

CLUTCH-SIZE DETERMINATION IN PRECOICIAL BIRDS: A STUDY OF THE COMMON EIDER

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ABSTRACT.—Clutch-size determination in the Common Eider (*Somateria mollissima*) was evaluated in a colony in northern Norway. Females in good body condition (determined from mass at hatching) produced large clutches and had a shorter incubation period than females with small body reserves. Females in good body condition cared for young (including adoption of the young of other females), while females in poor body condition abandoned their young soon after hatching. Repeatability (an upper limit to heritability) of clutch size, which for individual females varies from three to six eggs, does not differ significantly from zero. A hypothesis is proposed, suggesting that there is a trade-off involved in allocating body reserves to eggs, incubation, and care of chicks and that females use a particular clutch-size strategy related to their body condition and ability to care for young. Received 8 May 1992, accepted 12 May 1993.

LACK (1947, 1948) SUGGESTED that clutch size in altricial birds was ultimately limited by the ability of the parents to rear young. Although Lack's hypothesis has been somewhat modified (see Williams 1966, Charnov and Krebs 1974, Høgstvedt 1980), the idea of brood-size limitation has been supported by many studies (for reviews, see Klomp 1970, Dijkstra et al. 1990).

The adaptive significance of clutch size in birds with self-feeding precocial young is an enigma (Arnold and Rohwer 1991). Clearly, Lack's hypothesis for clutch-size determination in altricial birds cannot apply to precocial birds. A number of other hypotheses have been proposed (see Winkler and Walters 1983). The one most often applied is the egg-production hypothesis (Winkler and Walters 1983, Arnold and Rohwer 1991). This hypothesis was proposed by Lack (1967, 1968), who suggested that clutch size ultimately is limited by the hen's ability to allocate nutrient reserves to egg laying. However, except for studies on arctic-nesting geese (Ankney and MacInnes 1978), evidence corroborating the hypothesis is scarce.

A number of studies have shown that female waterfowl use body reserves for egg production (Ankney et al. 1991). However, use of body reserves for egg production has uncritically been used as evidence that available body reserves determine the optimal clutch size (Arnold and Rohwer 1991). Even if nutrient reserves influence number of eggs produced, there may be a trade-off between the use of body reserves for egg production and for later use during incu-

bation (Erikstad 1986, Gloutney and Clark 1991) and care of chicks (Lessells 1986, Bustnes and Erikstad 1991).

In this study we examine some of the hypotheses that have been put forth as possible explanations for within-season variation in clutch size. We outline a new hypothesis that combines several earlier ideas to show that clutch-size determination could be affected by an interaction of female body condition, egg predation, and parental care.

MATERIALS AND METHODS

The study was carried out in a Common Eider (*Somateria mollissima*) breeding colony near Tromsø in northern Norway (69°49'N, 18°15'E) in 1986-1989. The colony was on a 0.65-km² island (Grindøya) and contained 400 breeding pairs.

Searches were begun in early May when first nests were initiated. Nests were visited at one- or two-day intervals to determine laying dates and clutch sizes. A clutch was assumed to be complete and incubation to have begun when no new eggs were recorded during a period of three days. We determined intraspecific nest parasitism by detecting multiple eggs laid in a nest within 24 h. The frequency was very low (less than 1%; unpubl. data). All parasitic clutches were excluded from the analysis. Incubation was assumed to begin on the day that the final egg was laid and was completed when one chick had hatched.

Females were caught on the nest with a net at hatching and weighed using a spring balance (± 10 g). For a few females caught three to five days before hatching, we estimated hatching mass by using a daily mass

TABLE 1. Yearly variation ($\bar{x} \pm \text{SE}$) in clutch size, laying date (May), body mass at hatching, and length of incubation period in Common Eiders from northern Norway. Sample size in parentheses.

