest, being particularly marked (1-way ANOVA;  $F = 30.5$ ;  $n = 52$ ;  $P < 0.001$ ). As previously, a range test was subsequently conducted, to identify exactly where these differences lay: Tukey's H.S.D. indicated that significant differences occurred between a- and b-, b- and c-, and a- and c-eggs, hence confirming an overall trend for decreasing egg incubation period with position in the clutch.

**Table 2.** Mean incubation periods ( $\pm$  S.E.), with respect to laying order, for 3-egg clutches only.

Egg order.	Sample size ( <i>n</i> ).	Mean incubation period (days).
A	(11)	28.82 $\pm$ 0.30
B	(26)	27.27 $\pm$ 0.22
C	(15)	25.43 $\pm$ 0.29

**(iii). Fate of eggs.**

Failure of an egg to hatch can be allocated to one of a variety of categories, according to the underlying reason. In the present study, there were three such categories, which are included in Table 3. Samples are again grouped according to clutch size and position of each egg within the clutch. Values in the table relate to the proportion of eggs from a particular sample, which either hatched, went missing, were broken between visits, or were “addled” (the result of infertility or embryo death).

**Table 3.** Hatching success and causes of failure, each expressed as a proportion of the total sample size (*n*), with respect to clutch size and laying order within each clutch.

Clutch size.	Egg order.	Sample size ( <i>n</i> ).	Hatched.	Missing.	Broken.	Addled.
1 egg	A	(12)	0.42	0.42	0.08	0.08
2 eggs	A	(20)	0.70	0.20	0	0.10
	B	(20)	0.70	0.10	0	0.20
3 eggs	A	(43)	0.81	0.14	0.05	0
	B	(42)	0.88	0.10	0.02	0
	C	(42)	0.57	0.14	0.07	0.22

Looking firstly at hatching success, the only significant difference with respect to laying order within a clutch is that for c-eggs, the proportion of eggs successfully giving rise to a chick is smaller than the clearly similar values obtained for both a- and b-eggs from a 3-egg clutch (Pearson chi-squared = 12.1;  $n = 127$ ;  $P < 0.01$ ).

Next, comparing eggs of the same laying order within different clutch sizes, the only noteworthy difference is that the success of lone a-eggs was considerably less than that of the same order egg in a clutch of two, and was approximately half that calculated for a nest containing three eggs. Again using chi-squared, this difference between the single egg and a-eggs from larger clutches was also confirmed as being significant (Pearson chi-squared = 0.034;  $n = 75$ ;  $P < 0.05$ ).

## **Section Two: Chick growth data.**

### **(i) Effect of position in the clutch.**

Firstly, looking solely at broods containing 3 chicks, an index of body size was calculated for every chick which had been assigned a position within the clutch. This index combined both beak and tarsus lengths to obtain an overall measure of chick size. However, to make the relative contribution from these two measurements equal (tarsus lengths being much greater in absolute terms than those for beaks), it was necessary first to standardize these two variables (Norusis 1991), so that within a sample, each variable had a mean value of zero, with a standard deviation of one. Such standardized measurements are known as z-scores, with the size index being calculated for each chick by summing the scores obtained for beak and tarsus.

Body weight was then regressed upon the index representing body size (after Hamer *et al* 1993), with the residuals obtained in turn being expressed as a proportion of the predicted weight. For each chick, the resulting figure was then used as a measure of body condition (i.e. how well the chick was growing), and will be referred to in this and following sections as the “growth index” (within these following

