

SELECTIVE CORRELATION OF EGG SIZE WITH CHICK MORTALITY IN THE BLACK-HEADED GULL (*LARUS RIDIBUNDUS*)

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Parsons (1970) and Nisbet (1973) found in the Herring Gull (*Larus argentatus*) and the Common Tern (*Sterna hirundo*), respectively, a strong positive correlation between egg size and chick survival. Davis (1975) has claimed that female age affects egg size in the Herring Gull. Thus the correlation between egg size and chick survival might be an artifact of the age structure of the population.

In the present study of the Black-headed Gull (*Larus ridibundus*) we wished (1) to find out whether egg size and chick survival are positively correlated, and, if so, (2) to discuss why this does not result as a continuous increase of egg size in populations, and (3) to examine the significance of egg size variation within clutches of larid species.

MATERIALS AND METHODS

Our study area is in the Kristinestad/Kristiinankaupunki archipelago (62°17'N, 21°20'E) on the coast of the Gulf of Bothnia, Finland. The two small islets (total area 800 m²) are open, partly covered by rather long grass, and located about 500 m from the mainland. The colony consists of about 500 pairs, while about twice as many more breed in a sanctuary 400 m north of the study area.

The colony was studied every afternoon for two hours between 28 May and 21 June 1974 and between 26 May and 12 June 1975, except for two cold and rainy days (3 June 1974 and 31 May 1975). Prolonged disturbance of the gulls was avoided, especially when the weather was bad.

The eggs of three-egg clutches were marked (130 clutches in 1974, 122 clutches in 1975). Egg length and breadth were measured to the nearest 0.1 mm. The date of laying of the first egg in each clutch was determined by water tests, using criteria shown in Figure 1. The criteria in Figure 1 apply most accurately for eggs of medium size, but less accurately for very small or large eggs (accuracy is approximately ± 5 days per one egg, but since the mean date of the clutch is taken, accuracy is even greater). The stage of incubation of each egg was given a three-number code which we found practical in handling large amounts of data for computer analyses. This method rapidly and exactly determines the distribution of laying dates of clutches in colonial species; for an example using larids, see Väisänen (1974:80).

Chicks were marked immediately after hatching. In a few clutches where the hatching order of two chicks was not recorded, we judged the heavier chick to have hatched first. The eggs in each clutch were denoted a, b, or c according to the hatching order. This probably corresponds to the order of laying, because the eggs normally hatch in the same sequence as

they are laid (Ytreberg 1956). One-day-old chicks were weighed to the nearest gram using a Pesola spring balance.

When the chicks began to hatch, a nest was surrounded by a fence of chicken wire, about 20–25 cm high and with a diameter of about 50 cm. The nests were checked daily for 4–12 days after hatching. When the chicks were more than eight days old, some of them were able to escape from the enclosures. Therefore, chicks 10 days of age or more are not analyzed in the present study. Fencing the nests enabled us to find the chicks on each visit with a minimum of disturbance.

From the length (EL) and breadth (EB) of the eggs, the shape index (ES) and volume (EV) were calculated using the formulae

$$ES = 100 \times EL/EB$$
$$EV = 0.45923 \times EL \times EB^2 + 1.333$$

where EV is given in cm³ and EL and EB in cm; the species-specific formula for EV is based upon Väisänen's (1969) regression method.

RESULTS

NESTING SUCCESS

The clutch sizes were determined 28 May 1974 and 26–28 May 1975 (Table 1). During

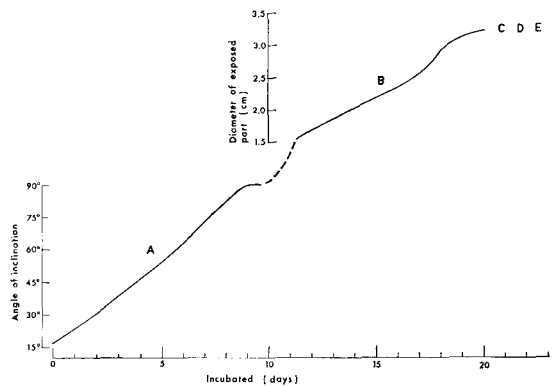


FIGURE 1. Criteria for determining incubation stage in eggs of the Black-headed Gull by submerging eggs in water. (A) Egg lying with small end on the bottom of beaker. The angle of long axis with bottom is measured to the nearest 15°. (B) Diameter of exposed part measured to the nearest 0.1 cm. (C) Shell cracked, (D) pipped and (E) the chick hatched. These criteria were derived from tests with 250 eggs whose date of hatching was subsequently recorded; their date of laying was calculated backwards using 24 days as the average duration of incubation.

TABLE 1. Clutch sizes in two years in Kristiinankaupunki.

		No. of eggs				Mean clutch size (\pm SD)
		1	2	3	4	
1974	N	5	50	253	1	2.81 \pm 0.44
	%	1.6	16.2	81.9	0.3	
1975	N	3	16	122	0	2.84 \pm 0.42
	%	2.1	11.4	86.5	0.0	

the study no eggs were plundered. Therefore the observed average number of eggs, 2.8, in both years, was probably close to the true clutch size. Clutch-size in our population was higher than that found in other investigations of Black-headed Gulls: Svårdson (1958) and Ytreberg (1960), 2.6 eggs; Goodbody (1955), 2.5; and Fredrikson (1940) 2.4.

The weather of May and June 1974 and in 1975 differed from the average temperature and rainfall for 1931 to 1960 (Kolkki 1966, Helimäki 1967) according to the monthly reports published by the Meteorological Central Institute of Finland. In 1974, June was considerably warmer than average; in 1975, June was cooler than average and rainfall was heavy in May and June. Due to a warmer spring (late April and early May), nesting took place about one week earlier in 1975 than in 1974 (Fig. 2). In both years, the hatching success of the chicks (average 90.6%) and survival to seven days of age (74.0%) were almost the same (NS, χ^2 test; Table 2). In both years, mortality of the chicks occurred mostly in the first two days of life (52% of chick mortality occurred during the first seven days of life; Fig. 3).

