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IS THERE AN OPTIMAL CLUTCH SIZE IN SNOW GEESE?

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Lack (1947, 1954) suggested that the average clutch size in a population reflects the number of eggs from which parents could rear the most young to an age of demographic independence. In nidicolous species (e.g., perching birds), he considered this number to be limited by the amount of food parents were able to provide for their young. In nidifugous species (e.g., waterfowl), he suggested that clutch size was limited by the availability of nutrients for the female around the time of laying, modified by the relative size of the egg. Clutch size in nidifugous species may also be limited by predation (Safriel 1975) or, more generally, by the ability of parents to provide care other than feeding between hatching and fledging (see Winkler and Walters 1983). Other modifications of Lack's hypotheses have integrated the benefits of producing young with their potential costs to parental survival (e.g., Cody 1966; Williams 1966; Charnov and Krebs 1974).

Hypotheses of clutch-size evolution generally predict that there is an optimum clutch size with reproductive fitness declining with increasing distance from that optimum. For nidicolous species, reproductive fitness is expected to decline with clutch size above a certain threshold because of the parents' inability to provide adequately for the young (Perrins 1964; Ricklefs 1968). The same trend is expected in nidifugous species when predation or parental-care costs increase with clutch or brood size (Perrins and Birkhead 1983). Lack reasoned that clutch size in nidifugous species reflects a trade-off between the number and size of eggs a female can produce from a finite food reserve and a positive correlation between hatchling survival and egg size (Lack 1968, p. 225). Those hypotheses claiming that clutch size has evolved in relation to maximum lifetime reproductive fitness assume that the increased costs of producing a large clutch need not stem from reduced offspring survival per se. Rather, such theories predict trade-offs between fecundity and parental survival such that individuals producing larger than average clutches show reduced survival and, hence, lower lifetime fitness.

The recurring theme in these hypotheses is, thus, that the most productive clutch size (in the sense of Charnov and Krebs 1974) is generally not the largest

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that could be produced. However, empirical evidence that clutch size is optimized by selection is underwhelming. Lessells (1986) concluded that of all clutch or brood manipulation experiments undertaken to date, about a third reported results consistent with this formulation. In many instances, the most productive clutch is larger than the average clutch size of the population (Andersson 1976; Loman 1980; Slagsvold 1982; Nur 1984*b*). Moreover, the negative correlation between fecundity and survival is not as ubiquitous as several theories predict. Several studies have failed to detect any consistent relationship between brood size and survival (Kluyver 1963; Perrins 1965; Bryant 1979; De Steven 1980; Smith 1981; Alerstam and Högstedt 1984). Indeed, some studies (e.g., Högstedt 1981) have even reported a positive correlation between clutch size and parental survival. In general, studies providing empirical support for the optimization of clutch size via a reduction in parental survival (Askenmo 1979; Nur 1984*a*) are outnumbered by those in which the expected trade-off between reproductive effort and survival was not detected.

Much of this research has relied on manipulation studies, in which the clutch size of individual birds is modified and the consequences on fitness are assessed. Moreover, most of it has centered on nidicolous species with the notable recent exceptions of the research by Rohwer (1985) and Lessells (1986). Neither of these studies found evidence that clutch (or brood) size in ducks or geese had been optimized through trade-offs involving either success at nesting and hatching or survival of offspring and parents. Rather, the evidence suggested that the relevant selection pressures operated before and/or during laying.

We have approached these issues from a somewhat different perspective by investigating the fitness of different segments of the population, segments being defined by their natural clutch size (Cooke et al. 1985; Rockwell, in press). If all components of fitness related to clutch size can be identified, we can address the question of whether individuals that lay different-sized clutches have different fitnesses. Manipulation experiments, by contrast, ask whether individuals laying a clutch of one size have different fitnesses if they are given a clutch of another size. Our approach allows us to ascertain whether selection is occurring and, if so, to determine its pattern. Given some knowledge of the genetics of the system, we can then predict the effects of selection on the population. Both aspects are critical to studies of natural selection in wild populations (Endler 1986). Considering the various hypotheses of clutch-size evolution, we expect selection to be stabilizing, such that clutch size and reproductive fitness are not related in a simple monotonic fashion.

This study examines the relation between clutch size and reproductive fitness in a population of lesser snow geese (*Anser caerulescens caerulescens*) breeding in the Canadian Arctic. We use a model of the snow goose life cycle in which successive life stages, from egg to breeding adult, are used to estimate components of fitness (Prout 1969; Bundgaard and Christiansen 1972; Cooke et al. 1985; Rockwell, in press). We assessed the relationship between natural variation in clutch size (the starting point in our model) and variation in each of the subsequent components of fitness. Specifically, we have ascertained whether various fitness components depend on the initial clutch size, established the relationship between clutch size and total fitness, and evaluated the pattern and intensity of selection affecting clutch size. The analyses are discussed in view of the observed mean and variance of clutch size in this population and the various hypotheses of clutch-size evolution, particularly as they apply to Arctic-breeding geese.