Year	Clutch size	Laying date	Hatching body mass (g)	Incubation period (days)
1986	4.2 \pm 0.1 (64)	24.3 \pm 0.3 (16)	1,391 \pm 45.9 (4)	24.0 \pm 1.0 (2)
1987	4.3 \pm 0.08 (106)	22.9 \pm 0.4 (29)	1,392 \pm 13.5 (52)	24.4 \pm 0.2 (17)
1988	4.5 \pm 0.06 (194) ^a	24.5 \pm 0.5 (64) ^a	1,421 \pm 13.7 (53)	24.0 \pm 0.2 (27)
1989	4.3 \pm 0.05 (227) ^a	21.5 \pm 0.6 (77) ^a	1,408 \pm 11.4 (90)	24.5 \pm 0.2 (29)
F-value	3.45	5.91	0.71	1.24
df	3 and 587	3 and 182	3 and 195	3 and 71
P-value	0.02	0.007	0.53	0.30

^a Significantly different from each other (Tukey HSD test; $P < 0.05$).

loss of females of $22.5 \pm \text{SE of } 9.3 \text{ g/day}$ (Bustnes and Erikstad 1991).

Nests were visited every second or third day during the last half of the incubation period to estimate total clutch loss (i.e. all eggs lost before hatching), partial clutch loss (one or more eggs disappeared in nests where at least one egg hatched), and hatching success (proportion of unpredated eggs hatched).

Females caught on their nests were individually marked with patagial tags (Bustnes and Erikstad 1990) or with nasal discs (Sudgen and Poston 1968). Females were classified as "abandoners" and "tenders" according to their posthatch behavior. Abandoners were females that gave up their young while tenders were females that cared for their own young and also adopted young from abandoners. Bustnes and Erikstad (1991) have provided further details of definitions and methods.

Data on hens nesting in more than one season were used to estimate repeatability (see Lessells and Boag 1987) of clutch size and laying date. Repeatability gives an upper limit to heritability and allowed us to estimate the relative importance of heritable and environmental components in the variation of traits. For a number of females we could also correlate directly the variation in clutch size from one year to the next with the corresponding variation in laying date and body mass.

Because some of the variables measured were not available for all females, a simultaneous test of all

variables in combination would have restricted sample size. Therefore, we performed separate analyses of the relationships between clutch size, body mass, laying date, and incubation time.

Data were organized and statistical tests made using the SAS statistical package (SAS Institute 1988). All tests are two-tailed with significance level set at $P < 0.05$.

RESULTS

Annual differences in mean hatching body mass and incubation period were not significant (Table 1). Annual differences in mean laying date (ranging from 21 May in 1989 to 24 May in 1988) and mean clutch size (ranging from 4.3 eggs in 1989 to 4.5 eggs in 1988) were small but significant.

Overall egg loss consists of total clutch loss, partial egg loss and unhatched eggs. Total clutch loss was the component that contributed most to total egg loss (Table 2) and tended to decrease with increasing clutch size (34% in three-egg clutches, 20% in six-egg clutches). Partial clutch loss (0.01–3.3%) and hatching loss (4.2–9.1%) contributed less to the total egg loss and showed no trend in relation to clutch size. None of the egg-loss components were significantly corre-

TABLE 2. Egg survival in Common Eider in relation to clutch size. Values are percentages of nests (eggs) displaying different components of egg survival. Data pooled over years and sample sizes given in parentheses (number of nests for total clutch loss, and number of eggs for the other three components). None of the components of egg size differed significantly ($P > 0.05$) with clutch size. The number of ducklings leaving nest increased with clutch size ($F_{3,235} = 11.6$, $P = 0.001$).

Component of survival	Clutch size			
	3	4	5	6
Total clutch loss	34.2 (38)	22.0 (100)	20.8 (91)	20.0 (10)
Partial clutch loss	0.9 (114)	3.3 (400)	1.8 (455)	0.0 (60)
Hatching success	95.8 (71)	91.3 (275)	93.0 (329)	90.9 (44)
$\bar{x} \pm \text{SE}$ (no. ducklings)	1.9 \pm 1.3 (38)	2.8 \pm 1.6 (100)	3.6 \pm 2.0 (91)	4.4 \pm 2.4 (10)

TABLE 3. One-way ANOVA and repeatability (*r*) of clutch size and laying date in Common Eiders.