VARIATION IN EGG DIMENSIONS AND THE WEIGHT OF CHICKS

Egg dimensions of the Black-headed Gull conform to the generalization (Väisänen 1969) that breadth is least variable, length and shape more variable, and volume most variable (Table 3). We also noted that the weight of the newly-hatched chick (CV \sim 11%) varies even more than egg volume. This may be explained partly by the fact that some chicks probably had been fed at the age of one day, while others had not. Decrease in egg volume from the b- to the c-egg is caused primarily by the shortening of the eggs. The c-chick weighs on an average 1.1 g (4.2%) less than the ab- (a or b) chicks.

Using Ytreberg's (1956) mean measurements of egg length and breadth, we calculated egg volumes and found that the

average volume in his population was 33.07 cm³, about 2% smaller than in our population. A comparison of egg volumes in the laying sequence with the average egg dimensions in the clutch gave the following values for a-, b- and c-eggs: Ytreberg, +2.2, +1.5 and -3.7; this study, +0.8, +0.7, and -1.5. In the Norwegian population the c-egg was proportionally smaller than in our population. Part of this difference may be because we labelled the eggs according to hatching order (but see discussion).

The correlation between egg length and breadth increases from the a-egg to the c-egg; i.e., the egg shape becomes more regular in the laying sequence (Table 4). From the correlations EL/ES and EB/ES one may conclude that the shape index depends more on length than breadth. Egg shape was not correlated with egg volume or chick weight.

Using stepwise regression to explain chick weight from the four dimensions (length, breadth, shape, volume), we found egg volume to be the best predictor (Table 4). Adding a second independent variable to the models explained more variation, but by only 2-3%. The best correlation was obtained between the mean weight of the chicks in a clutch (MJWE) and the mean volume of the eggs (MV; $R^2 = 70\%$). The model for the a-egg was poorest ($R^2 = 52\%$). Thus egg volume predicts fairly well the weight of a newly hatched chick. The later the chick is in the hatching sequence, the better the weight of the chick can be predicted by egg volume. Egg breadth and egg length are less accurate predictors of chick weight (Table 4).

CHICK MORTALITY AND EGG DIMENSIONS

Mortality in relation to chick age was similar in both years (Fig. 4). Since the mortality rates of the a- and b-chicks did not differ significantly, they were combined. The c-chicks, on the other hand, were not as successful as their siblings in either year. Compared to the c-chick, the survival advantage of the ab-chicks increased from 0.1% units on the first day of life to

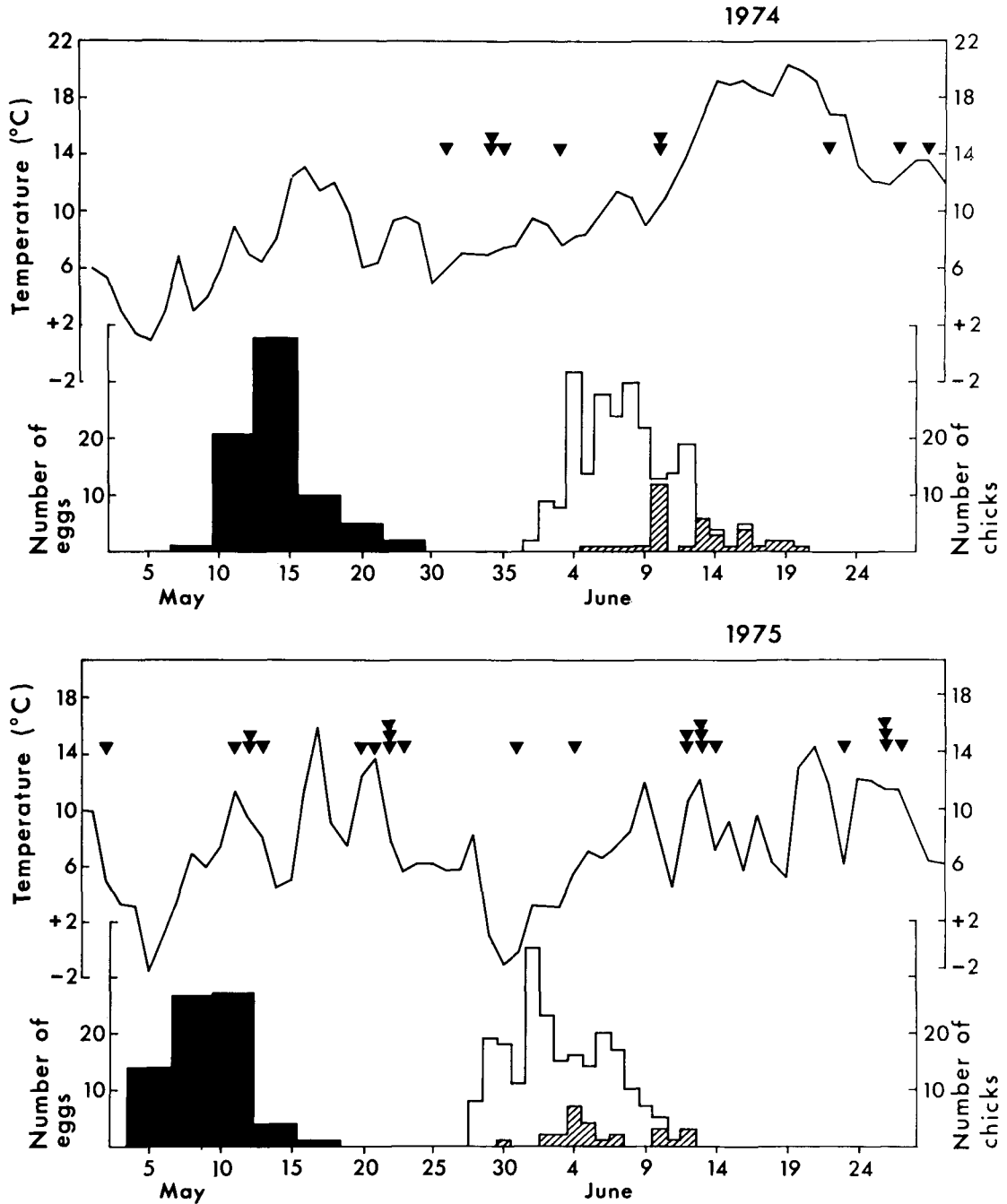


FIGURE 2. Time of laying and hatching of the eggs and death of the chicks in three-egg clutches in relation to climatic parameters. Clutch initiation dates (*shaded histogram*) with class interval of three days; hatch dates of eggs (*open histogram*) (1974 N = 231, 1975 N = 219) and death dates of chicks (*diagonal shading*) with class interval of one day. Mean daily temperature and precipitation (▼ = 2-8 mm, ▼ = 8-14 mm, ▼ = 14-20 mm) shown above.

