ON THE ADAPTIVE VALUE OF INTRACLUTCH EGG-SIZE VARIATION IN BIRDS

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ABSTRACT.—Using data from the field and the literature on 67 species of birds, we analyzed intraclutch variation in egg size, especially the deviation of the last egg from the clutch mean (D). Values of D are closer to zero in precocial than in altricial species; D is negatively correlated with body size in interspecific comparisons, i.e. large birds, including precocial species, lay small final eggs; and D is higher in open-nesting passerines (on average $D = +3.56\%$, 17 species) than in hole-nesting species (on average $D = -0.05\%$, 13 species). Within populations of birds, a negative relationship exists between D and clutch size, particularly in species that have a generally low value of D.

The results support the view that intraclutch variation in egg size has an ultimate, adaptive value. We suggest that birds adopting the "brood-reduction strategy" have a small final egg, particularly those birds with large clutches, whereas birds adopting the "brood-survival strategy" have a relatively large final egg, particularly those birds with large clutches. Received 5 December 1983, accepted 19 April 1984.

BIRDS possess several mechanisms by which they can adjust the magnitude and pattern of their breeding effort in relation to environmental conditions and to their own breeding condition. The most important of these factors is clutch size (Lack 1954, O'Connor 1978, Lundberg and Väisänen 1979). Other proposed mechanisms are the sex ratio of the brood (Trivers and Willard 1973, Howe 1976, Fiala 1981), egg quality (Schifferli 1973, Howe 1978, Ricklefs et al. 1978, O'Connor 1979, Högstedt 1981, Birkhead and Nettleship 1982), hatching pattern (Lack 1954, Ricklefs 1965), and intraclutch egg-size variation (Parsons 1970, 1976; Howe 1976; Rydén 1978; Ojanen et al. 1981). When clutch-size adjustments and the influence of nest predation are excluded, a pronounced variation still is found among birds in the proportion of eggs that are successful. The hatchability of the eggs (Koenig 1982) and nestling mortality vary significantly. In many passerine birds, for example, nestling mortality from starvation is rather low (Nice 1957, Ricklefs 1969, Slagsvold 1982a), compared with that of some birds of prey in which one of the two young in the brood always dies (Stinson 1979, Edwards and Collopy 1983). It has been assumed that birds that lay relatively many eggs in relation to the number of young that they are normally able to feed (e.g. raptors) have adopted a brood-reduction strategy that en-

ables them to adjust the number of offspring they rear in relation to the environmental conditions that prevail during the nestling stage. This is brought about by hatching asynchrony, a phenomenon that results in a size hierarchy within the brood (Lack 1954, Ricklefs 1965, Hahn 1981, Slagsvold 1982a). Clark and Wilson (1981), however, cited data on the hatching patterns of several species of altricial birds and claimed that, rather than supporting the brood-reduction hypothesis, these data supported predictions adduced from a model based on the probabilities of nest failures occurring. In many species of passerine birds egg size increases with laying order, and this phenomenon is indeed difficult to explain by means of the brood-reduction hypothesis (Clark and Wilson 1981).

In the present paper, we report the results of an inter- and intraspecific comparison made with regard to such within-clutch egg-size variation. A large body of data now exists for a wide variety of bird species, and the time is ripe for a comparative analysis. The patterns of such egg-size variation seem fundamental to an understanding of overall reproductive strategies in birds.

THEORY

It has been assumed that the intraclutch variation in the size of birds' eggs has an ultimate,
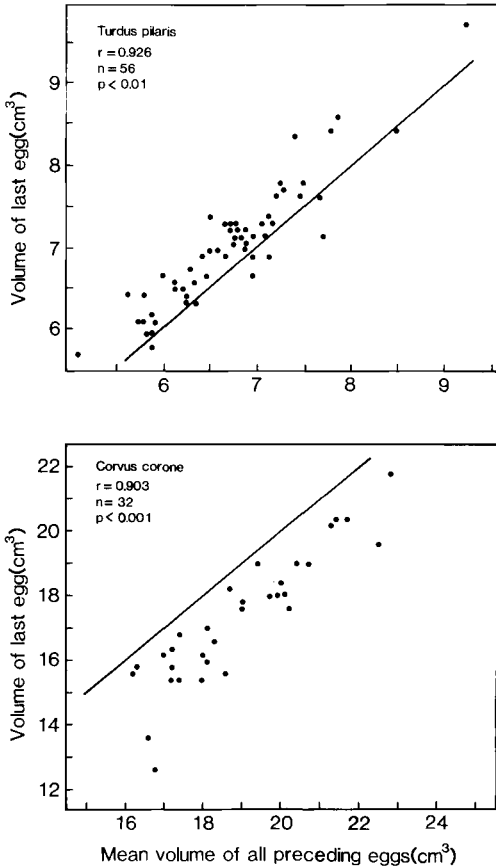
Fig. 1. The volume of the final egg laid in a clutch plotted against the mean value of the egg volume of all the preceding eggs laid in the same clutch. Data from Fieldfare and Hooded Crow clutches of 4 or 5 eggs. The $y = x$ lines have been entered.