METHODS

Data were collected from 1973 to 1984 as part of a larger investigation of the breeding biology of lesser snow geese (*Anser caerulescens caerulescens*) at La Perouse Bay, Manitoba. A full description of the study site is given by Jefferies et al. (1979). Each season the colony is subdivided into several intensive study areas. Daily searches of these areas provide information on about 500 individual nests per year, including dates of establishment and hatch, the identity of the attendant pair, clutch size, and reproductive success. Subsequent searching of areas of non-intensive study provides less-complete information on approximately 2500 nests per year. Hatchling goslings are fitted with monel web tags identifying their natal nest.

During the adult molt (and just before the goslings fledge), about 35% of the individuals are captured in a series of banding drives. At this time, all goslings and unmarked adults are marked with individually coded, plastic leg bands. Recaptures of web-tagged goslings provide information on post-hatching gosling mortality and brood sizes at fledging. Recapture of marked individuals provides estimates of the age structure of the colony, as well as information on adult survival and gosling recruitment. At present, 45%–50% of the female members of the approximately 8000 breeding pairs are so marked. The proportion of marked males is considerably less, since few males return to their natal colony to breed (Cooke et al. 1975).

We use a general compartmental fitness model (fig. 1) modified from one introduced earlier (Cooke et al. 1985) to estimate the relative reproductive fitness of individuals producing clutches of different sizes. (For details regarding terminology and estimation procedures, see Cooke et al. 1985 and Cooke and Rockwell 1988). Briefly, the *fecundity components* of fitness, which are regarded as those spanning the period from egg laying to the fledging of goslings, include the following factors.

Total clutch laid (TCL) is the total number of eggs laid in a nest.

Clutch size at hatching (CSH) is the number of eggs in a nest when at least one egg hatches.

Goslings leaving the nest (GLN) is the total number of goslings leaving a nest (nests are included only if $CSH > 0$).

Brood size at fledging (BSF) is the total number of goslings that survive to just before fledging. (For our purposes BSF is always greater than 0, since total brood loss is considered a separate variable below.)

Egg survival ($P_1 = CSH/TCL$) is the proportion of the total number of eggs laid still present in the nest at hatch. Differences between TCL and CSH reflect partial clutch loss (PCL) during the incubation period.

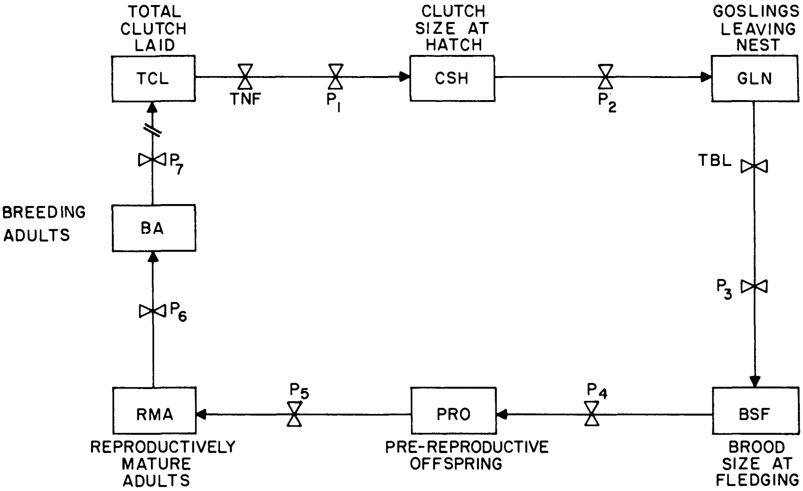

FIG. 1.—Components of fitness for the lesser snow goose. The state variables and transition probabilities trace the reproductive output of a single nest from the total clutch laid through various pre-fledging losses, recruitment, and adult survival (of the offspring from that nest) to, ultimately, the contribution of those offspring to their own clutches. The variables and probabilities are defined in the text. (After Cooke et al. 1985.)

Hatching success (P_2 = GLN/CSH) is the proportion of eggs in the nest that hatch. Differences between CSH and GLN reflect unfertilized, addled, or rotten eggs, and goslings abandoned at the nest.

Fledging success (P_3 = BSF/GLN) is the proportion of goslings leaving the nest that fledge. Differences between BSF and GLN reflect partial brood loss (PBL) during the post-hatching interval.

Although values of less than one for the last three variables indicate some decrement in fitness between stages of the reproductive cycle, they do so only for individuals that hatch at least one gosling or have at least one gosling leave the nest, not for individuals that fail to produce any goslings whatsoever. To account for these cases, we define two additional variables.