21.7% units on the seventh and 34.8% units on the ninth day of life.

When the clutches were arranged according to the date of the first egg laid, the lowest mortality was found in clutches laid

between 7 and 15 May; chick mortality increased markedly in clutches laid between 16 and 21 May (1974), especially in the c-eggs (Fig. 5). Mortality was also somewhat higher in clutches laid 4-6 May than in

TABLE 2. Hatching success per egg laid and chick survival to the age of seven days in three-egg clutches for two years.

	Hatching success		Chick survival	
	%	No. of eggs	%	No. of chicks
1974	89.9	(297)	72.9	(255)
1975	91.7	(288)	75.9	(141)
1974 + 1975	90.6	(585)	74.0	(396)

clutches completed between 7 and 15 May. The high mortality of late chicks in 1974 coincides with warm weather (cf. Ytreberg 1956, Harris 1964) but c-chicks were disproportionately affected (Fig. 5).

During both seasons, mortality of the chicks in the first week was seen to depend very strongly upon egg volume and the weight of newly hatched chicks (Table 5). The results of these years are so similar that the data can be combined in the classes ab-, c- and abc-eggs. Mortality was zero for the heaviest chicks and for those hatched from the largest eggs, but was very high in the smallest eggs and chicks. The differences were greater for the c-chicks than for a- and b-chicks. Mortality of the c-chicks decreased steadily with the increase of egg volume and very sharply with the increase of chick weight.

In order to compare the effects of different variables upon chick mortality, the familiar normalization was made by reducing from the different egg dimensions and chick weights the 1974-75 mean of the variable in question and dividing the rest by the standard deviation. The transformed means thus be-

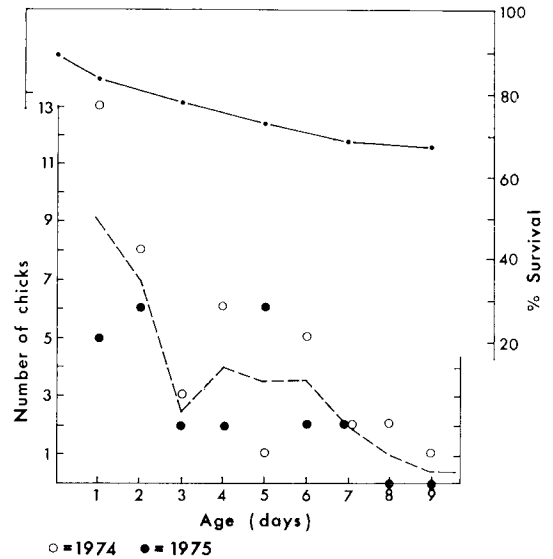


FIGURE 3. Number of dead chicks found during the first nine days after hatching (below) and survival of the chicks of the population for 83 three-egg clutches during at least nine days in 1974 or 1975. Dashed line shows the mean for 1974 and 1975.

came zeros and standard deviations one. Because the distributions were \pm normal, there remained too few observations outside the range ± 2.5 for the analysis (Table 6).

Accordingly, mortality was considered in five classes: class means are -2, -1, 0 (= \bar{x}), +1 and +2, and class intervals = 1 and the observations of classes -3 and +3 will be included in classes -2 and +2, respectively. Chick weight (Fig. 6.1) clearly affected survival, especially in very small chicks. In the classes of larger chicks the survival per-

TABLE 3. Variation in egg dimensions and chick weight in relation to the hatching sequence (\sim laying sequence). Number of observations for a-, b- and c-eggs is 156 (Σ N 468) and for chick weights, 125 (Σ N 375).

		a	b	c	abc
Length (mm)	\bar{x}	52.37	52.05	51.81	52.07
	SD	2.13	2.03	2.04	2.08
	CV	4.1	3.9	3.9	4.0
Breadth (mm)	\bar{x}	36.81	36.90	36.56	36.76
	SD	1.05	1.10	1.02	1.06
	CV	2.9	3.0	2.8	2.9
Shape	\bar{x}	142.32	141.10	141.73	141.72
	SD	6.32	5.53	5.33	5.75
	CV	4.4	3.9	3.8	4.1
Volume (cm ³)	\bar{x}	33.97	33.94	33.19	33.70
	SD	2.50	2.68	2.55	2.60
	CV	7.4	7.9	7.7	7.7
Chick weight (g)	\bar{x}	26.00	25.94	24.87	25.61
	SD	2.78	2.75	2.78	2.77
	CV	10.7	10.6	11.2	10.8

TABLE 4. Explanation of the hatching weight of the chick by egg dimensions. EL = egg length, EB = egg breadth, ES = egg shape, EV = egg volume (cm³), JWE = chick weight (g); ML = clutch length (mean for the three eggs of the clutch; a, b, and c in the hatching sequence), MB = clutch breadth, MS = clutch shape, MV = clutch volume, MJWE = mean chick weight. R² indicates the fraction of variance explained by a model.