Source of variation	<i>F</i>	df	<i>r</i>	<i>P</i>
Clutch size	0.93	60,73	-0.03	ns
Laying date	2.33	21,26	0.38	0.05

lated with clutch size. The number of ducklings leaving the nest increased with clutch size (ranging from 1.9 for three-egg clutches to 4.4 among six-egg clutches; Table 2). The results show that the most productive clutch size (six eggs) is larger than the commonest clutch size (four eggs). There was no repeatability in clutch size while approximately 38% of the phenotypic variation in laying date arose from differences between individuals (Table 3).

Pooled data over years show a positive relationship between clutch size and female hatching body mass, but the explained variance was very low ($r^2 = 0.09, n = 58, P = 0.02$). There was no similar relationship between clutch size and laying date ($r^2 = 0.04, n = 58, P = 0.12$).

Individual hens varied their clutch size by a maximum of three eggs from one year to the next. This equals the maximum range of normal clutches (three to six eggs). Variation in relative mass at hatching explained a significant proportion of this clutch-size variation (Fig. 1). Seven females increased their clutch size from one year to the next, 11 laid smaller clutches, and 6 had a similar clutch size ($X^2 = 0.83, df = 2, P = 0.66$), suggesting that there was no directional change in clutch size with age. There were no similar relationships between differences in hatching body mass from one year to the next and laying date ($r^2 = 0.10, n = 26, P > 0.05$), or between clutch size and laying date ($r^2 = 0.04, n = 25, P > 0.05$).

Clutch size was larger among tenders than

TABLE 4. Body mass in grams ($\bar{x} \pm SD$) at hatching in relation to clutch size among females caring for their young (tenders) and females abandoning their young after hatching (abandoners). Sample size in parentheses.

Clutch size	Abandoners	Tenders
3	1,371 \pm 74 (10)	1,436 \pm 125 (3)
4	1,348 \pm 78 (19)	1,438 \pm 126 (27)
5	1,410 \pm 93 (9)	1,455 \pm 48 (5)
6	1,300 (1)	1,446 \pm 48 (5)
\bar{x}	1,367 \pm 82 (39)	1,446 \pm 108 (63)

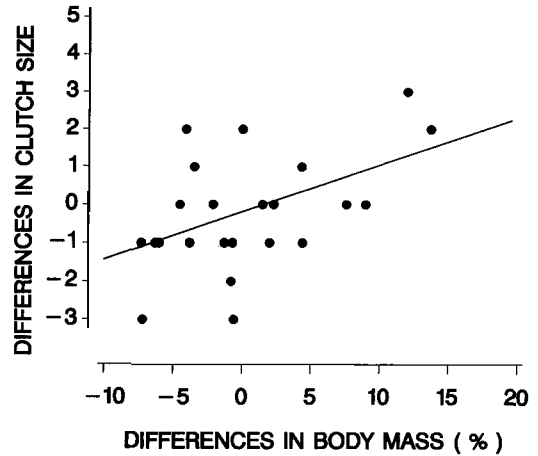


Fig. 1. Relationship between relative changes (%) in body mass of individual females at hatching from one year to the next and the accompanying change in clutch sizes ($Y = -0.35 + 0.50X; r^2 = 0.40, P < 0.01, n = 26$). Presented as raw data, but arcsin transformed for analysis.

abandoners (4.6 ± 0.09 vs. $4.0 \pm 0.11, F_{1,102} = 13.8, P = 0.003$). Tenders also had shorter incubation periods than abandoners (24.0 ± 0.58 vs. $25.0 \pm 0.58, F_{1,30} = 4.91, P = 0.03$), but the dates of egg laying were similar (23.3 ± 0.7 vs. $20.9 \pm 1.9, F_{1,30} = 2.26, P = 0.14$).