adaptive value (Paludan 1952, Parsons 1970, Nisbet and Cohen 1975, Howe 1976, Rydén 1978, Lundberg and Väisänen 1979, O'Connor 1979, Edwards and Collopy 1983). This cannot yet be considered as proven, as the variation may simply reflect the condition of the egg-laying female (cf. Pinowska 1979, Drent and Daan 1980, Ojanen et al. 1981, Houston et al. 1983). The assumption seems reasonable, however, as distinctly different patterns are found between species, differences that are difficult to explain from energetic constraints alone [see also the experiments done by Paludan (1952) and Parsons (1976), and the review by Klomp (1970)]. For instance, the Fieldfare (*Turdus pilaris*) produces, relative to parental body size, a

larger egg mass per clutch than does the Hooded Crow (*Corvus corone cornix*). Yet the final egg laid by the Fieldfare is, in general, larger than the preceding eggs laid in the same clutch, whereas the final egg of the Hooded Crow is not larger than its preceding eggs (Fig. 1).

The results of several studies have indicated that the chances of survival of any particular nestling are related to the size of the egg from which it hatched (Parsons 1970; Schifferli 1973; Murton et al. 1974; O'Connor 1975, 1979; Ryder 1975; Howe 1976; Nisbet 1978; Lundberg and Väisänen 1979; Williams 1980a; Moss et al. 1981; Birkhead and Nettleship 1982), and we found that the final eggs of both the Black-billed Magpie (*Pica pica*) ($t = 3.56$, df = 15, $P < 0.01$) and the Hooded Crow ($t = 2.74$, df = 8, $P < 0.05$) that did not hatch were significantly smaller than those that did hatch (Table 1).

If the egg-size variation within the clutch has an adaptive value, this variation may be related to the hatching pattern of the bird. Richter (1982) argued that the nest-failure model of Clark and Wilson (1981) is not a biologically plausible, general explanation for hatching asynchrony, but rather is an alternative to the brood-reduction hypothesis, applying to species whose nestlings seldom starve but who frequently suffer nesting failures. Thus, some species of birds may hatch asynchronously to facilitate brood reduction, others to escape heavy nest predation (Tyrväinen 1969, Hussell 1972).

If such different breeding strategies do exist, viz. a "brood-reduction" and a "brood-survival" strategy, they may be accompanied by differences in intraclutch egg-size variation (cf. O'Connor 1978, 1979). In birds that hatch their eggs asynchronously, the nestling that hatches from the last-laid egg is at a disadvantage compared with its siblings. Laying a small final egg may therefore be another mechanism that facilitates brood reduction. On the other hand, birds adopting the brood-survival strategy are expected to have an egg-size increase with the laying order (Clark and Wilson 1981).

MATERIAL AND METHODS

Bird nests were located near Trondheim (63°N, 10°E), Norway, during the period 1980–1982. We found that there was a correlation between the relative size of the final egg laid within a clutch and the general egg-size variation within the same clutch,

TABLE 1. Mean volume (cm³) of Black-billed Magpie and Hooded Crow eggs.[a]

	Pica pica			Corvus corone		
	Mean	SD	n	Mean	SD	n
All eggs, complete clutches	8.98	1.09	520	18.46	2.08	518
Last eggs laid (hatched)	9.68	0.93	8	16.14	1.11	8
Last eggs laid (did not hatch)	7.87	1.16	9	14.77	0.44	2

[a] From nests in the vicinity of Trondheim (present study).

i.e. if the final egg was relatively small, there was also a decrease in the size of the eggs from the first to the penultimate egg. When we expressed the relationship between egg size and laying order of the $x - 1$ first eggs for each clutch by means of a regression slope and compared the value of this slope with the relative size of the final egg laid for the same clutch, we found $r = 0.55$ (16 clutches, $P < 0.05$) for the Hooded Crow. Thus, we use only the relative size of the final egg laid, calculated as the percentage deviation from the mean size of all the eggs in the clutch (D-value), in our comparisons. The final egg is more frequently identified than the other eggs in the clutch, and it is also biologically relevant to use this measure, as the hypotheses mentioned above pay special attention to the condition of the last young hatched.

Using field data and data from the literature, we estimated egg volume from egg length (L) and maximal breadth (B) by means of the formula $0.51\ LB^2$ (Hoyt 1979), except where otherwise stated (Appendix). Thus, all eggs within a clutch were assumed to have the same shape. Although this is not necessarily true, at present we do not have enought data available on egg-shape variation within clutches to adjust the volumes calculated. We compared the D-value calculated from egg-volume data with that calculated from fresh-egg-weight data for the same species and found a high correlation. Using only measurements of the same clutches for each species (at least four clutches measured), we found that $r = 0.98$ (9 species, $y = 0.973x + 0.19$); when adding 5 species with measurements mostly of the same clutches we found also that $r = 0.98$ (14 species, $y = 0.986x + 0.28$); excluding penguins, we found that $r = 0.87$ (9 species, $y = 0.941x + 0.45$).