Correlations	a-egg (125)				b-egg (125)				c-egg (125)				abc-eggs (375)			
	EB	ES	EV	JWE	EB	ES	EV	JWE	EB	ES	EV	JWE	EB	ES	EV	JWE
EL	.21	.79	.69	.44	.38	.71	.74	.52	.43	.72	.77	.61	.34	.74	.73	.53
EB		-.44	.85	.66		-.39	.90	.71		-.32	.90	.74		-.38	.89	.71
ES			.10	-.09			.04	-.03			.11	.07			.09	.02
EV				.72				.76				.80				.77

Regression models				Clutch means (125)				
			R ²		MB	MS	MV	MJWE
a-egg	JWE = -1.82 + 0.820 EV		52.0%					
b-egg	JWE = -0.97 + 0.792 EV		57.9%	ML	.40	.72	.76	.60
c-egg	JWE = -3.27 + 0.848 EV		64.5%	MB		-.34	.90	.78
abc-eggs	JWE = -2.43 + 0.832 EV		58.9%	MS			.10	.36
Clutch means	MJWE = -2.57 + 0.836 MV		70.1%	MV				.84

centages were about the same, 90 on an average. The c-chicks were less successful than ab-chicks in all classes. The same phenomena as with chick weight were observed with egg volume (Fig. 6.2) and chick survival. The disadvantage of the c-chick in the -2 class was as high as 35%, compared with the ab-chicks. The relationship of egg breadth (Fig. 6.3) and chick survival was almost linear in the ab- and abc-eggs. In the c-chicks there was considerable difference between the three smallest and two largest breadth classes. The ab-eggs of medium length (Fig. 6.4) were some 25% units more successful than the smallest eggs and some 5% more successful than the longer eggs. The diagram for the egg shape (Fig. 6.5) differs from the others. In classes close to the

mean (-1, ±0 and +1) the survival values are about the same and the difference between the ab- and c-eggs is also largest there. Chicks from broad short eggs were more successful than those from narrow long ones.

When comparing the relationships of different variables to chick survival (Fig. 6.6) in small eggs (class -2), we can order the variables in the following way: mortality is highest in lightest chicks and survival increases by 10% in the dimensional variables: volume, length and breadth, in this order. It is, thus, most fatal for a chick to be light at hatching, and least disadvantageous to be hatched from an egg with small breadth. In the +2 class the best survival (~ 100%) is found in chicks hatched from the eggs with the largest volume or breadth. The difference

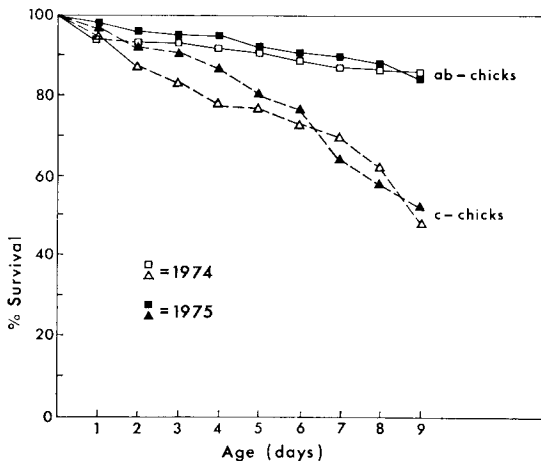


FIGURE 4. The survival of chicks in 1974 (open) and 1975 (black), the ab- and c-chicks shown separately.

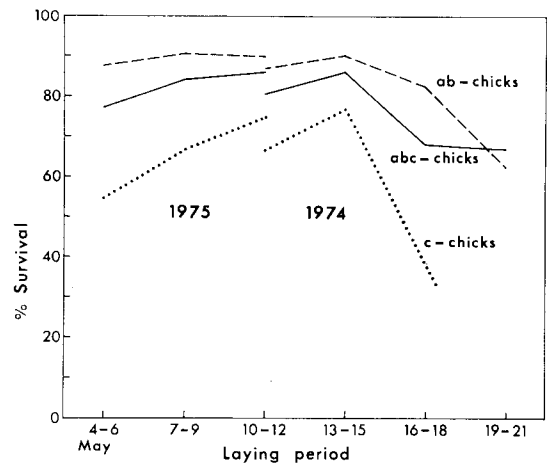


FIGURE 5. Relationship between the date of laying of the clutch and the first seven days of post-hatching chick survival.

TABLE 5. Survival of chicks (in %/N) of different egg sizes and hatching weights in the first week after hatching. Letters a, b and c refer to the hatching order (~ = the laying order) of the eggs in the clutches of three eggs.

Egg volume (cm ³)	1974		
	ab	c	abc
24-26	100.0/ 1	50.0/ 2	66.7/ 3
27-29	75.0/12	33.3/ 6	61.1/18
30-32	76.3/38	61.9/21	71.2/59
33-35	94.5/55	76.7/30	88.2/85
36-38	88.9/27	100.0/ 5	90.6/32
39-41	100.0/ 5	100.0/ 2	100.0/ 7

Egg volume (cm ³)	1975		
	ab	c	abc
24-26	-	-	-
27-29	50.0/ 2	0.0/ 2	25.0/ 4
30-32	83.8/37	61.1/18	76.4/55
33-35	90.7/43	68.8/16	84.7/59
36-38	100.0/20	100.0/ 3	100.0/23
39-41	100.0/ 5	-	100.0/ 5

Egg volume (cm ³)	1974 + 1975		
	ab	c	abc
24-26	100.0/ 1	50.0/ 2	66.7/ 3
27-29	71.4/14	25.0/ 8	54.5/ 22
30-32	80.0/75	61.5/39	73.7/114
33-35	92.9/98	73.9/46	86.8/144
36-38	93.6/47	100.0/ 8	94.5/ 55
39-41	100.0/10	100.0/ 2	100.0/ 12

Hatching weight (g)	1974		
	ab	c	abc
16-18.9	-	100.0/ 1	100.0/ 1
19-21.9	66.7/ 6	20.0/10	37.5/16
22-24.9	82.4/34	66.7/12	78.3/46
25-27.9	92.7/41	95.2/21	93.5/62
28-30.9	91.3/23	85.7/ 7	90.0/30
31-33.9	100.0/ 7	100.0/ 1	100.0/ 8
34-36.9	100.0/ 1	-	100.0/ 1