Total nest failure (TNF). A nest was considered a total failure if all the eggs were preyed upon or abandoned before any hatching occurred.

Total brood loss (TBL). The absolute incidence of TBL between hatch and fledging cannot be estimated since the failure of a brood to appear in the pre-fledging sample need not imply that the entire brood died, but only that it was not recaptured (Cooke and Rockwell 1988). However, a minimum estimate of TBL may be obtained from the proportion of nests with marked parents and more than one gosling leaving the nest from which the marked parents but no goslings were recaptured in the pre-fledging sample.

Evolutionary constraints on clutch-size variation need not be limited to fecundity selection. They may also involve clutch or brood size, dependent offspring, or parental survival (Rockwell et al. 1985). The following are the relevant *viability components* (see fig. 1).

Pre-reproductive offspring (PRO) is the number of fledglings surviving until they become reproductively mature.

Reproductively mature adults (RMA) is the number of surviving fledglings that have become reproductively mature.

Breeding adults (BA) is the number of reproductively mature adults that breed.

Pre-reproductive survival (P_4) is the vector of age-specific survival probabilities for immature birds.

Reproductive maturation (P_5) is the vector of probabilities that an individual is reproductively mature by age x.

Adult survival (P_6) is the vector of age-specific survival probabilities for reproductively mature adults.

Repeat breeding (P_7) is the probability that an individual that has bred at time t will breed at time $t + 1$.

Offspring survival was estimated by two independent techniques. The first is concerned strictly with viability and involves estimates of the proportion of marked goslings, from clutches of a particular size, which were reported killed during the pre-reproductive period. These marked goslings are called recoveries and their numbers are based on the return of U.S. Fish and Wildlife Service bands. The second measure, recruitment (PR), incorporates both pre-reproductive survival (P_4) and maturation (P_5) and is based on the number of goslings recaptured in the colony at least 2 yr after their initial marking date (see Rockwell et al. 1985). Estimates of relative recruitment rates from clutches of different sizes are based entirely on females, which are much more likely to return to their natal colony (Cooke et al. 1975). Recapture of marked adults (both males and females) in subsequent years permits estimates of relative adult survival in relation to reproductive effort and reproductive success in the preceding year (for details, see Rockwell et al. 1985).

Two standard statistical techniques were employed in these analyses, namely, analysis of variance (ANOVA) and multidimensional contingency analysis (MDCA). The application of these techniques to this type of data is explained elsewhere (Cooke et al. 1985; Rockwell et al. 1985). The test statistic for MDCA is the log-ratio χ^2, abbreviated here as G.

RESULTS

Variation in Clutch Size

Clutches of lesser snow geese normally range from 1 to 7 eggs. Occasionally, nests contain 8 to 12 eggs, but these represent less than 1% of the 30,615 nests studied since 1973. Thus, we have restricted our analyses to clutches with 7 or fewer eggs. The relative distributions of clutch sizes, at the time each female began incubating, are shown in figure 2 for 11 yr of the study and for the data pooled over these years. (The sample sizes in 1979 were too small to yield meaningful comparisons and were not included in any analyses.)