Those mean values of egg size that were based on egg-weight data (see Appendix) were first reduced by 8% (Manning 1978) before being used in the analyses in order to make them comparable with egg-volume data, because the specific weight of fresh eggs is above unity. In the Appendix, the relative size of the final egg laid is calculated for various populations. In the interspecific comparisons, the weighed mean D-value for each species is used. The data have been presented separately for particular clutch sizes in the Appendix in all cases where the sample size

per clutch size was at least five nests. Body weight, as used in this paper, refers to the weights of adult females recorded in spring and was taken from the same papers from which the egg-measurement data were obtained, wherever possible, or from other sources, mainly from Hartman (1961), Haftorn (1971), and Clench and Leberman (1978).

RESULTS

Penguins.—Measurements of penguin's eggs are included in the Appendix to allow a comparison to be made with those of other birds, but these data were not used in our analyses because of the peculiar biology and unique phylogenetic position of penguins (e.g. Williams 1981). Most of the species would have fitted nicely into the patterns that emerged because, in all penguins except those belonging to the genus *Eudyptes*, the final egg laid in a clutch was smaller than the others. The second (final) egg of *Eudyptes* spp. is unique, however, in being much larger than the first one laid, and, generally, the nestling that hatches from this second egg is the only one to survive (Gwynn 1953, Warham 1975). The large final egg of *Eudyptes* spp. is very difficult to explain, as it seems to contradict what theory would predict.

Precocial and altricial birds.—If the relative size of the eggs in a particular clutch represents an adaptive mechanism that facilitates brood reduction, or prevents it from occurring, then we should expect to find such a mechanism primarily among altricial species of birds, as most of these species hatch asynchronously (Clark and Wilson 1981) in contrast to precocial birds. Thus, we predict that the deviation of the size of the final egg laid from that of the mean size of all the eggs in the clutch will be closer to zero in precocial than in altricial species of birds.

The results of our analyses support this prediction (Table 2), although the data for the pre-

TABLE 2. Comparison of the relative size of the final egg laid.[a]

Species group	Number of species	Mean deviation (%)	SD	Mann-Whitney U-test
Non-passerines				
Precocial	9	−0.68	1.77	$U_s = 35$
Altricial	19	−3.91	3.61	$P < 0.02$
Passerines				
Hole-nesters	13	−0.05	2.82	$U_s = 37$
Open-nesters	17	3.56	3.56	$P < 0.002$

[a] Data from Appendix; those for the penguins excluded.

cocial birds were rather few and mostly referred only to waders, and whether or not waders should be regarded as precocial may be questioned. The relative size of the final egg was rather similar in altricial and precocial species as a whole (−0.29, $n = 49$, for altricial, and −0.68, $n = 9$, for precocial), but the standard deviation was much higher in altricial birds, *viz.* 4.64 versus 1.77 ($P < 0.001$, test between the variances). The mean egg size of ducks (Koskimies 1957, Bezzel 1968) and of Willow Ptarmigan (*Lagopus lagopus*; Moss et al. 1981) seems to decrease as the laying sequence progresses, but this is not true of Black Swans (*Cygnus atratus*; Cutten 1966).

Body size.—Large birds are less vulnerable to nest predation than are small birds, and, thus, they would be expected to follow the brood-reduction strategy. Moreover, they lay relatively smaller eggs than those of smaller birds (Heinroth 1922, Lack 1968, Rahn et al. 1975), and the energy cost of incubating an egg is also relatively less for such birds (Ricklefs 1974). Large birds, therefore, would not seem to be so rigorously constrained by egg production and incubation, although this does not prove that
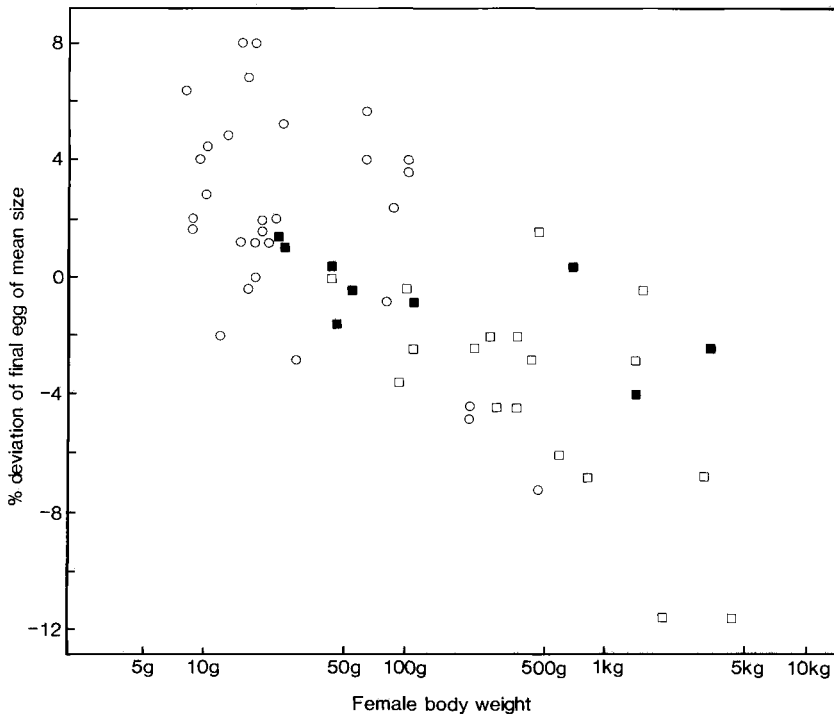

Fig. 2. The relative size of the final egg laid plotted in relation to the body weight of the adult female: $D = 7.66 - 1.776 \cdot \ln(\text{body weight})$. Mean values for each species have been used (from Appendix, penguins excluded). Symbols: open circles = passerine species; open squares = altricial, nonpasserine species; solid squares = precocial, nonpasserine species.