Hatching weight (g)	1975		
	ab	c	abc
16-18.9	-	-	-
19-21.9	50.0/ 2	25.0/ 4	33.3/ 6
22-24.9	70.8/24	72.7/11	71.4/35
25-27.9	92.7/41	66.7/15	85.7/56
28-30.9	100.0/24	75.0/ 4	96.4/28
31-33.9	100.0/ 4	-	100.0/ 4
34-36.9	-	-	-

Hatching weight (g)	1974 + 1975		
	ab	c	abc
16-18.9	-	100.0/ 1	100.0/ 1
19-21.9	62.5/ 8	21.4/14	36.4/ 22
22-24.9	77.6/58	69.6/23	75.3/ 81
25-27.9	92.7/82	83.3/36	89.8/118
28-30.9	95.7/47	81.8/11	93.1/ 58
31-33.9	100.0/11	100.0/ 1	100.0/ 12
34-36.9	100.0/ 1	-	100.0/ 1

in survival of the extreme classes (-2 and +2) is about 50% in chick weight and egg volume, and about 30% in egg length and breadth.

CHICK SURVIVAL IN RELATION TO THE AVERAGE PARAMETERS OF THE CLUTCH

Finally, we studied the dependence of chick survival upon the relative sizes of the eggs within the clutch. The following variables were chosen for study: S = chick survival during the first seven days of age (number of chicks alive at the age of seven days, range 0-3); mean length (ML), mean breadth (MB), mean shape (MS), mean volume (MV), and MJWE of the eggs in a clutch, and the mean weight of a newly hatched chick; range values within a clutch (the difference between the largest and the smallest egg/chick, usually a - c) in relation to length (RL), breadth (RB), shape (RS), volume (RV) and chick weight (RJWE). The data consisted of 86 three-egg clutches, in which each variable was measured and each young had been under observation for seven days.

In the population studied, chick survival was highest when the mean egg size and mean chick size were high, and when within-clutch differences were small (Fig. 7). The survival of the chicks was better the larger the mean of the clutch in egg length ($P < 0.01$; one way analysis of variance between the four clutch classes), egg breadth ($P < 0.05$), egg shape (NS), egg volume ($P < 0.01$) and chick weight ($P < 0.01$). Chick survival was higher when within-clutch variability of egg length ($P < 0.01$) or egg volume was small ($P < 0.05$).

DISCUSSION

CORRELATION BETWEEN EGG SIZE AND CHICK MORTALITY

Post-hatching survival was first found to be related to egg size in the Herring Gull (Parsons 1970; the data for 1970 in Davis 1975). However, Davis (1975) found that this correlation broke down in the second year of his study, 1972; he concluded that "the correlation between egg-size and chick survival in 1970 (and in the results of Parsons 1970) may be an artefact of the age structure."

In the Common Tern, egg size is correlated with survival of chicks hatched from third eggs (two small sets of data with the same results, Nisbet 1973). Since we found a clear correlation between egg size and chick mortality in the present study, Davis's 1972

TABLE 6. Number of ab- and c-eggs in the classes of normalized data for Figure 6.

	Classes								
	-3	-2	-1	±0	+1	+2	+3		
Egg length	ab	1	16	49	108	50	18	3	245*
	c	-	11	25	45	19	5	-	105*
Egg breadth	ab	-	18	52	79	74	21	1	245
	c	2	7	27	43	21	5	-	105
Egg shape	ab	-	16	69	88	57	10	5	245
	c	-	5	31	40	22	7	-	105
Egg volume	ab	1	11	52	89	74	16	2	245
	c	2	8	25	46	20	3	1	105
Chick weight	ab	1	7	58	55	62	16	8	207
	c	3	12	23	26	17	4	1	86

* Proportionately more ab- than c-chicks were studied for the first week after hatching because the observation period was restricted.

results appear to be deviant and based on few data. In 1972 he observed that medium-sized chicks, hatched from medium-sized eggs, unexpectedly were successful compared with young hatched from large eggs. In weight classes of larger young, with high mortality, the material consisted of 37 young, 46% of which fledged (Davis 1975: Table 5). The small data base may have been affected by disturbance caused by the investigator, which

he mentioned. His conclusions on the effect of the age of the Herring Gull female upon egg size were also based on only seven females.

Coulson (1963) did not find any correlation between age and egg dimensions in the Black-legged Kittiwake (*Rissa tridactyla*), but his data were likewise scanty. In the Arctic Tern (*Sterna paradisaea*) egg volume increased slightly with age, according to Coul-