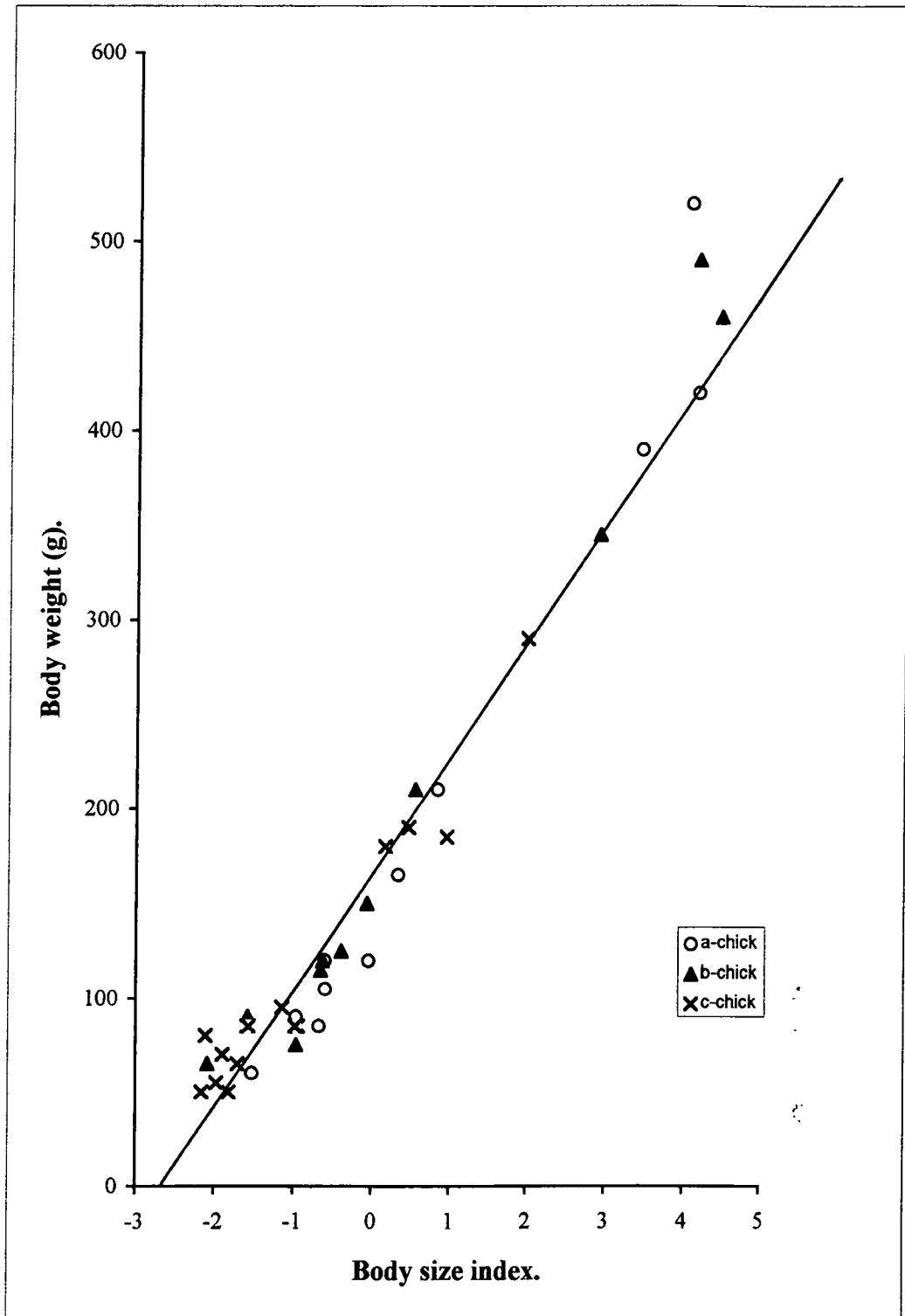
sections, new indices of size and growth have to be calculated each time, due to the different combinations of chicks contributing to the sample data sets).