TABLE 3. Multiple correlation analysis of the relative size of the final egg.[a]

Species group	n	Simple correlation coefficients			Partial regression[b]		Multiple correlation coefficient
		Body weight[c]	Nest site[d]	Clutch size	Body weight[c]	Nest site[d]	R
Nonpasserines	28	−0.65***	−0.22	0.05	−0.64***	−0.03	0.66***
Passerines	30	−0.54**	0.49**	−0.07	−0.58***	0.54***	0.76***
Total	58	−0.74***	−0.04	0.35**	−0.85***	0.28**	0.79***

[a] Same data as used in Table 2; ** $P < 0.01$, *** $P < 0.001$.
[b] Standardized regression coefficients after inclusion of the two variables; clutch size yielded no significant contribution and was omitted.
[c] Log values for body weight of adult females.
[d] Hole-nesters vs. open-nesters.

these processes are less demanding in such birds (cf. Houston et al. 1983). The costs should preferably not be measured in energy units but in the cost of obtaining the amount of energy needed. Ricklefs (1974) concluded that the energetic cost of egg production relative to BMR in passerine birds does not change with body weight but that such a change is found in other groups of species.

If large birds have a tendency to lay a relatively greater excess of eggs per clutch than do small birds (i.e. not in absolute terms but in relation to the number of young that they are able to feed; e.g. raptors, Edwards and Collopy 1983), then most mortality will be due to starvation, a situation promoting the brood-reduction strategy. Thus, we would expect that large birds would be less likely to attempt to raise the last-hatched young and thus would not tend to give it a size advantage. We would therefore expect that a negative relationship should exist between the mean body size of a bird species and the relative size of the final egg laid in the clutch. The results support this prediction (Fig. 2, Table 3). The tendency for the final eggs laid by small birds to be relatively large was found to be as true for altricial birds ($r = -0.77$, $n = 49$, $P < 0.001$) as for precocial birds ($r = -0.74$, $n = 9$, $P < 0.05$). The log values of the body weights of adult females were used in these calculations, although the values of the correlation coefficients obtained for the relative size of the final egg plotted against the log value of the mean egg volume were of similar magnitude.

Open-nesting and hole-nesting passerine species.—
Open-nesting species of passerines lay fewer eggs per clutch than do hole-nesters, not only in absolute terms (Nice 1957, Lack 1968) but perhaps also in relation to their ability to rear the brood (Slagsvold 1982a). The hatchability of their eggs seems to be higher (Koenig 1982), but they also suffer a higher rate of nest predation (Lack 1968). Thus, open-nesters may be more likely to show hatching asynchrony as a response to nest failure and would be expected to try to offset the disadvantage to the last-hatched young (the brood-survival strategy). We therefore predict that open-nesters lay relatively larger final eggs than do hole-nesters.

The results support the prediction (Tables 2 and 3). In hole-nesters, the last egg laid was similar in size to the preceding eggs laid, whereas in open-nesters the final egg was about 4% above mean size. For passerine birds, the correlation coefficient for the relationship between the relative size of the final egg laid and the log values of body weight was $r = -0.54$ ($n = 30$, $P < 0.01$). When the type of nesting site was included, a further 28.6% of the variation could be accounted for. The multiple correlation coefficient then obtained was $R = 0.76$ (Table 3), accounting for a total of 58% of the variation among the passerine species in the relative size of the final egg laid.

*Clutch size.—*Within species, but not between species (Table 3), a negative correlation was found between the relative size of the final egg laid and clutch size. This is shown by counting the number of cases when a decrease or an increase in the mean D-value was found for an increase in clutch size from x to $x + 1$ eggs (Fig. 3). The D_{x+1} values were less than the respective D_x values in as many as 18 of the 24 investi-
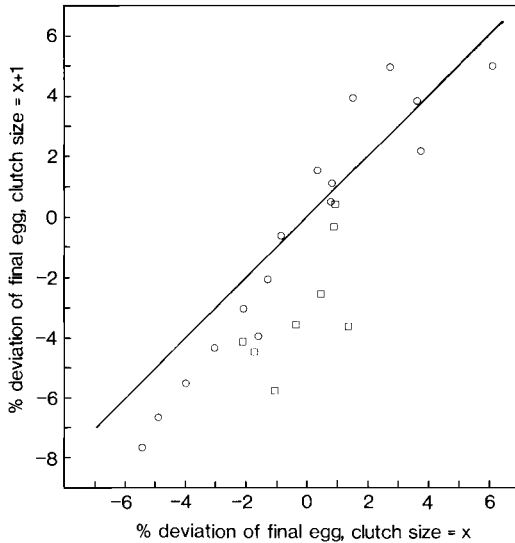
Fig. 3. The relative size of the final egg laid plotted against successively increasing clutch size (data from Appendix, penguins excluded). The $D_{x+1} = D_x$ line has been entered. Symbols as in Fig. 2.