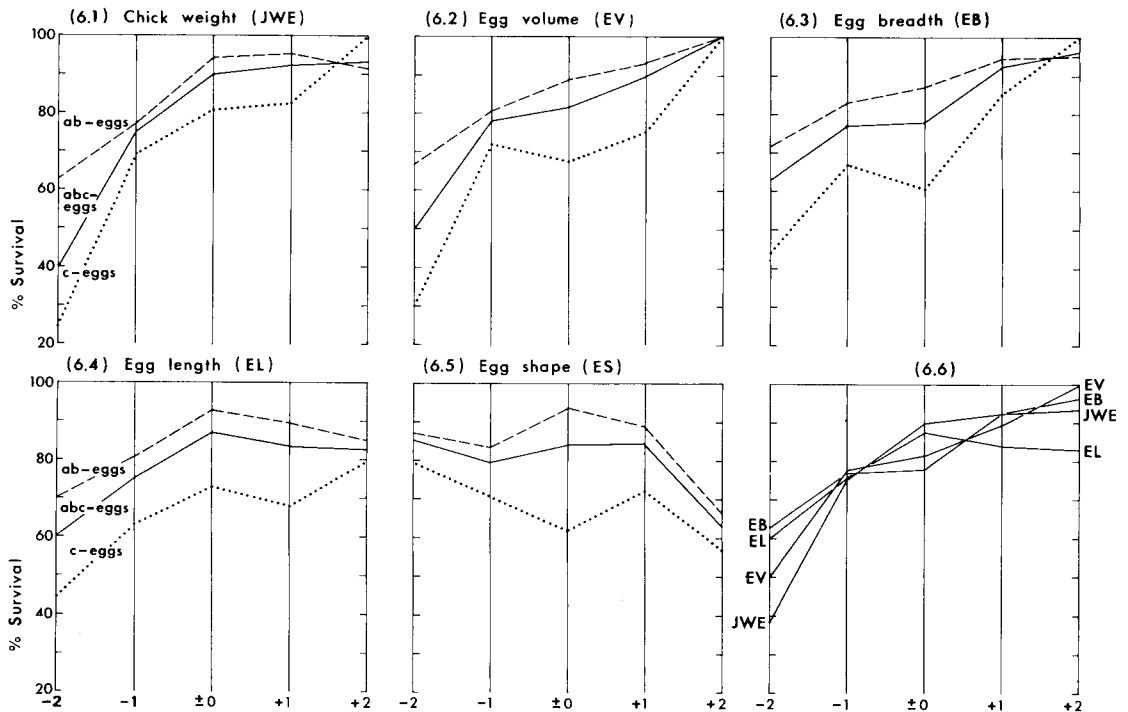


FIGURE 6. Chick survival in the first week after hatching in relation to various egg dimensions and chick size variables (normalized classes). Values for the first two eggs (ab), the third (c) egg and all eggs (abc) of the clutch are given for (6.1) chick weight, (6.2) egg volume, (6.3) egg breadth, (6.4) egg length, (6.5) egg shape and (6.6) diagrams for abc-eggs for JWE, EV, EL and EB. Numbers of observations in Table 6.

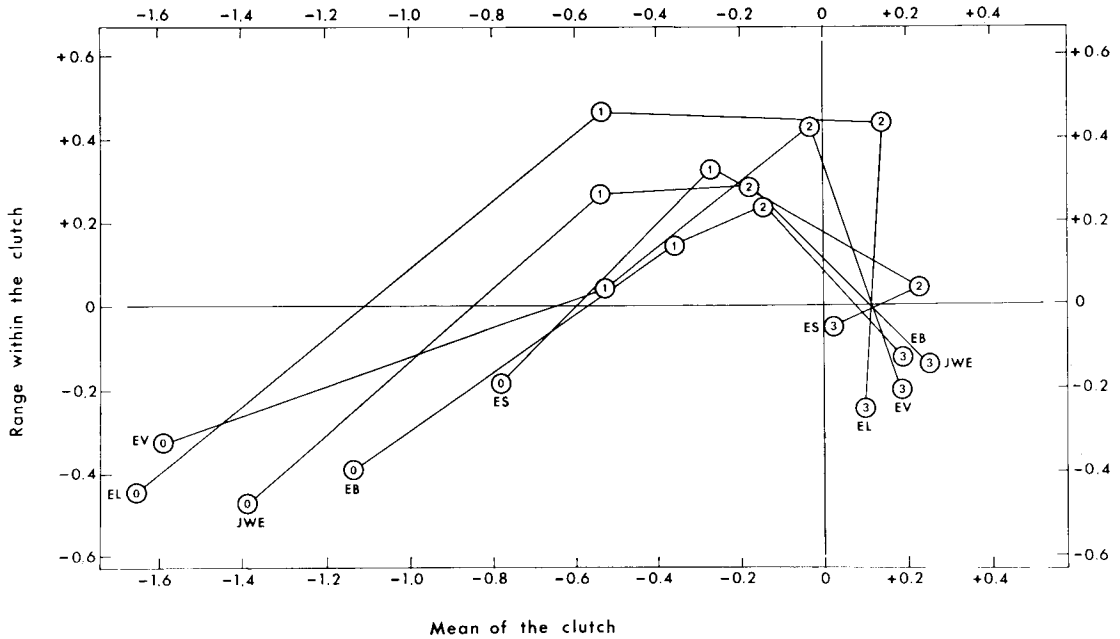


FIGURE 7. Normalized means for the four clutch-survival classes: no chicks ($N = 3$ clutches), one chick ($N = 7$), two chicks ($N = 25$) and all three chicks ($N = 51$) alive after the first week after hatching. Mean of the eggs of the clutch (x-axis) and the range between the eggs within the clutch (y-axis) are graphed for the following variables: egg length (EL), breadth (EB), shape (ES) and volume (EV), and the weight of the newly-hatched chick (JWE).

All three chicks died, if mean was very small and range was also small; one or two chicks died, if mean was larger and range large; all three chicks survived, if mean was large and range small (= three large eggs of rather similar size in the clutch). For statistical significance of the differences between the classes, see text.

son and Horobin (1976). Using their data, we calculate that the mean for three-year-old birds was 7.0% and for four- to five-year-olds, 1.8% smaller than the mean of six-year or older birds. Samples were not, however, from the same marked females in various age classes. The effect of age on egg size was masked in a year when much less food was available and the mean egg volume reduced by about 3% from the normal mean.

SELECTION PRESSURES FOR LARGE EGG SIZE

Heritability (h^2) roughly means the heritable part of variation. Heritability values range from zero (all variation is due to environmental factors) to one (all variation is due to additive genetic factors). The heritability of egg size in the Great Tit (*Parus major*) breeding in natural environments has been estimated using daughter-dam regression. The h^2 of egg weight in the Oxford population was 0.72 ± 0.11 (Jones 1973) and that of egg volume in the Oulu population (northern Finland) 0.86 ± 0.29 (Ojanen et al. 1979). However, in most bird species that have been studied a fairly large part of variation in egg size seems to be heritable, 0.5–0.7. This can

be estimated from the phenotypical female component by measuring a sample with several clutches from each female (Ojanen et al. 1979). We know of no estimates of heritability for larids. In the Black-headed Gull we observed that selection favors large mean egg size in a clutch. If the heritability of the egg size of larids was close to the above-mentioned 0.5, and if opposite selection pressures were missing, the egg size of populations would increase rapidly. Even if h^2 was no more than about 0.1, opposite pressures still must be prominent, as there is no progressive increase in the egg sizes of gulls. For future research, we propose that the following hypothetical factors oppose the selection for large egg size:

1. It is of advantage to breed early (cf. the Great Tit results by Perrins 1965) and yet at the same time as the other pairs of the colony. Thus, if a female were to increase egg size in the early spring, when there is often less food available, she might be delayed from the others.