**Table 4.** Mean growth indices ( $\pm$  S.E.) of chicks from 3-chick broods, with respect to position in the nest.

Chick position.	Sample size ( $n$ ).	Mean growth index ( $\pm$ S.E.).
A	(11)	-0.101 $\pm$ 0.041
B	(11)	0.103 $\pm$ 0.120
C	(15)	0.285 $\pm$ 0.140

The mean values obtained for this growth index, with respect to position of the chick within the nest, can be seen in Table 4. There was no significant difference among groups (1- way ANOVA;  $F = 2.73$ ;  $n = 37$ ;  $P = 0.08$ ). This result agrees with what one would expect, based upon Figure 2 (overleaf): here, a plot of chick weight against body size index illustrates that the points for each category of chick almost all fall close to the overall regression line, such that no clearly visible difference exists between categories, in terms of their chicks positions with respect to which side of the line they lie upon.

**Figure 2.** Body weight plotted against body size index for a-, b- and c-chicks from 3-chick broods only.



**(ii) Effect of clutch size.**

To examine the effect of clutch size upon chick growth, perhaps the most obvious approach would be to compare broods containing only a single chick, with respect to whether the nest had an original compliment of either 1, 2, or 3 eggs. However, the fact that most adult females laid three, or at least two eggs, and that generally more than one of these hatched successfully, in turn created insufficient data on single-chick broods to allow analysis.

Therefore, instead it was decided to investigate the growth of two-chick broods, with respect to whether they arose from a clutch of two or three eggs (as there is now known to be no significant difference in growth with respect to position in the nest for 3-chick broods, combined with the fact that the same is also likely to be true for nests containing two nestlings, such division of chicks within broods shall be dispensed with. Therefore, in this, and the following analysis, data from nests in which laying or hatching order could not be determined, can still be utilized, hence increasing sample sizes to a point where more satisfactory statistical analyses may be conducted).

**Table 5.** Means of within-brood mean chick growth indices ( $\pm$  S.E.), with respect to clutch size, and for two-chick broods only.

<b>Clutch size.</b>	<b>Sample size (<i>n</i>).</b>	<b>Mean of within-brood mean chick growth indices (<math>\pm</math> S.E.).</b>
2-eggs	(10)	0.011 $\pm$ 0.105
3-eggs	(13)	-0.062 $\pm$ 0.052

Following calculation of size and growth indices for each individual nestling in the manner previously detailed, these values were next averaged across chicks within each nest, to produce a mean chick growth index for each brood. In turn,

means of these values were calculated with respect to clutch size (see Table 5). Statistical analysis found there to be no differences between groups (t-test for equal variances;  $t$ -value = 0.68;  $n$  = 23;  $P$  = 0.30). Hence, nestlings in a 2-chick brood from a 2-egg clutch display similar growth to those in a 2-chick brood which came from a clutch originally containing 3 eggs.

**(iii) Effect of brood size.**

As position in the nest and clutch size had no effects upon growth, it was possible to conduct a single analysis of the influence of brood size, which did not control for these variables, and hence utilized the vast majority of chick data collected. To begin with, new size and growth indices were therefore calculated for each young bird, with the latter again being used to create a mean chick growth index for each brood. Also similarly to above, in turn means of these values are calculated, but this time with respect to brood size (Table 6). Statistical analysis found there to be no significant difference between any two groups (1-way ANOVA;  $F$  = 1.26;  $n$  = 50;  $P$  = 0.29). Put simply, mean chick growth within a brood was similar regardless of whether the nest contained 1, 2 or indeed 3 offspring.

**Table 6.** Means of within brood mean chick growth indices ( $\pm$  S.E.), with respect to brood size.

<b>Brood size.</b>	<b>Sample size (<math>n</math>).</b>	<b>Mean of within-brood mean chick growth indices (<math>\pm</math> S.E.).</b>
1 chick	(13)	-0.024 $\pm$ 0.035
2 chicks	(24)	-0.0005 $\pm$ 0.058
3 chicks	(13)	0.122 $\pm$ 0.083