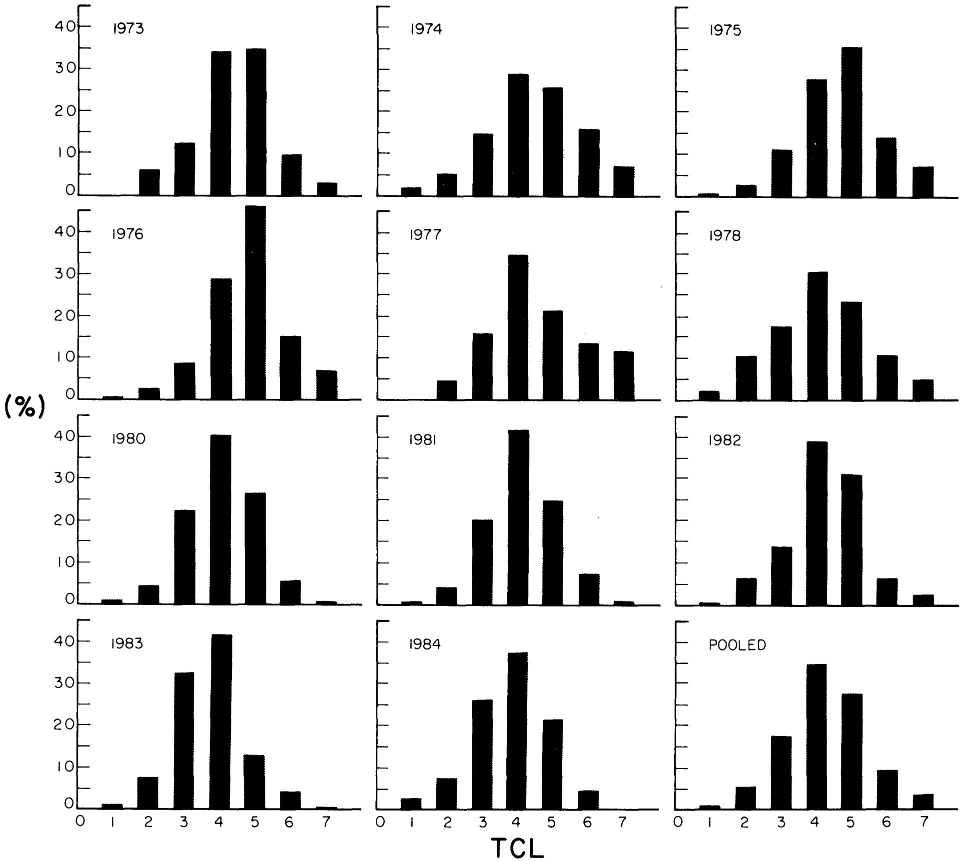

FIG. 2.—Relative distributions of total clutch laid (TCL) for lesser snow geese at La Perouse Bay. The total sample sizes for each graph are 1973, 164; 1974, 340; 1975, 283; 1976, 201; 1977, 121; 1978, 217; 1980, 295; 1981, 321; 1982, 375; 1983, 212; 1984, 222; pool, 2751.

Because intraspecific nest parasitism (ISNP) occurs in lesser snow geese, eggs in a given nest may not all belong to the attendant pair. Snow geese have a plumage dimorphism controlled by a single-locus, two-allele system, with blue dominant to white, such that rates of ISNP can be estimated from the frequency of blue goslings in the nests attended by two white parents (Cooke and Mirsky 1972). The annual rate of ISNP has ranged from 5% to 12% over the course of our study. Preliminary analyses of the relationship between ISNP and clutch size indicate that the probability of a nest's containing eggs laid by a non-attendant female increases disproportionately with clutch size until approximately 38% of the 6-egg clutches and 96% of the 7-egg clutches contain one or more parasitic snow goose eggs. This result is consistent with the work of Ankney (1974) and Hamann (1983), who did not collect any females containing more than six post-ovulatory follicles. We consider the effect of ISNP on the various fitness components in the following sections.

TABLE 1

REPRODUCTIVE SUCCESS AND VARIATION IN CLUTCH (BROOD) SIZE (%)

CLUTCH-SIZE MEASURE	COMPONENT OF REPRODUCTIVE SUCCESS	CLUTCH OR BROOD SIZE							LOG-RATIO χ^2 (df)
		1	2	3	4	5	6	7	
TCL	TNF	44.8 (29)	23.5 (153)	12.1 (487)	8.7 (969)	7.8 (772)	9.1 (263)	9.0 (100)	55.8*** (6)
	PCL		1.8 (114)	14.0 (420)	16.1 (853)	18.6 (687)	34.1 (226)	45.8 (83)	104.9*** (5)
	PBL		11.1 (9)	37.3 (59)	61.5 (117)	68.9 (90)	76.5 (17)	80.0 (15)	29.7*** (5)
	TBL	33.3^a (3)		13.0 (23)	8.3 (60)	5.6 (36)	8.3^b (12)		2.4 (4)
CSH	PBL		17.9 (117)	52.1 (357)	68.4 (735)	71.8 (493)	78.8 (118)	76.9 (26)	160.1*** (5)
	TBL	20.0 (5)	11.5 (52)	13.9 (144)	5.4 (299)	6.8 (192)	3.6^b (55)		12.5* (5)
GLN	PBL		19.8 (162)	57.9 (430)	70.9 (724)	73.9 (422)	84.4^b (96)		193.5*** (4)
	TBL	16.7 (18)	10.4 (67)	10.5 (171)	6.4 (296)	6.2 (161)	2.6^b (38)		7.0 (5)

NOTE.—Entries give percent of nests displaying the indicated component. Data are pooled over years. Sample sizes in parentheses. TCL, total clutch laid; CSH, clutch size at hatching; GLN, goslings leaving nest; TNF, total nest failure; PCL, partial clutch loss; PBL, partial brood loss; TBL, total brood loss.

[a] Clutch sizes 1 and 2 pooled.

[b] Clutch sizes 6 and 7 pooled.

* $P < 0.05$.

*** $P < 0.001$.

Fecundity Selection: Rates of Total and Partial Failure

Overall reproductive success of snow geese is related in part to predation intensity resulting both in total nest failure (TNF) and partial clutch loss (PCL) during incubation and in partial brood loss (PBL) and total brood loss (TBL) during brood rearing (Cooke and Rockwell 1988). If, for example, large clutches were more prone to failure, then predation would reduce the fitness of individuals producing such clutches. In this section, we examine the relationship between clutch size and TNF, PCL, PBL, and TBL. Because sample sizes within years were insufficient, data were pooled over years.