2. Body size and egg size seem to be controlled partly by independent and partly by the same (pleiotropic) polygenes (cf. results

on the domestic fowl [*Gallus gallus*], Festing and Nordskog 1967) and selection pressures opposed to large body size might act indirectly, decreasing egg size.

3. The larger the mean egg size of a female, the more energy is required to produce the clutch. This strain influences a female's other activities of incubating the clutch and caring for the young.

4. In the Common Tern, courtship-feeding seems to be of great nutritional importance to a female at the time when she is forming eggs (Nisbet 1973). A large egg size would then be restricted by a male's ability to bring food to a female.

IMPORTANCE OF EGG SIZE VARIATION WITHIN CLUTCHES

Variation of egg dimensions within clutches is considerably smaller in several other avian species than in larids (Väisänen et al. 1972; also see Ojanen et al. 1979). In regulating the production of young, is it possible in larids to speak of a mechanism based on *egg size*, as opposed to one based on *clutch size* such as is found in many passerines (Ojanen et al. 1979)?

Since in larid clutches the third egg is about 4% smaller than the other eggs, calculated from the clutch mean (Väisänen et al. 1972), the mortality of the c-chick is expected to be higher, as has been ascertained in this study and others referred to above. Mortality of the c-chick is increased also by later hatching time as well as ethological factors (see Parsons 1970). The "effective" number of eggs in a gull clutch is thus really not two or three, but something intermediate, because the eggs are not equal as far as their probability of producing chicks is concerned.

The third egg produces a chick in favorable conditions, especially if plenty of food is available during the first days of life. Possibly the size of the population is regulated thus: if the pair density is low in relation to food resources, there is enough food for the c-young and relatively often it is fledged. If, on the other hand, the population is at the upper limits of resources in relation to the amount of food available when the chicks are reared, the survival of the c-chick is poor; in most cases it dies within a few days and so food is saved for the other young.

Let us compare this mechanism with that apparent in many passerine birds. In the Great Tit, for example, the size of the clutch varies considerably within the female (especially within the season) but the within-clutch

differences in egg dimensions are small (Ojanen et al. 1978, 1979); in other words, it is advantageous to produce one egg less in unfavorable conditions, in order to give chicks better nutrition. By decreasing egg size the survivorship of all young in the clutch would be lower.

Our examples of mechanisms based on egg size and clutch size for regulating the production of young are, of course, extremes—intermediate cases are to be found. Shorebirds, for example, usually have a constant clutch size, but within-clutch differences in egg dimensions are small (Väisänen et al. 1972, Väisänen 1977). There is no advantage to shorebird chicks, who seek their own food, being unequal as far as the influences of egg size are concerned. In owls, on the other hand, the hatching sequence of the young causes strong competition for food, which probably masks tiny differences in juvenile survival resulting from the variations in egg size within the clutch. Still there are species (e.g., the Great Tit; Ojanen et al. 1979) in which individual clutch size varies strongly, but within-clutch differences in egg size are small (and hatching takes place synchronously). Comparison of these with larids in our model for regulating production of young helps us to understand the importance of variation in egg dimensions.

In the Herring Gull, Parsons (1976) found that the presence of the a-egg stimulates brooding behavior. Further, he found that the onset of incubation affects the size of the c-egg (7.4% smaller than the a-egg), especially reducing the amount of albumen (8.1%) and to a lesser degree the size of the yolk (2.2%). There could be some advantage in laying a smaller c-egg, as it would reduce the incubation period of this egg and therefore the asynchrony of hatching within the clutch and the mortality of the c-chick.

In the Black-headed Gull we found that selection favors small differences in egg size within clutches, i.e., it tends to decrease the differences in egg size within a clutch. This conclusion implies that in larids egg size differences within the clutch are partly controlled genetically. In this case the reduction of the c-egg due to the onset of incubation may be partly regulated genetically, if the mechanism described in the Herring Gull (above) also exists in other gull species.

In our study area, differences in size between the ab-eggs and the c-egg were, on the average, small compared with the Oslo material (Ytreberg 1956, also see Results).

This is just what might be expected if selection had decreased the difference in size between the ab- and the c-eggs during the recent huge increase of this population. The variation in egg dimensions within a larid clutch must not be interpreted as environmental variation. Note too that a study of heritability requires separating the heritability of the mean egg size in a three-egg clutch as well as that of the size difference between the ab- and the c-egg.

Our model for regulating population size, partly based on egg size, might be able to stabilize a larid population of certain size in an aquatic habitat. The mechanism might be especially effective in a species whose life-span is long and annual production of young is small. Here we may draw attention to two types of evolutionary patterns based on demographic parameters, r- and K-selection (MacArthur and Wilson 1967, see also Pianka 1970, 1972): (1) r-selection is selection for reproductive potential, favoring rapid increase in populations, accompanied by selection for early reproduction, rapid development and short life. Species that are relatively r-selected occur in unpredictable environments, their mortality is often catastrophic (nondirectional, density-independent), and population size varies in time. (2) K-selection favors competitive ability through specialization for efficient exploitation of limited resources in fairly constant and/or predictable environments. In such species mortality is more directed (density-dependent), population size is at or near carrying capacity of the environment, body size is larger, reproduction is delayed and life-span is longer.

The species taken as examples for our regulation mechanisms, the Great Tit and the larids, also exemplify r- and K-selection, respectively (body size, age and rate of reproduction, fluctuation in population size). Southwood (1976) named the Blue Tit (*Parus caeruleus*) as an extreme example of an r-selected bird species. Of course, K-selection may, owing to recent population increase, temporarily have relaxed in our Black-headed Gull population. Regulating the production of young may thus be related to r-selection when based on clutch size, and related to K-selection when based on egg size.