TABLE 4. Correlation coefficients between the relative size of the final egg laid and (A) the mean egg volume for the same clutch, and (B) the date of egg laying (first egg).

Species	Clutch size	n	A Against mean egg volume	B Against laying date[a]
Turdus pilaris	5	24	−0.24	−0.21
	6	32	−0.05	0.07
	4–7	61	−0.15	−0.03
Pica pica	6	12	−0.15	0.57
	7	8	0.18	0.67
	8	7	0.05	0.05
	3–9	36	−0.01	0.40*
Corvus corone	4	9	0.30	−0.53
	5	23	0.23	0.31
	3–6	39	0.21	0.05

[a] *P < 0.05.

gated cases ($\chi^2 = 6.00$, $P < 0.02$). Notice also that more of the data plotted in Fig. 3 lay below the $D_x = D_{x+1}$ line for those species that yielded low D_x values than for those that yielded high D_x values. In other words, this decrease of the relative size of the final egg seems to be more pronounced in species adopting, by our interpretation, the brood-reduction strategy than in those adopting the brood-survival strategy. For instance, the average plot for each of the 6 large species in Fig. 3 fell below the line as compared with the average plot for only 5 of the 9 small species [large species: magpie (210 g) or larger; small species: Fieldfare (103 g) or smaller].

Mean egg'volume and time of egg laying.—We collected field data to determine whether or not there is any relationship between the relative size of the final egg, the mean egg volume of the same clutch, and the time of egg laying (Table 4) on the Fieldfare and the Hooded Crow (open-nesters, the latter with a body weight of 489 g) and the magpie (hole-nester). In none of these species was any tendency found in those individual birds that lay large eggs to lay a particularly deviant (either small or large) final egg in the clutch (Table 4), nor was there any consistent tendency for the final egg in clutches laid late in the breeding season to be particularly small or large (Table 4). The only statis-

tically significant correlation obtained was that for the magpie, when the data for all clutch sizes were pooled. The partial correlation coefficients obtained were also nonsignificant for all three bird species investigated when clutch size and egg laying date were kept constant.

DISCUSSION

The results of the present study support the view that the intraclutch variation in the size of birds' eggs is a mechanism that has an ultimate, adaptive value that is used in combination with asynchronous hatching. The eggs of most altricial bird species hatch asynchronously (Clark and Wilson 1981). A large final egg will increase the probability that the nestling hatched from such an egg will fledge successfully. Thus, the parents that practice the brood-survival strategy will benefit from certain advantages offered by asynchronous hatching, other than facilitation of a reduction in brood size, such as a shortening of the time between the onset of egg laying and the time the first nestling fledges (Tyrväinen 1969) and a staggering of the periods of peak food demand by the young (Bryant 1978).

We consider that the contrast between the relative size of the final egg of open-nesting and that of hole-nesting species of passerines is of particular importance in providing a clue for an understanding of the breeding strategies adopted by birds in general. The open-nesting
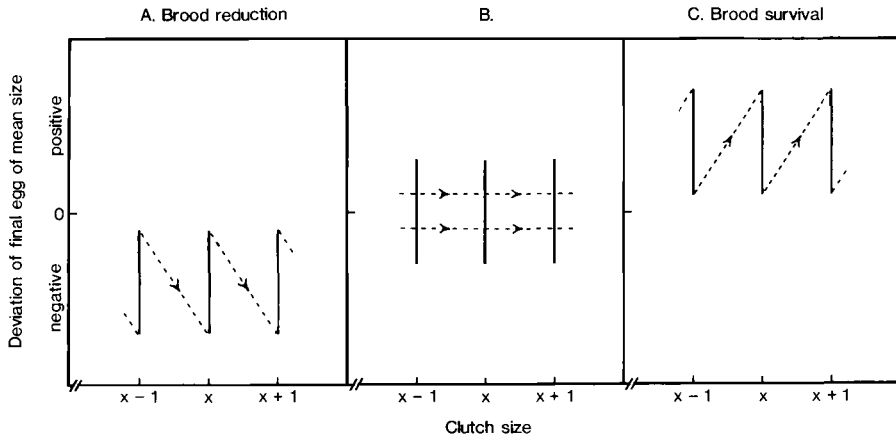
Fig. 4.   Proposed relationship between the relative size of the final egg laid and change of clutch size, for three patterns of breeding strategies. A third dimension has also been included, *viz.* the conditions for breeding, illustrated by the dashed lines (arrows indicating expected change as conditions are improved).

passerines lay fewer eggs than the hole-nesters, but the final egg they lay in a clutch is large. The smaller clutch size of open-nesters cannot therefore simply be explained by energetic constraints on the egg-laying females. There are at least three explanations for the reduction in clutch size: the higher costs of incubating many eggs, in particular in open nests (Biebach 1981, Slagsvold 1982a); the increased mortality of nestlings because of overcrowding and falling out of the nest (Slagsvold 1982a); and the higher rate of nesting failures. Open-nesting passerines run a serious risk of nesting failure because of a sudden onset of bad weather and a high degree of nest predation (Nice 1957, Ricklefs 1969). These factors may select for a reduction in the number of eggs laid in each single attempt to nest and for an increase in the ability of open-nesters to renest quickly (Skutch 1949, Snow 1978, Ewald and Rohwer 1982, Slagsvold 1982b).