TNF depends significantly on clutch size (table 1). The increased failure rate of clutches of one and two eggs makes a major contribution to the total heterogeneity. This high contribution was established by asking whether there were subsets of clutch sizes within the total range on which TNF does not depend. In this particular case, TNF was independent of clutch size in the range of three to seven eggs ($G\,[3\text{–}7] = 6.84$, df $= 4$, $P = 0.14$). Because G is additive, we concluded that the significant effect in table 1 stems primarily from clutch sizes of one and two. (This approach is used throughout to identify classes that contribute to overall effects; Bishop et al. 1975.)

The enhanced rate of TNF in these small clutches reflects at least two factors.

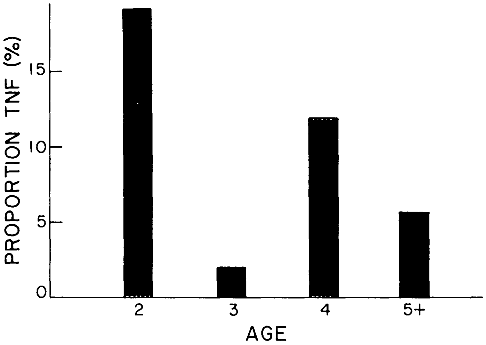

FIG. 3.—Female age and proportion of total nest failure (TNF) for lesser snow geese at La Perouse Bay. The sample sizes for the age classes are, in order, 26, 48, 59, 251.

First, for clutches of one and two eggs, loss of one or two eggs, respectively, must result in TNF, whereas for larger clutches, it results in only PCL. Second, clutches of one and two eggs are more prevalent among young, inexperienced breeders (Rockwell et al. 1983) and lack of age or experience possibly contributes to enhanced failure. Analysis of a sample of females of known age indicated that TNF does not depend significantly on the TCL ($G = 1.54$, df = 4, $P = 0.82$) but does depend primarily on female age ($G = 9.14$, df = 3, $P = 0.03$). A major contributor to this effect is the enhanced failure rate of 2-yr-olds (G [3–7] = 4.64, df = 2, $P = 0.1$), a category including only first-time breeders (fig. 3). Thus, the principal cause of the increased rate of TNF for small clutches is youth and/or inexperience rather than small clutch size per se.

An indication of some level of predation at the nest during incubation, PCL also depends on TCL (table 1), with low incidence rates for two-egg clutches (1.8%) and relatively higher rates for six- and seven-egg clutches (34.1% and 45.8%, respectively). The low value for two-egg clutches probably reflects the inclusion of only single-egg predation events for these nests in the sample since higher predation results in TNF. If two-egg clutches are excluded, most of the remaining variation is due to the enhanced loss rates among six- and seven-egg clutches (G [3–7] = 71.39, df = 4, $P < 0.01$), with three- to five-egg clutches showing little heterogeneity (G [3–5] = 4.22, df = 2, $P = 0.12$).

Partial brood loss depended on all three measures of fecundity (table 1). Since the three measures are themselves highly correlated (r[TCL-CSH] = 0.83, r[TCL-GLN] = 0.77, r[CSH-GLN] = 0.89; df = 308; $P < 0.01$ for all values), we examined the pattern of dependence in detail only for GLN (the state variable immediately preceding the depredations that result in PBL). Broods of two goslings had a disproportionately lower incidence of PBL, the incidence increasing markedly for brood sizes of three and more (table 1). The major contributors to total heterogeneity are the two-gosling broods. Like nest failure, this effect may result because predation events in small broods are more likely to lead to TBL rather than PBL, thereby reducing overall rates of PBL. This effect may also reflect a higher incidence of young, inexperienced females among the parents of

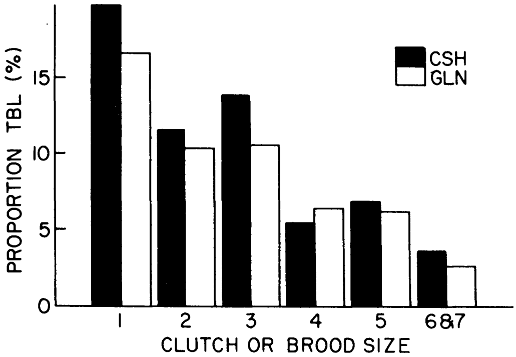

FIG. 4.—The incidence of total brood loss (TBL) as a function of clutch size at hatching (CSH) and goslings leaving the nest (GLN) for lesser snow geese at La Perouse Bay. The sample sizes for the clutch and brood classes are, in order, for CSH, 5, 52, 144, 299, 192, 55; for GLN, 18, 67, 171, 296, 161, 38.

the smaller broods. To assess this explanation, we examined the effects of GLN and female age on PBL with a sample of known-age individuals. The analysis indicates that PBL does not depend on age ($G = 5.38$, df $= 3$, $P = 0.15$) but does depend almost exclusively on GLN ($G = 44.82$, df $= 4$, $P < 0.01$). Thus, PBL is not a consequence of parental age but, rather, of brood size per se.