SUMMARY

The correlation between dimensions of 450 eggs and chick mortality in the Black-headed Gull was studied in 1974 and 1975 in a colony in Finland. Egg dimensions were measured

and the date of laying, hatching sequence of eggs, hatching weight of the chicks, as well as survival of 350 chicks during the first week of living were determined.

Survival rates of a- and b-chicks were not different, but c-chicks, which hatched from eggs 4% lighter in weight had 20% higher mortality. The chick weight and egg dimensions were put in the following order of importance in relation to chick survival: hatching weight of the chick (most important), egg volume and egg breadth, egg length, and egg shape. In normalized data the survival (seven days) of chicks from eggs of the smallest volume class (-2 from the mean) was 50%, in somewhat larger eggs (-1) 78%, and in the largest eggs (+2) 100%. The survival values for the weight classes of the chicks were 39%, 75% and 92% (classes -2, -1, and in the third value classes ± 0 , +1 and +2 together). The results were similar in both years. In clutch-based analyses, selection seemed to favor large mean egg and chick sizes, but decreased within-clutch differences in egg and chick sizes.

Selection pressures, which prevent a continuous increase of egg size in larids, are discussed. A mechanism based on egg size for regulation of production of young is presented, as opposed to a mechanism based on clutch size for regulation of production of young. The former can be found in larids, and is related to K-selection; the latter can be found in many passerines, e.g. the Great Tit, and is related to r-selection.

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LITERATURE CITED

- COULSON, J. C. 1963. Egg size and shape in the Kittiwake (*Rissa tridactyla*) and their use in estimating age composition of populations. Proc. Zool. Soc. Lond. 140:211-217.
- COULSON, J. C., AND J. HOROBIN. 1976. The influence of age on the breeding biology and survival of the Arctic Tern *Sterna paradisaea*. J. Zool. 178:247-260.
- DAVIS, J. W. F. 1975. Age, egg-size and breeding success in the Herring Gull *Larus argentatus*. Ibis 117:460-473.
- FESTING, M. F., AND A. W. NORDSKOG. 1967. Response to selection for body weight and egg weight in chickens. Genetics 55:219-231.
- FREDRIKSON, K. A. 1940. Om skrattnåsens häckning

- på skärgårdsklippor och orsakerna till utflyttningen. *Ornis Fenn.* 17:59–63.
- GOODBODY, I. M. 1955. The breeding of the Black-headed Gull. *Bird Study* 2:1–119.
- HARRIS, M. P. 1964. Aspects of the breeding biology of the gulls, *Larus argentatus*, *L. fuscus* and *L. marinus*. *Ibis* 106:432–456.
- HELMÄKI, U. I. 1967. Tables and maps of precipitation in Finland, 1931–1960. *Meteorological Yearbook of Finland* 66 (Suppl. 2):1–22.
- JONES, P. J. 1973. Some aspects of the feeding ecology of the Great Tit *Parus major* L. Ph.D. thesis, Oxford University, Oxford.
- KOLKKI, O. 1966. Tables and maps of temperature in Finland during 1931–1960. *Meteorological Yearbook of Finland* 65 (Suppl. 1a):1–42.
- MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, NJ.
- NISBET, I. C. T. 1973. Courtship-feeding, egg-size and breeding success in Common Terns. *Nature* 241:141–142.
- OJANEN, M., M. ORELL, AND R. A. VÄISÄNEN. 1978. Egg and clutch sizes in four passerine species in northern Finland. *Ornis Fenn.* 55:60–68.
- OJANEN, M., M. ORELL, AND R. A. VÄISÄNEN. 1979. Role of heredity in egg size variation in the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scand.* 10:(in press).
- PARSONS, J. 1970. Relationship between egg size and post-hatching chick mortality in the Herring Gull (*Larus argentatus*). *Nature* 288:1221–1222.
- PARSONS, J. 1976. Factors determining the number and size of eggs laid by the Herring Gull. *Condor* 78:481–492.
- PERRINS, C. M. 1965. Population fluctuations and clutch-size in the Great Tit, *Parus major* L. *J. Anim. Ecol.* 34:601–647.
- PIANKA, E. R. 1970. On r and K selection. *Am. Nat.* 104:592–597.
- PIANKA, E. R. 1972. r and K selection or b and d selection. *Am. Nat.* 106:581–588.
- SOUTHWOOD, T. R. E. 1976. Bionomic strategies and population parameters. In R. M. May [ed.], *Theoretical ecology*. Blackwell Scientific Publications, Oxford.
- SVÄRDSON, G. 1958. Biotop och häckning hos skrattnåsen (*Larus ridibundus*). *Vår Fågelvärld* 17:1–23.
- VÄISÄNEN, R. A. 1969. Evolution of the Ringed Plover (*Charadrius hiaticula* L.) during the last hundred years in Europe. A new computer method based on egg dimensions. *Ann. Acad. Sci. Fenn. A IV* 149:1–90.
- VÄISÄNEN, R. A. 1974. Timing of waterfowl breeding on the Krunnit Islands, Gulf of Bothnia. *Ornis Fenn.* 51:61–84.
- VÄISÄNEN, R. A. 1977. Geographic variation in timing of breeding and egg size in eight European species of waders. *Ann. Zool. Fenn.* 14:1–25.
- VÄISÄNEN, R. A., O. HILDÉN, M. SOIKKELI, AND S. VUOLANTO. 1972. Egg dimension variation in five wader species: the role of heredity. *Ornis Fenn.* 49:25–44.
- YTREBERG, N.-J. 1956. Contribution to the breeding biology of the Black-headed Gull in Norway. Nest, eggs and incubation. *Nytt Mag. Zool.* 4:5–106.
- YTREBERG, N.-J. 1960. Some observations on egg-laying in the Black-headed Gull (*Larus ridibundus* L.) and the Common Gull (*L. canus* L.). *Nytt Mag. Zool.* 9:5–15.

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