As mentioned above, it is possible that the birds use within-clutch egg-size variation to adjust the clutch and the brood to the prevailing conditions for breeding, although no direct evidence exists as far as we know. Figure 4 illustrates three possible patterns of these adjustments on the individual-bird level. For a certain clutch size, it is assumed in Fig. 4A that a positive relationship exists between the relative size of the final egg laid and the prevailing breeding conditions. The switch from one level of clutch size to a higher level at im-

proved conditions (indicated by dashed lines and arrows) is one from a clutch of *x* eggs, with a relatively large final egg, to a clutch of $x + 1$ eggs, with a relatively small final egg. Figure 4C represents just the opposite pattern, whereas a third possibility, that no such relationship exists at all between clutch size and the relative size of the final egg laid, is illustrated in Fig. 4B.

We would expect the pattern in Fig. 4A to apply in species of birds that have adopted the brood-reduction strategy; if the clutch is increased by one egg, it is important that this egg is a small one so that the brood-reduction mechanism would operate effectively. On the other hand, birds adopting the brood-survival strategy should lay a particularly large final egg on the changeover from *x* to $x + 1$ eggs or at least a final egg of no reduced size, because the last young to hatch would be more at a disadvantage in a large brood (i.e. Fig. 4C or B).

The patterns in Fig. 4 are qualitatively supported by the results given above (Fig. 3). We encourage further studies of these relationships, however, as possible concomitant changes in general egg size and in hatching pattern have not been included in the model because they are not known. For instance, if the general egg size is small, it may be of greater importance that the final egg is large than when all eggs are large. Moreover, if the conditions for breeding are improved, it is possible that the mechanism of response adopted by

birds is to hatch more synchronously. This would improve the probability of survival of the young hatched from the final egg laid, and then no concomitant change in the relative size of the final egg may be needed (i.e. the pattern shown in Fig. 4B may then be expected).

If the mean egg size of a clutch reflects the conditions for breeding (e.g. Högstedt 1981), we would expect a positive correlation to be found between mean egg size and the relative size of the final egg laid for species adopting the brood-reduction strategy but not for those adopting the brood-survival strategy (cf. Fig. 4). Thus, for selected clutch-size levels, we would expect positive correlation coefficients to be found for the magpie and the Hooded Crow, and negative values for the Fieldfare. Table 4 indicates that 6 of 7 coefficients had the predicted sign. The random probability that all, or all-but-one, of the coefficients should have the predicted sign is $P = 8 \cdot (0.5)^7 = 0.063$ (one-tailed test). Statistically, however, no single coefficient significantly deviated from zero (Table 4).

Karlsson (1983) provided European Starlings (*Sturnus vulgaris*) with extra food. The birds advanced the time of egg laying and laid larger eggs, but they changed neither clutch size nor the relative size of the final egg laid (which was 1.9% and 1.0% smaller than the mean egg size, respectively, for the experimental and control clutches). Thus, this species seems to represent the pattern in Fig. 4B. It should be added, however, that, although the availability of food at the time of egg laying influences the condition of the female at this stage of the breeding period, it may not necessarily indicate to the female that the conditions for rearing young would be favorable later on. When provided experimentally with additional food, passerines lay larger eggs but do not seem to respond by laying larger clutches (Ewald and Rohwer 1982, Karlsson 1983; see Slagsvold 1982a for further references).

We would like to stress that the two breeding "strategies" proposed, brood reduction and brood survival, are indeed not well-documented entities and that a greater amount of loss by brood reduction following hatching asynchrony has not been demonstrated convincingly (Clark and Wilson 1981; but see Hahn 1981, Slagsvold 1982a). Thus, the existence of two such breeding strategies is possible but has not yet been proved. The present data support the in-

terpretation of the relative size of the final egg as an indication of a brood-reduction or a brood-survival strategy. The model shown in Fig. 4 is comprised of three dimensions: clutch size, relative size of final egg, and condition for breeding (dashed lines). Preferably, as mentioned above, we should also have included two more dimensions: general egg size of the clutch and the hatching pattern. Unfortunately, we have not yet information available for doing this, but we hope that our study would encourage further research to find out if, and how, birds use and combine all these factors to maximize their reproductive fitness.

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APPENDIX. Data from the literature and from our fieldwork on the clutch sizes, egg volumes, and sizes of last eggs laid of a number of species.