For all clutch-size categories, abandoners tended to be lighter at hatching than tenders (Table 4). An analysis of covariance (PROC GLM) shows that behavior (abandoning/tending) has a clear effect statistically on hatching body mass ($F = 14.93, P = 0.002$), whereas the variance accounted for by clutch size ($F = 0.30, P = 0.58$), and that for the interaction between clutch size and behavior ($F = 0.12, P = 0.73$) were very small.

The length of the incubation period (range 22-27 days) was negatively correlated with hatching body mass (Fig. 2), but was not related to clutch size ($r^2 = 0.01, P = 0.33$).

To separate the effect of clutch size and body mass on the likelihood that females should abandon or tend their brood, we used a logistic regression (PROC LOGISTIC) with binary response (abandoners = 0, tenders = 1). The analyses show that both hatching body mass ($X^2 = 9.2, P = 0.002$) and clutch size ($X^2 = 8.4, P = 0.004$) statistically influence the behavior. The relationship is given by the equation:

$$\text{logit}(p) = -14.003 + 0.94C + 0.007M, (1)$$

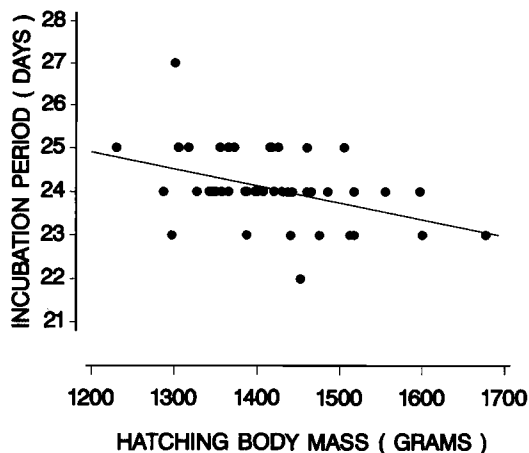


Fig. 2. Relationship between hatching body mass of females and length of incubation period ($Y = 29.4 - 0.004X$; $r^2 = -0.18$, $P = 0.003$, $n = 47$).

where $\text{logit}(p)$ is the log odds function (SAS Institute 1988), C is clutch size, and M is body mass in grams. This model fits well since the likelihood-ratio test for the interaction is non-significant ($P > 0.05$). The equation suggests that the chance the female will tend her brood increases with both hatching body mass and clutch size, and that females with large clutches may tend their brood at a lower body mass than females with small clutches.

DISCUSSION

The main results in this study can be summarized as follows. There is no support for the hypothesis that available body reserves alone (egg-formation hypothesis) determine the within-season variation in optimal clutch size in eiders. We did obtain a positive correlation between body mass and clutch size. In addition, individual females nesting in more than one season produced larger clutches in years when they had a larger body mass at hatching. However, females with large body mass also had shorter incubation periods, and they cared for both their own young and adopted those of females that abandoned their young. These results support the idea that there may be an optimal trade-off between use of body reserves for egg laying and for later use during incubation and chick care.

Repeatability of reproductive components.—The

repeatability of clutch size varies greatly from species to species. Laurila (1988) and Lessells et al. (1989) reviewed several studies where repeatability of clutch size ranged from -0.17 to 0.58 . The value of -0.03 from our study is at the low end of this scale. High partial egg predation may obscure repeatability estimates. However, it is unlikely that there is such an effect in our estimate since partial clutch loss was very low in our study (Table 2).