The incidence of TBL increases as clutch size decreases (fig. 4). TBL shows a significant overall dependence on CSH, with increased rates of TBL associated with smaller clutches. When CSH > 3, TBL is independent of clutch size. A similar trend is evident in the relationship between TBL and GLN (fig. 4), with the lack of significance undoubtedly resulting from reduced statistical resolving power. Since loss rates for families of two or three goslings or for families of four or more goslings show no detectable differences, the data were pooled within these classes. Analysis of the pooled data for brood-size classes of one, two or three, and four or more indicates significant dependence of TBL on GLN, with loss rates decreasing with increasing brood-size class ($G = 6.52$, df $= 2$, $P < 0.05$).

Again, these effects may be a consequence of clutch or brood size per se or of a preponderance of young, inexperienced individuals among the parents of the smaller clutch or brood sizes. Analysis of a sample of females of known age (fig. 5) indicates that TBL does not depend on age for either CSH or GLN (CSH, $G = 2.03$, df $= 3$, $P = 0.57$; GLN, $G = 1.19$, df $= 3$, $P = 0.59$) but does depend significantly on CSH ($G = 13.89$, df $= 6$, $P = 0.03$) and GLN ($G = 10.62$, df $= 4$, $P = 0.03$). We conclude that smaller than average clutches and broods are more likely to suffer TBL during the post-hatching period and that this increase is not due simply to a preponderance of young or inexperienced individuals.

Fecundity Selection: Transition Probabilities in Successful Nests

The survival of eggs and offspring before fledging in nests that do not fail totally is related to clutch or brood size in several species (Ricklefs 1968; Perrins and

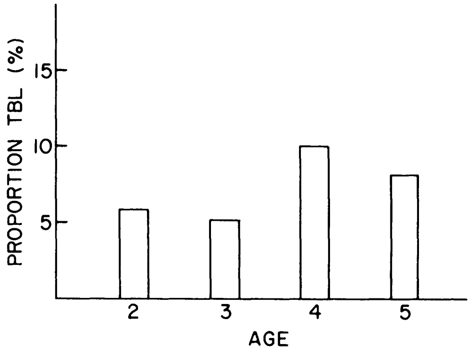

FIG. 5.—Female age and the rate of total brood loss (TBL) with respect to goslings leaving nest for lesser snow geese at La Perouse Bay. The sample sizes are, in order, 17, 38, 49, 132.

Moss 1975; Bryant and Westerterp 1983). In our component-fitness model (fig. 1), such effects would appear as dependence of a transition probability, egg survival (P_1), hatching success (P_2), or fledging success (P_3), on TCL, CSH, or GLN, respectively.

We investigated this possibility with three independent data sets: (1) a set (LF) of 308 families for which all four fecundity measures (TCL, CSH, GLN, BSF) and all three transitions (P_1, P_2, P_3) were available; (2) a set (LH) of 1413 families for which only the measures of TCL, CSH, GLN, and the transitions P_1 and P_2 were available; (3) a set (HF) of 1468 families for which only the measures CSH, GLN, BSF, and the transitions P_2 and P_3 were available. The LF sample is ideal for our purposes since all measures are from a single set of individuals and emerging trends are therefore unlikely to result from pooling across different individuals for which data from only part of the life cycle are available. Unfortunately, the sample size is small, particularly when apportioned over the various clutch sizes. For this reason, the other samples, with their large sample sizes, were also used to detect relationships that might not appear in the LF sample.

Our analyses ask whether there is significant variation in egg survival (P_1), hatching success (P_2), or fledging success (P_3) with respect to TCL, CSH, or GLN. Since the transitions (P_1, P_2, P_3) are numerically constrained by the size of the clutch or brood (e.g., in a clutch of two eggs, P_1 can only equal 0.5 or 1.0), we analyzed deviations from expected values based on the null hypotheses that P_1, P_2, and P_3 were independent of clutch and brood sizes. The data took the form $d_{ij} = X_{ij} - \mathrm{E}(X_i)$, $i = 2, 3, \ldots, 7$, $j = 1, 2, \ldots, n(X_i)$, where X_{ij} is the jth observation in clutch- or brood-size class i. The expected value of the ith class is $\mathrm{E}(X_i)$, which is given by $\mathrm{E}(X_i) = P_k\, i$, where P_k is the mean probability across all clutch- or brood-size classes in the sample for the transition in question ($k = 1, 2, 3$; egg success, hatching success, or fledging success, respectively), and $n(X_i)$ is the total number of observations in the ith class for a given data set (LF,LH,HF). The d_{ij} are thus deviations of the jth individual from the expected value of the ith class under the null hypothesis that the relevant transition probabilities are independent of clutch or brood size.