Species	Clutch size (range)	n	Mean egg volume (cm³)	Relative size of last egg (%)[a]	Source
Megadyptes antipodes	2	296	129.75	−0.28	Richdale 1957
Pygoscelis papua	2.19 (2–3)	16	123.91	−4.71	Gwynn 1953
	2	?	137.50[b]	−2.55	Williams 1980b
Pygoscelis adeliae	2	9	108.24	−3.40	Taylor 1962
	3	10	100.73	−10.47	Taylor 1962
	2.53 (2–3)	19	104.29	−7.12	Taylor 1962
	2	15	120.50	−2.07	Reid 1965
Eudyptes chrysolophus	2	13	114.32	24.31	Gwynn 1953
	2	?	127.50[b]	22.75	Williams 1980b
Eudyptes atratus	2	5	118.98	23.95	Warham 1975
Eudyptes crestatus	2.10 (2–3)	10	84.01	16.49	Gwynn 1953
	2	?	92.50[b]	17.84	Williams 1980b
Eudyptes pachyrhynchus	2	121	101.44	8.09	Warham 1974
Eudyptes robustus	2	23	102.16	12.87	Warham 1975
Spheniscus demersus	2	?	106.00[b]	−0.94	Williams 1980b
Phalacrocorax aristotelis	2	5	48.75[b]	0.92	Snow 1960
	3	40	49.22[b]	−0.34	Snow 1960
	4	10	51.00[b]	−3.53	Snow 1960
	3.09 (2–4)	55	49.50[b]	−0.81	Snow 1960
	2	26	45.04	0.90	Coulson et al. 1969
	3	127	46.97	0.47	Coulson et al. 1969
	4	38	44.75	−2.59	Coulson et al. 1969
	3.06 (2–4)	191	46.27	−0.07	Coulson et al. 1969
Ciconia ciconia	6	3	102.69	−6.67	Bloesch 1982
Branta canadensis	3.89	19	138.64	−2.53	Manning 1978
Melanitta fusca	ca. 8.5	12	88.93	ca.−4	Koskimies 1957
Aquila verreauxii	2	1	99.83	−4.33	Meyburg 1974
	2	22	122.60	−12.09	Gargett 1977
Hieraaetus fasciatus	2	1	97.89	−11.72	Meyburg 1974
Haematopus moquini	2	21	54.06	0.23	Summers and Cooper 1977
Charadrius hiaticula	4	23	10.99	−0.47	Väisänen et al. 1972

APPENDIX. Continued.

Species	Clutch size (range)	n	Mean egg volume (cm³)	Relative size of last egg (%)[a]	Source
Calidris temminckii	4	20	6.14	1.23	Väisänen et al. 1972
Calidris minutilla	4	11	6.54	1.36	Miller 1979
Calidris alpina	4	9	10.36	−1.66	Väisänen et al. 1972
Gallinago gallinago	4	8	15.79	−0.67	Tuck 1972
Phalaropus lobatus	4	9	6.59	0.36	Väisänen et al. 1972
Larus novaehollandiae	2	51	38.65	−1.09	Mills 1979
	3	12	35.97	−5.78	Mills 1979
	2.19 (2–3)	63	38.14	−1.98	Mills 1979
Larus atricilla	2.79 (2–3)	19	42.57	−4.18	Preston and Preston 1953
	3	5	39.31	−5.76	Schreiber and Lawrence 1976
Larus ridibundus	3	105	34.73	−3.66	Ytreberg 1956
	3	125	35.88	−1.56	Lundberg and Väisänen 1979
Larus delawarensis	3	43	51.78	−4.65	Vermeer 1969
	3	82	53.47	−2.12	Ryder 1975
Larus canus	3	138	49.69	−4.35	Barth 1967
Larus fuscus	3	62	71.25	−6.29	Paludan 1952
	3	59	73.21	−3.81	Harris 1964
	3	68	74.47	−4.70	58°N, Barth 1967
	3	44	69.50	−6.83	63°N, Barth 1967
	3	8	66.56	−6.70	69°N, Barth 1967
Larus argentatus	3	57	91.23	−6.48	Paludan 1952
	3	100	78.84	−7.79	Harris 1964
	3	18	92.37	−3.56	58°N, Barth 1967
	3	76	88.73	−5.39	63°N, Barth 1967
	3	59	94.00	−5.00	69°N, Barth 1967
	3	103	79.39	−7.33	Parsons 1972
	3	453	77.87	−7.17	Davis 1975
Larus californicus	3	18	72.58	−4.13	Behle and Goates 1957
	3	55	70.15	−6.83	Vermeer 1969
Larus marinus	3	35	101.36	−1.80	Harris 1964
	3	16	109.33	−2.72	58°N, Barth 1967
	3	93	107.95	−3.29	63°N, Barth 1967
	3	74	113.47	−2.79	69°N, Barth 1967
Rissa tridactyla	2	104	44.79	−2.09	Coulson 1963
	3	33	45.23	−4.12	Coulson 1963
	2.24 (2–3)	137	44.90	−2.58	Coulson 1963
	2	68	45.22	−2.09	62°N, Runde and Barrett 1981
	2	376	47.53	−1.77	69°N, Runde and Barrett 1981
	3	27	46.90	−4.47	69°N, Runde and Barrett 1981
	2.07 (2–3)	403	47.49	−1.95	69°N, Runde and Barrett 1981
Sterna dougallii	2	63	19.95[b]	−2.26	Nisbet and Cohen 1975
Sterna hirundo	3	22	20.09	−1.33	Gemperle and Preston 1955
	3	64	21.20[b]	−1.89	Nisbet and Cohen 1975
	3	112	19.61	−4.56	Gochfeld 1977
	3	10	20.24[b]	−4.59	Nisbet 1978
Columba palumbus	2	5	20[b]	2.00	Murton et al. 1974
	2	2	19.48	1.31	Present study
Apus apus	2	129	3.56[b]	1.40	O'Connor 1979
	3	49	3.50[b]	−3.63	O'Connor 1979
	2.28 (2–3)	178	3.55[b]	0.02	O'Connor 1979
Apus melba	3	21	5.92	−0.39	Arn-Willi 1960
Tachycineta bicolor	5	10	1.86[b]	3.76	Zach 1982
	6	24	1.79[b]	2.14	Zach 1982
	5.71 (4–7)	41	1.81[b]	2.09	Zach 1982
Hirundo rustica	5.00 (4–6)	12	1.93	1.54	Ålbu pers. comm.
Troglodytes aedon	5	11	1.41	2.75	Kendeigh et al. 1956
	6	13	1.38	4.98	Kendeigh et al. 1956
	5.59 (4–7)	29	1.39	4.40	Kendeigh et al. 1956