Our figure of repeatability is closest to that found in several studies of geese, which have a nesting strategy very similar to that of eiders in that they rely heavily on stored body reserves during the entire nesting cycle: Snow Geese (*Anser caerulescens*) 0.10 – 0.26 (Lessells and Boag 1987, Lessells et al. 1989); and Arctic-nesting Canada Geese (*Branta canadensis hutchinsii*), 0.17 (MacInnes and Dunn 1988). Laurila (1988) also reported a repeatability of 0.31 for Common Eiders from southern Finland. This significant repeatability reported on eiders from southern Finland may be a result of a more stable environment than in northern Norway.

We observed a significant repeatability (0.38) in laying date. This may seem contradictory since laying date and clutch size are often closely linked in birds (large clutches are generally laid early in the season; for reviews, see Klomp 1970, Winkler and Walters 1983). However, eiders have a common brood-rearing strategy, where several females may assist each other and where some females abandon their young to others (e.g. Munro and Bedard 1977a,b, Eadie et al. 1988, Bustnes and Erikstad 1991). In our study area more than 40% of all females were abandoners, and most young were adopted by brood-caring females. The broods also leave the colony area within a few days of hatching. Such a brood-rearing strategy may create strong stabilizing selection on laying date (hatching date), thereby guaranteeing that clutches hatch synchronously. Females in poor condition may lay small clutches early in the season to ensure that their young will be adopted by high-quality females that nest early. Other studies of eiders have also reported a tendency for females to nest at the same time in consecutive years (Spurr and Milne 1976, Laurila and Hario 1988).

Body mass and incubation.—The length of the incubation period was not related to clutch size, but was positively correlated with body mass at hatching. One possible interpretation is that females with a large body mass at hatching also have a large body mass at the start of the in-

incubation period. A high body mass during incubation may increase nest attentiveness and decrease the incubation period, as well as reduce predation risk as described for other ground-nesting birds (Erikstad et al. 1982, Aldrich and Raveling 1983, Erikstad 1986, Gloutney and Clark 1991). Eiders feed little after the start of egg laying and lose about 46% of their body mass before the eggs hatch (Korschgen 1977, Parker and Holm 1990). However, some authors mention that females may feed, especially at the end of the incubation period (for references, see Swennen et al. 1993). A large decrease in nest attentiveness when the body mass reaches some lower threshold has been described for Canada Geese (Aldrich and Raveling 1983). A strategy to allocate body reserves for incubation may be very profitable in eiders. In our study, the rate of egg predation was about 30%, but in another study of eiders from the High Arctic, Ahlén and Andersson (1970) reported that only 27% of the eggs hatched. Swennen et al. (1993) noted that in eiders nearly all eggs lost to predators are lost when the female leaves the nest (see also Mehlum 1991).

Productivity of different clutch sizes.—The number of ducklings leaving the nest increased with clutch size and was highest for six-egg clutches. The survival of ducklings from different clutch-size categories is difficult to study in eiders due to their common brood-rearing strategy. However, as shown by Bustnes and Erikstad (1991), there is no relationship between the proportion of ducklings that survive until the age of five to six weeks and the brood/creche size. Although we do not know the recruitment level of birds from different clutch sizes to the breeding population (which is a better estimate of fitness), our results suggest that the most productive clutch size is larger than the commonest clutch size. Similar results have been obtained in a number of studies of birds (e.g. Klomp 1970), and several hypotheses have been proposed to account for this observation (for review, see Price and Liou 1989, Power et al. 1989).

The optimal clutch-size.—Since precocial birds do not feed their young, it has been assumed that parental effort is not affected by clutch size or brood size (for reviews, see Lack 1967, 1968, Klomp 1970, Winkler and Walters 1983; but also see Safriel 1975, Erikstad and Andersen 1983, Lessells 1986).

As shown in our study, Common Eiders have a highly variable clutch-size strategy depending on their body mass, and large clutches pro-

duce more ducklings than small clutches. Time-budget data and data on chick survival from different brood/creche sizes do not show any relationship between brood size and parental ability (Bustnes and Erikstad 1991). Nevertheless, the optimal clutch size may be affected by ability of the females to care for young. Females with large body reserves produce large clutches, have a short incubation period, care for their own young, and adopt young from other females. Females in poor body condition produce smaller clutches, have a longer incubation period, and abandon their young. At hatching, brood abandoners have depleted their body reserves below that of tenders at all clutch-size categories.