## CHAPTER 4: DISCUSSION.

### Section One: Egg parameters.

#### (i) Egg Volume.

Considering the wealth of documented cases which describe the occurrence of a decrease in egg volume with laying sequence, particularly with respect to the c-egg (Paludan 1951, Preston & Preston 1953, Coulson 1953, Parsons 1972, 1975a, Nisbet & Cohen 1975, Hahn 1981, Pierotti & Bellrose 1986, Reid 1987b, Bolton 1991, Sydeman & Emslie 1992, Bollinger 1994), the discovery of a similar trend during the present study was perhaps only to be expected. It is interesting to note, however, that the current results are very similar to those obtained by Paludan (1951), also studying *L. fuscus*: looking specifically at the size difference between a- and c-eggs, the previously cited figure of 9.4 % obtained by this researcher compares with the 9.5 % of the present study. However, it would appear that such an exact size disparity is not intrinsic to the species: whilst Royle obtained a lower, but relatively similar value of 8.3 %, Bolton *et al* (1992) found control c-eggs to be on average 13.3 % smaller in volume than control a-eggs.

Although not a subject addressed by the results of the current study, there is some debate as to the mechanism responsible for the egg size asymmetry observed within a clutch, particularly with respect to the much smaller c-egg. The reduced size of this third-laid egg has been attributed to the effect of a limited nutrient (food) supply during the pre-laying period (Pierotti & Bellrose 1986), as, according to Bolton *et al* (1992) this egg in particular may be expected to be the most sensitive to variation in food availability or quality (presumably because the adult female will by this stage have fewer reserves upon which to draw in order to make up for any shortfalls in nutrient availability from the environment). Similarly, Reid (1987b) concluded that the small size of c-eggs was a non-adaptive effect of food supply, as courtship feeding of the female by the male declines with initiation of the clutch (i.e. laying of the first egg).

Indeed, food supplementation experiments have shown that an increased supply of nutrients allows females to lay larger eggs. For example, Bolton *et al* (1992) found that birds provided with supplementary egg-protein produced eggs which were on average 10 % bigger than controls. However, the latter study, together with others such as that by Hiom *et al* (1991) also found that, whilst the extra food produced a somewhat greater increase in the size of the c-egg relative to that induced for the a- and b-eggs, nevertheless, the size differential between members of a clutch, although reduced, was still maintained. This suggests that food availability or quality represents only part of the explanation.

Evidence that females may indeed to some extent control egg size regardless of nutrient availability, can be obtained from egg-removal experiments, such as those of Parsons (1971, 1976) conducted upon *L. argentatus*: following the removal of the a-egg from a nest soon after it was laid, the subsequent difference between a- and c-eggs was significantly less marked, so that the latter approximated to the size of the b-egg. Such evidence suggests that c-egg size in unmanipulated clutches is actually adaptive. Furthermore, the lower volume of the c-egg is known to be the result of a reduced albumen rather than yolk content, the latter being indispensable to the life and growth of the embryo (Parsons 1976). This has led to the conclusion that the proximal cause of the smaller c-egg is the onset of incubation before the full clutch has been laid (due to the a-egg stimulating brooding behaviour), hence reducing the level of albumin secretion during the formation of the c-egg (see Parsons 1972; for an in depth description of the pre-laying mechanism of egg development, see Parsons 1976).

Overall, therefore, it seems probable that both food availability and (more importantly) the onset of incubation, together contribute to within-clutch egg size asymmetry, particularly with respect to the c-egg.

Turning to the effects of clutch size upon egg volumes, the lack of a significant difference between eggs occupying the same position within clutches of different sizes in this study (Table 1) tends to contradict the findings of Parsons (1976) for *L. argentatus* and Houston *et al* (1983) for *L. fuscus*, where females laying smaller clutches also laid smaller eggs.

Clutch size is primarily determined by the level of pre-breeding body protein reserves (Houston *et al* 1983, Bolton *et al* 1992). Also, it is known that egg size positively correlates with chick size, growth and probability of fledging (Schiferli 1973, Nisbet 1978, Bolton 1991), and that there exists a minimum size, below which the resulting chick has little chance of surviving to independence (Parsons 1976). As such, whilst potential reproductive success of the adult female can increase via production of a greater number of eggs (which is likely to lead to more offspring), success can also increase by laying larger eggs (so that each offspring has a greater probability of survival).