APPENDIX. Continued.

Species	Clutch size (range)	n	Mean egg volume (cm³)	Relative size of last egg (%)[a]	Source
Prunella modularis	5.50 (5–6)	2	2.07	1.32	Present study
Erithacus rubecula	6	3	2.65[b]	0.20	Chappell 1948
Luscinia luscinia	5	10	2.54	5.06	Pryl 1980
Phoenicurus phoenicurus	7	4	1.82	−0.22	Ojanen et al. 1981
Turdus merula	5	15	7.15[b]	2.40	Rydén 1978
Turdus pilaris	5	24	6.81	3.66	Slagsvold 1982a
	6	32	6.77	3.85	Slagsvold 1982a
	5.54 (4–7)	61	6.79	3.86	Slagsvold 1982a
Turdus philomelos	5	?	5.86[b]	4.01	Pikula 1971
Turdus iliacus	5	5	4.95[b]	6.13	Present study
	6	6	4.97	4.99	Present study
	5.55 (5–6)	11	4.96	5.51	Present study
Sylvia atricapilla	4	1	2.03	7.93	Present study
Phylloscopus collybita	5.60 (5–6)	5	1.16	6.30	Groebbels et al. 1930
	6	1	1.27	6.07	Present study
Phylloscopus trochilus	4	1	1.03	2.14	Groebbels et al. 1930
Muscicapa striata	5	1	1.86	6.87	Present study
Ficedula hypoleuca	6	49	1.64	0.79	Ojanen et al. 1981
	7	36	1.69	1.12	Ojanen et al. 1981
	6.42 (6–7)	85	1.66	0.96	Ojanen et al. 1981
	5	8	1.65	0.38	Present study
	6	11	1.69	1.51	Present study
	7	12	1.64	3.91	Present study
	6.19 (5–8)	32	1.66	2.35	Present study
Parus palustris	8	1	1.24	−1.86	Present study
Parus ater	8.00 (7–9)	2	1.16	1.48	Present study
Parus caeruleus	ca. 11.5	23	1.12	2.20	Winkel 1970
	10.67 (10–11)	3	1.08	6.06	Present study
Parus major	ca. 11.9	55	1.74[b]	0.91	Gibb 1950
	ca. 10.0	27	1.60	1.63	Winkel 1970
	9	17	1.65	0.85	Ojanen et al. 1981
	10	14	1.62	0.49	Ojanen et al. 1981
	9.45 (9–10)	32	1.64	0.67	Ojanen et al. 1981
	10	1	1.61	0.29	Present study
Pica pica	6	12	9.73	−1.59	Present study
	7	8	10.05	−3.98	Present study
	8	7	9.83	−5.51	Present study
	6.47 (3–9)	36	9.77	−4.96	Present study
Corvus monedula	5	11	10.51	−4.89	Antikainen 1978
	6	12	10.39	−6.69	Antikainen 1978
	5.10 (3–6)	29	10.44	−4.51	Antikainen 1978
	6	1	10.33	−6.55	Zimmermann 1951
Corvus corone	4	9	19.29	−5.33	Present study
	5	23	18.29	−7.58	Present study
	4.64 (3–6)	39	18.52	−7.22	Present study
Sturnus vulgaris	5	18	6.69	−0.93	Ojanen et al. 1981
	6	14	6.85	−0.73	Ojanen et al. 1981
	5.44 (5–6)	32	6.76	−0.84	Ojanen et al. 1981
Passer domesticus	2	44	2.29[b]	−1.29	Pinowski and Myrcha 1977
	3	221	2.33[b]	−2.10	Pinowski and Myrcha 1977
	4	315	2.25[b]	−3.02	Pinowski and Myrcha 1977
	5	74	2.20[b]	−4.35	Pinowski and Myrcha 1977
	3.64 (2–5)	654	2.27[b]	−2.74	Pinowski and Myrcha 1977
Fringilla coelebs	4.86 (4–5)	7	2.19	2.07	Present study
Carduelis tristis	5.26 (5–6)	27	1.41	4.74	Holcomb 1969
Dendroica petechia	4	4	1.58	4.05	Schrantz 1943
Emberiza schoeniclus	7	1	1.93	7.82	Present study
Quiscalus quiscula	5	40	6.58[b]	3.50	Howe 1976

[a] Deviation (in %) of the size of the final egg laid from that of the mean size of all the eggs in the clutch.
[b] Mean egg weight.