Giving up one's young after hatching is costly in terms of reproductive success, since the ducklings from brood-tending females survive the first five to six weeks better than ducklings from brood abandoners (Bustnes and Erikstad 1991). This may explain how such a strategy can become evolutionarily stable. Since abandoning and adoption of young are not obligate individual strategies but change between years (Bustnes and Erikstad 1991), we suggest that individuals lay different clutch sizes depending on their body mass and their ability to care for young.

The likelihood that females should tend their brood was related not only to body mass, but also to clutch size. Females hatching large clutches tended their brood at a lower body mass than females hatching small broods. This result suggests a trade-off between current and future reproduction. Female body condition at hatching may affect female survival (for review, see Dijkstra et al. 1990), while tending young will increase the value of parental care through increased survival of the ducklings.

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LITERATURE CITED

- AHLÉN, I., AND Å. ANDERSSON. 1970. Breeding ecology of an Eider population on Spitsbergen. *Ornis Scand.* 1:83-106.

- ALDRICH, T. W., AND D. G. RAVELING. 1983. Effects of experience and body weight on incubation behaviour of Canada Geese. *Auk* 100:670-679.
- ANKNEY, C. D., AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of Lesser Snow Geese. *Auk* 95:459-471.
- ANKNEY, C. D., A. D. AFTON, AND R. T. ALISAUSKAS. 1991. The role of nutrient reserves in limiting waterfowl reproduction. *Condor* 93:1029-1032.
- ARNOLD, T. W., AND F. C. ROHWER. 1991. Do egg formation costs limit clutch size in waterfowl? A skeptical view. *Condor* 93:1032-1038.
- BUSTNES, J. O., AND K. E. ERIKSTAD. 1990. Effects of pagital tags on the laying date and egg size of Common Eiders. *J. Wildl. Manage.* 55:216-218.
- BUSTNES, J. O., AND K. E. ERIKSTAD. 1991. Parental care in the Common Eider *Somateria mollissima*: Factors affecting abandonment and adoption of young. *Can. J. Zool.* 69:1538-1545.
- CHARNOV, E. L., AND J. R. KREBS. 1974. On clutch size and fitness. *Ibis* 116:217-219.
- DIJKSTRA, C., A. BULT, S. BIJLSMA, S. DAAN, T. MEIJER, AND M. ZIJLSTRA. 1990. Brood size manipulations in the Kestrel (*Falco tinnunculus*): Effects on offspring and parental survival. *J. Anim. Ecol.* 59:269-285.
- EADIE, J. MCA., F. P. KEHOE, AND T. D. NUDDS. 1988. Pre-hatch and post-hatch brood amalgamation in North American Anatidae: A review of hypothesis. *Can. J. Zool.* 66:1709-1721.
- ERIKSTAD, K. E. 1986. Relationship between weather, body condition and incubation rhythm in Willow Grouse. *Fauna Norv. Ser. C, Cinclus* 9:7-12.
- ERIKSTAD, K. E., R. BLOM, AND S. MYRBERGET. 1982. Territorial Hooded Crows (*Corvus corone*) as predators on Willow Grouse (*Lagopus lagopus*) nests. *J. Wild. Manage.* 46:109-114.
- ERIKSTAD, K. E., AND R. ANDERSEN. 1983. The effect of weather on survival growth rate and feeding time in different sized Willow Grouse broods. *Ornis Scand.* 14:249-252.
- GLOUTNEY, M., AND R. G. CLARK. 1991. The significance of body mass to female dabbling ducks during late incubation. *Condor* 93:811-816.