Indeed, above a minimum viable egg size, there is some debate as to whether egg or clutch size should take priority: according to Ricklefs (1973), when clutch size is greater than one, it is the number of eggs which should be adjusted before egg size, whilst Bolton (1991) has argued the opposite: that because a decrease in clutch size represents a quantum reduction in reproductive potential, then egg size should be adjusted first. Overall, this implies that, across the full range of reserves available to females, an individual with fewer reserves than average should produce smaller, not fewer eggs (i.e. change egg size first), whilst one with greater reserves should lay more, rather than larger eggs (i.e. change clutch size first).

In fact, regardless of the exact nature of the balance in priorities between changing egg and clutch size, there should nevertheless exist approximate threshold levels of female body protein reserves, which determine the number of viable eggs laid. Between two adjacent thresholds, there will then exist females with a range of protein reserves, but which all lay the same number of eggs: females at the higher end of the range (having more reserves) would be expected to produce larger eggs than those lower down.

Also, assuming that, within a population, the overall frequency distribution of female body protein reserves follows a normal distribution, then the result of an investigation concerning how clutch size influences egg size, will depend upon where the above thresholds (which are static) intersect this distribution (whose absolute position along an axis of protein reserves varies according to the supply of resources to females). Therefore, alternative findings from other studies are not necessarily

contradictory, but might instead reflect differences in food availability during the pre-laying period.

From the above mechanism, the current finding of no correlation between egg and clutch sizes has two possible explanations: firstly, food supplies (and hence, body protein reserves) were so low that the thresholds for laying 1, 2 and 3 eggs all fell beyond the peak of the normal distribution, and so there were more females laying smaller than larger eggs in each of the clutch sizes. Alternatively, food supplies (probably similar to those described later with respect to the post-hatching period) may have been so good that the same thresholds all fell the other side of the peak, with more females laying larger than smaller eggs in each clutch size.

### **(ii) Incubation period.**

The reduction in mean incubation period with respect to laying sequence (from a- through to c-egg) agrees with the trend noted by previous studies upon *L. fuscus*, such as Hebert & Barclay (1988), and more recently Royle (1995), who recorded that, on average b-eggs took 1.66 days less to incubate than a-eggs, whilst the difference between the former, and c-eggs was a further 1.14 days. (These compare to respective values of 1.55 and 1.84 days obtained during the current study).

Such a trend is perhaps to be expected, as incubation period is itself related in part to egg size. Specifically, the energy requirement for embryonic development is related to the surface area and weight of an egg, with the result that larger eggs require longer incubation periods. However, a further contributing factor to the overall trend may be related to behavioural changes in the parent bird, as Parsons (1972) has shown that incubation during the laying period is only partly effective. This would tend to result in cooling of embryos within earlier laid eggs, thus delaying their development.

### **(iii) Hatching success.**

Previous studies such as those of Parsons (1970) and Bolton *et al* (1992) found there to be no difference in hatching success of eggs with respect to laying order. Although the present study also obtained similar results for a- and b-eggs, hatching

success of c-eggs was however significantly lower. For all three eggs, a similar proportion of individuals went missing, most probably as a result of intra-specific predation (see later). In contrast, only c-eggs were ever noted as failing to hatch, and indeed over 20 % of them were added. Similar results were obtained by Royle (1995).