TABLE 2

Results of Two-Factor anova's Examining the Influence of Total Clutch Laid (TCL) and Year on Clutch Size at Hatching (CSH), CSH and Year on Goslings Leaving the Nest (GLN), and GLN and Year on Brood Size at Fledging for the Three Data Sets LF, LH, and HF

	Data Set and Transition Probabilities						
	LF			LH		HF	
Source	P_1	P_2	P_3	P_1	P_2	P_2	P_3
Year	2.0	3.8	13.0*	14.2***	3.9	14.7***	27.5***
	(10)	(10)	(10)	(10)	(10)	(10)	(10)
X = TCL for P_1 CSH for P_2 GLN for P_3	10.1	0.8	13.6	4.9	24.9***	8.0***	32.8***
	(5)	(5)	(5)	(5)	(5)	(5)	(5)
Year × X	21.0*	14.2	30.6	18.8[a]	15.0	22.4***	47.1**
	(40)	(39)	(36)	(47)	(45)	(45)	(42)
Error	89.8	78.8	166.5	405.5	541.9	344.3	990.8
	(249)	(246)	(245)	(1350)	(1340)	(1407)	(1390)

Note.—Data sets are defined in the text. The data are individual deviations from the expected value of a particular clutch- or brood-size class under a null model that transition probabilities (e.g., from TCL to CSH) are independent of clutch (brood) size. Entries are sums of squares; degrees of freedom are in parentheses. Only values with symbols are significant.

[a] $P = 0.067$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

The effects of year and fecundity measure on the individual deviations were evaluated with two-factor anova's (table 2). Although significant year-by-fecundity measure interactions occur for some measures in some samples, the anova design is such that the main effects are uncontaminated by the interaction component. Mean deviations from the expected values (i.e., means of d_{ij}) for each clutch-size and brood-size category are presented in figure 6. The analyses of the three data sets yield qualitatively similar patterns, with discrepancies appearing only in those categories with small sample sizes.

Egg survival (fig. 6*A*) showed little variation across clutches of two to five eggs with no departure from the average expectation in this range. However, there is evidence of decline among six- and seven-egg clutches, with a posteriori contrasts of the LF and LH samples indicating a significant difference in egg survival between clutches of two eggs and those of six or seven eggs. A similar trend is shown for hatching success (fig. 6*B*) with little variation and no departure from expectation among clutches of two to five eggs, but a decrease in success for six-egg clutches and a further decrease for clutches of seven eggs. For fledging success (fig. 6*C*), contrasts using the LF sample show significant differences between broods having six goslings and those having two or three. Contrasts using the HF sample indicate differences between broods of two or three goslings and broods of five or six goslings. In both cases, the fledging success of the smaller broods is greater than expected.