- HØGSTEDT, G. 1980. Evolution of clutch size in birds: Adaptive variation in relation to territory quality. *Science* 210:1148-1150.
- KLOMP, H. 1970. The determination of clutch size in birds. A review. *Ardea* 58:1-124.
- KORSCHGEN, C. E. 1977. Breeding stress of female eiders in Maine. *J. Wildl. Manage.* 41:360-373.
- LACK, D. 1947. The significance of clutch size. *Ibis* 89:302-352.
- LACK, D. 1948. Natural selection and family size in the Starling. *Evolution* 2:95-110.
- LACK, D. 1967. The significance of clutch-size in waterfowl. *Wildfowl* 18:125-128.
- LACK, D. 1968. Ecological adaptation for breeding in birds. Chapman and Hall, London.
- LAURILA, T. 1988. The role of genetic factors on clutch size and egg dimensions in the Common Eider *Somateria mollissima*. *Finnish Game Res.* 45:11-18.
- LAURILA, T., AND M. HARIO. 1988. Environmental and genetic factors influencing clutch size, egg volume, date of laying and female weight in the Common Eider *Somateria mollissima*. *Finnish Game Res.* 45:19-30.
- LESSELLS, C. M. 1986. Brood size in Canada Geese: A manipulation experiment. *J. Anim. Ecol.* 55:669-689.
- LESSELLS, C. M., AND P. T. BOAG. 1987. Unrepeatable repeatabilities: A common mistake. *Auk* 104:116-121.
- LESSELLS, C. M., F. COOKE, AND R. F. ROCKWELL. 1989. Is there a trade-off between egg weight and clutch size in wild Lesser Snow Geese (*Anser c. caerulescens*)? *J. Evol. Biol.* 2:457-472.
- MACINNES, C. D., AND E. H. DUNN. 1988. Components of clutch size variation in Arctic nesting Canada Geese. *Condor* 90:83-89.
- MEHLUM, F. 1991. Egg predation in a breeding colony of the Common Eider (*Somateria mollissima*) in Kongsfjorden, Svalbard. *Norsk Polarinst. Skr.* 195:37-45.
- MUNRO, J., AND J. BEDARD. 1977a. Creche formation in the Common Eider. *Auk* 94:759-771.
- MUNRO, J., AND J. BEDARD. 1977b. Gull predation and creching behaviour in the Common Eider. *J. Anim. Ecol.* 46:799-810.
- PARKER, H., AND H. HOLM. 1990. Patterns of nutrient and energy expenditure in female Common Eider nesting in Svalbard. *Auk* 107:660-668.
- POWER, H. W., E. D. KENNEDY, L. C. ROMAGNANO, M. P. LOMBARDO, A. S. HOFFENBERG, P. C. STOUFFER, AND T. R. MCGUIRE. 1989. The parasitism insurance hypothesis: Why starlings leave space for parasitic eggs. *Condor* 91:753-765.
- PRICE, T., AND L. LIOU. 1989. Selection on clutch size in birds. *Am. Nat.* 134:950-959.
- SAFRIEL, U. N. 1975. On the significance of clutch size in nidifugous birds. *Ecology* 56:703-708.
- SAS INSTITUTE. 1988. SAS/STAT user's guide: Statistics, release 6.03. SAS Institute, Inc., Cary, North Carolina.
- SPURR, E. B., AND H. MILNE. 1976. Factors affecting laying date in the Common Eider. *Wildfowl* 27:107-109.
- SUDGEN, L. G., AND H. J. POSTON. 1968. A nasal marker for ducks. *J. Wildl. Manage.* 32:484-496.
- SWENNEN, C., J. C. H. URSEM, AND P. DUIVEN. 1993. Determinate laying and egg attendance in Common Eiders. *Ornis Scand.* 24:48-52.
- WILLIAMS, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *Am. Nat.* 100:687-690.
- WINKLER, D. W., AND J. R. WALTERS. 1983. The determination of clutch size in precocial birds. *Curr. Ornithol.* 1:33-68.