It seems possible that there exists a minimum size below which an egg will not be viable, even to hatching (as opposed to hatching successfully, but subsequently having little chance of producing a viable chick), and it may be that in the present study, some c-eggs were below this threshold. Also, whilst further c-eggs may have failed to hatch because they remained unfertilized, yet another proportion might have done so because of a disruption or cessation of incubation behaviour. For instance, Beer (1966) reported that, for Black-headed Gulls *Larus ridibundus*, the presence of chicks in the nest curtails adult incubation. Similarly, *L. argentatus* parents typically neglect their last-to-hatch (c-) egg during the period before the chick emerges, allowing its mean temperature to drop by about 4 degrees-C, to near 33 degrees-C (Lee *et al* 1993, Evans *et al* 1995). If the temperature falls further, a reduction in (or indeed suspension of) development may occur, often leading to the death of the late-stage embryo. Indeed, neglect during even the pipped egg stage has been interpreted as a cause of mortality in a significant proportion (up to 11 %) of Herring Gull terminal eggs on a study site in Newfoundland (Haycock & Threlfall 1975). Hence, parental neglect may well account for a number of the instances of egg failure recorded in the current study (assuming that similar behaviour is exhibited by the closely related *L. fuscus*).

The significantly lower proportion of single eggs found to give rise to chicks in the present study, compared to a-eggs from 2- and 3-egg clutches (Table 3), was mainly a result of a far greater proportion of single eggs going missing. The main cause of this, and indeed egg loss in general for *L. fuscus* upon Walney, tended to be predation by conspecifics, and also by *L. argentatus*. This has been documented by Brown (1967), and Henley (1979), the former noting that, apart from gulls, the number of potential predators of eggs or chicks upon the island is small. Therefore, the lower hatching success of single egg clutches can be most satisfactorily explained in terms of why they suffer greater predation.

As predation did not always involve the loss of the entire clutch, and assuming that the predator does not differentiate between a-, b- and c-eggs, then the above result may have been influenced by an increasing “dilution of predation pressure” within ever larger clutches. For example, if, in a particular situation a predator is (for whatever reason) limited to taking perhaps only one egg, then in a clutch of three, the a-egg has a 33.3 % chance of being taken, in a clutch of two, this rises to 50 %, but in a single-egg clutch it increases dramatically to 100 %.

However, Brouwer & Spaans (1994) studying *L. argentatus* found that, whilst controlling for clutch size, egg predation was nevertheless strongly correlated to clutch volume. Having also excluded the possibility of a predator-linked selection mechanism, they concluded that lower quality birds not only lay smaller eggs, but also exhibit less efficient parental care during the incubation period. As lower quality individuals also lay fewer eggs, it seems likely that the greater predation of lone a-eggs in the current study is likewise primarily due to less efficient parents putting their clutches at greater risk of predation: a similar suggestion to that of Parsons (1975) who stated that birds laying smaller clutches may have a lower incubative drive.

Such an explanation predicts that hatching success of a-eggs should also decrease from 3- to 2-egg clutches, mainly as a result of the poorer protection of eggs afforded by parents of the latter. Whilst the current results do follow such a trend, the differences are not great enough to be significant. Although the chances of an a-egg being the subject of a predatory attack might increase less from 3- to 2-egg, than from 2- to 1-egg clutches (as in the earlier example), the apparently secondary nature of any such effect means that the current result could be interpreted more readily as suggesting that the difference in parental efficiency between adults laying two, and those laying three eggs, is less than that between birds laying two, and those laying only one egg.

## Section Two: Chick growth.

### **(i) Effect of position in the clutch.**

In the present study, the lack of any significant differences between the growth of a-, b- and c-chicks agreed with results obtained by Royle (1995). In particular, the similarity of c-chick growth to that of its two siblings is, however, contradictory to numerous instances in the literature which refer to a condition seen in many gull (and other species), called the “third chick disadvantage.” Put simply, it is known that smaller eggs give rise to chicks which are not only skeletally smaller but also lighter for their size than those from larger eggs (Furness 1983, Bolton 1991). Furthermore, because *L. fuscus* displays asynchronous hatching (Griffiths 1992), the c-chick is also the last to enter the brood, so that the elder chicks present will not only have frequently been larger at hatching, but have now also experienced a “head start” in subsequent growth. Hence, the considerably smaller c-chick often has difficulty in competing successfully with older brood members for food brought back by the adults (Graves, Whiten & Henzi 1991).

As such, in many gull studies, it is a common observation that the last hatched chick displays reduced growth, compared with that of its siblings (e.g. Lundberg & Vaisanen 1979, Viksne & Janaus 1980, Furness 1983, Hebert & Barclay 1986, Pierotti & Bellrose 1986, Reid 1987b). Associated with reduced growth, these studies also found an increased level of mortality amongst c-chicks. However, chick mortality (with respect to position in the nest, clutch or brood size) was not formally investigated during the present study, and it would be difficult to draw conclusions from the data obtained, as the fate of many chicks remained unclear. The problem, similar to that noted by Brown (1967), was that on Walney the thick vegetative cover and mobility of chicks made it often difficult to find marked youngsters (a problem compounded in the current study by the prevalence of nearby rabbit burrows, into which young birds often retreated at the advance of the researcher). Whether such individuals died, or survived to fledging therefore remains unclear.

Returning to c-chick growth, the result of the current study could be interpreted as supporting the proposal of Ricklefs (1973): that, except in cases of

starvation, chick growth is inflexible, and generally takes place at some physiological maximum rate, determined by factors such as the rate of cell division. However, there exist a variety of alternative explanations, which predict similarity of growth between all brood members, even though chick growth is taken as being flexible below some upper limit.

One such explanation could be that there were abundant supplies of food available to the parent birds, so that it was possible to feed all three chicks without them needing to compete for this resource. Indeed, the local area is known to possess a rich variety of food resources, such that gulls from Walney may have a diet containing earthworms and terrestrial vertebrates taken from the surrounding land, together with domestic waste from refuse tips (one of which is situated just north of the colony), and a variety of marine shellfish and other organisms taken from Morecambe Bay and the Irish Sea. Other food sources can include discarded fish offal (which, together with refuse, was cited by Spaans (1971) as creating an abundance of food, leading to a rapid increase in populations of *L. argentatus* during the beginning of the 1970s), eggs and chicks of neighbouring gulls, sheep and cattle feed taken from fields, and waste scraps taken from litter bins, streets and gardens (Sibly & McCreery 1983).

Furthermore, it has in the past been suggested (Lack 1954, 1966) that the third egg is laid precisely to take advantage of situations where there is an abundance of food. Indeed, Bolton *et al* (1992) state that, as *L. fuscus* is an opportunist scavenger, at the time of egg laying, it is difficult for the parents to acquire a reliable indication of food availability later in the season. Therefore, this species may lay as many eggs as possible (within the upper limit set by incubation and/or brood rearing capacity), to take advantage of any abundance of food which may subsequently arise, and that, if instead, food supplies fail, then the third chick, being the least able to compete, and representing the chick into which least investment has been placed, will be the first to die, hence causing “brood reduction”. However, there are no data available to provide an indication of how abundant local food supplies were in 1995, with respect to the number of gulls dependent upon these resources. Therefore, the level of food availability remains speculative.

Another, somewhat similar explanation relates to the nature of the data used to estimate chick growth in the present study. As many young birds could not be found after only the second or third visit to the brood, estimates of individual chick growth within a nest were often based upon measurements of relatively young nestlings. Such small chicks would in turn have relatively low food requirements, easily met by the parents. Hence, at this stage all three chicks would in theory be able to acquire sufficient food to meet their needs, and would therefore grow at similar rates.

However, even though it was rarer to successfully catch older chicks at a time when all three brood members were known still to be alive, the associated estimates of growth may still (perhaps somewhat surprisingly) have contributed to the finding that growth was similar for all three chicks. According to Hussell (1972) and Bryant (1978) this could occur from the effects of asynchronous hatching, such that the staggered development of siblings prevents the maximum food requirements of all members of the brood from occurring at the same time ("peak load reduction"). This reduces any limiting effect of food supply, so that even older a-, b- and c-chicks may display similar growth.

Finally (and somewhat contradictory to the suggestion of peak load reduction), a yet further possibility relates to the fact that, although *L. fuscus* displays asynchronous hatching, the degree of asynchrony will to some extent be influenced by within-clutch differences in egg incubation periods. Whilst (as previously detailed) this difference between a- and b- eggs in the present study was similar to that found by Royle (1995), c-eggs took 1.84 days less to hatch than b-eggs, compared to only 1.14 days in the latter study. Overall, therefore, it is possible that the degree of hatching asynchrony may often have been relatively low during the current study.

As such, at hatching there would be less difference in the competitive abilities of brood members, with the opportunity for any one chick to dominate its siblings being reduced. Hence, all chicks would possess more equal feeding opportunities, and as a result would display less marked differences in growth, as found by Hebert & Barclay (1986), who manipulated hatch asynchrony within *L. argentatus* clutches.

However, whilst, in many instances during the present study, all members of a three egg clutch did indeed hatch between consecutive nest visits, this represented an interval of time in the order of 2-3 days. Studies such as Royle (1995) found that,

although the c-egg hatched considerably later than the a- and b-egg, the total a- to c-hatch interval was nevertheless only 1.45 days. Furthermore, Hebert & Barclay (1986) state that, for *L. argentatus*, normal hatch asynchrony occurs with a- to c-hatch intervals above as little as 24 hours. Therefore, whether normal hatch asynchrony was indeed reduced in some instances during the current study, cannot be directly verified.

Overall, whilst potential explanations for the similarity of c-chick growth to that of its elder siblings include not only that of inflexible chick growth, but also a number of alternatives which accommodate the contrary view, all remain somewhat speculative.

#### **(ii). Effect of brood size and clutch size.**

In the present study, the lack of significant differences in mean chick growth within broods of different sizes could also be viewed as favourable evidence for the inflexibility of chick growth. However, this result is at odds with the work of Bolton (1991), who found that brood size had a negative effect upon chick growth. Furthermore, Graves *et al* (1984) found that, for *L. argentatus* there was a significant difference in the proportional weight gain of chicks between those broods where there were three chicks in the brood for 3 days or more, and those where either only two chicks were hatched, or there were three chicks for 2 days or less.

If chick growth is in fact flexible, one possible explanation for the result of the current study relates to parental quality. As previously cited, better quality adults lay larger clutches, on average. It follows that these in turn (excepting egg losses) lead to larger broods, relative to those of poorer quality individuals. Therefore, although the overall food demand of a brood increases with the number of chicks present, the higher quality parents of these larger broods also represent those members of the breeding population which are best able to meet such requirements (if quality is defined in terms of ability to obtain resources). Hence, chick growth could well be similar across brood sizes. Also, such a mechanism would not contradict the above cited studies of Bolton (1991), and Graves *et al* (1984), where initial clutch size was controlled for. They were studying how the loss of a brood member allowed parental

effort to be divided amongst a smaller number of remaining chicks, which could indeed lead to subsequently greater growth of the latter.

From the above explanation, it seems reasonable to infer that, in cases where a high quality female which laid 3 eggs subsequently lost one such egg (to, for example, predation), then the ensuing brood could have a higher mean level of growth than that of a 2-chick brood produced by a lower quality female, who could only lay two eggs in the first place. However, in this study mean nestling growth in 2-chick broods from 2-egg clutches did not differ significantly from that of 2-chick broods which came from clutches originally containing three eggs.

As other studies have found that effects of adult quality and experience are apparent only during years with poor food supply (e.g. Hamer & Furness 1991), the absence of a relationship between clutch size and chick growth in the current study provides support for the earlier suggestion (made when discussing the similarity of growth within broods) that there may have existed an abundance of food during the nestling period.

In conclusion, of the possible alternative explanations to that based upon Ricklefs (1973) for the similarity of mean chick growth, this time within broods of different sizes, food abundance during the above period is a more appropriate suggestion than one involving parental quality.

## **CHAPTER 5: APPENDIX.**

Meaningful summary tables would by necessity reiterate in an unchanged form many of the measurements taken “in the field”. Therefore, instead, the complete set of original records are included in a separate binder.

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