It is likely that much of the decline in success associated with clutches of six

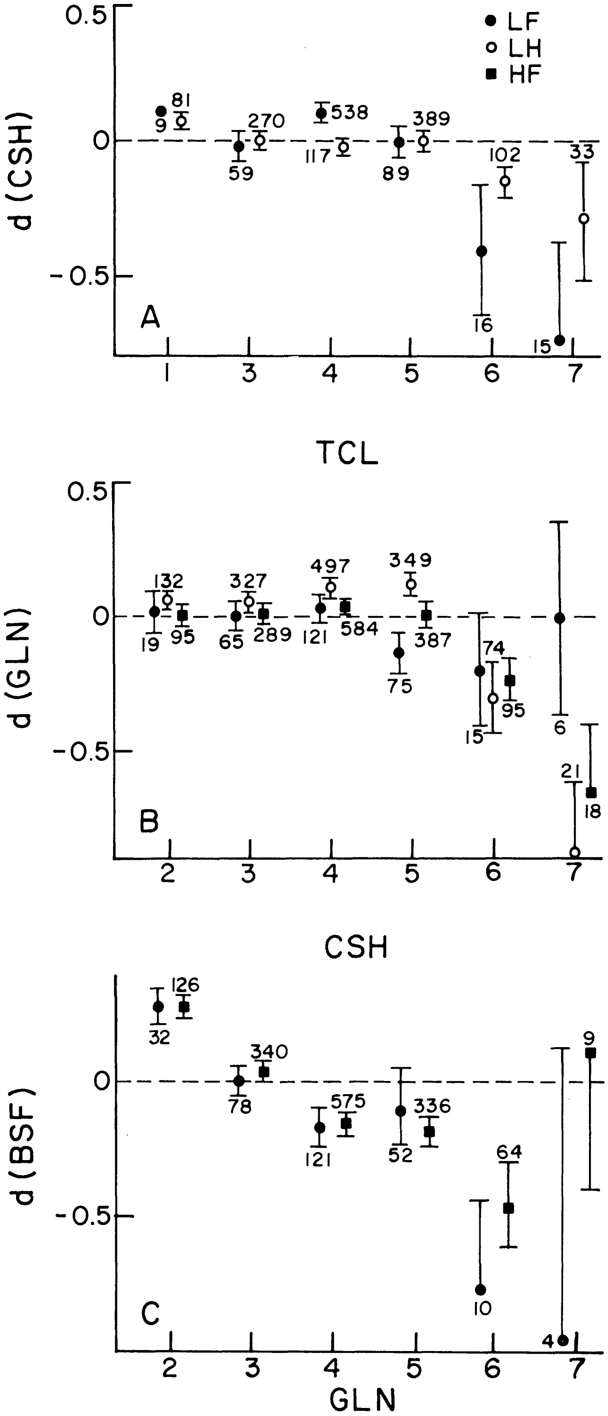

FIG. 6.—Relation of transition probabilities and clutch or brood size. Mean deviations and standard errors of the response variable from the expected value of a particular category of clutch (brood) size under the null hypothesis that transition probabilities (i.e., P_1 = egg survival, P_2 = hatching success, P_3 = fledging success) are independent of their preceding state variable. Numbers are sample sizes.

and particularly of seven eggs is related to ISNP. As mentioned earlier, at least 96% of the seven-egg clutches contain one or more foreign eggs. Recent analyses (D. Lank et al., MS) indicate that a disproportionate number of eggs that failed to hatch were parasitic eggs. Further, many of these eggs failed because they were laid after the "host" female had begun incubation. Given the short time between hatching and departing the nest for feeding areas in this species (Cooke and Rockwell 1988), a reduced level of laying asynchrony by parasites could result in goslings that, even though they hatch, either hatch too late to leave the nest with their more mature nest mates or never reach the feeding areas with their families.

Offspring Survival

The effect of reproductive effort on offspring survival was examined by comparing recovery and recruitment rates across various clutch (brood) sizes. Comparative estimates of pre-reproductive survival were based on recoveries of goslings marked between 1973 and 1982. The total reporting interval (ages 0 to 4, where 0 represents fledging) was partitioned into two periods, the first covering year 1 and the second covering years 2 through 4. For each period, the number of recovered offspring was contrasted with the number not recovered, obtained by subtracting the number of offspring recovered before and during the period of interest from the number of originally marked goslings. It is important to note that, for both survival and recruitment, the contrasts and estimates involve the number of fledglings that could have been recovered or recruited from a particular clutch or brood. For example, if CSH is 5 and only three of the goslings fledged, the recovery and recruitment estimates for that nest would be based on three fledglings. (For statistical details, see Rockwell et al. 1985.)

There was no evidence of significant higher-order interactions involving the recovery variable (R) and natal year (Y) or offspring sex (S) for any clutch- or brood-size measure except TCL, for which the term involving TCL, R, and Y was significant at $P < 0.04$. Since no effects involving recovery and sex were significant, the data were pooled over sex and natal year (table 3). Subsequent analyses indicate that recovery rates were independent of clutch (brood) size. Recovery rates were also homogeneous for the second period (G [R TCL] = 4.70; G [R CSH] = 7.88; G [R GLN] = 7.78; G [R BSF] = 9.96; all df = 6; all $P > 0.10$).

Close examination of table 3 suggests that offspring from clutches of seven eggs show elevated recovery rates. Recovery rates from clutches for which TCL is 7 are more than double that of smaller clutches (19.2% vs. 8.2%, $G = 5.7$, df = 1, $P = 0.017$). The same pattern is found for CSH (17.4% vs. 8.5%, $G = 8.9$, df = 1, $P < 0.01$). Thus, although pre-reproductive offspring survival, as estimated by band recoveries, is independent of clutch (brood) sizes of one to six, we found evidence of decreased survival of fledged offspring from clutches where seven eggs were originally present.

As explained above, reduced pre-fledging success in seven-egg nests may be related to a developmental lag in parasitic eggs, resulting from their being laid after incubation had begun. Although the reduced post-fledging survival associated with seven-egg clutches is based on the proportion of fledged goslings that are recovered, laying asynchrony, insufficient to prevent hatching or fledging, may

TABLE 3

THE INFLUENCE OF FECUNDITY ON FIRST-YEAR PRE-REPRODUCTIVE SURVIVAL IN LESSER SNOW GEESE

	FECUNDITY MEASURE							
	TOTAL CLUTCH LAID		CLUTCH SIZE AT HATCHING		GOSLINGS LEAVING NEST		BROOD SIZE AT FLEDGING	
CLUTCH OR BROOD SIZE	%	*N*	%	*N*	%	*N*	%	*N*
1	0.0	1	4.3	23	11.4	44	7.8	179
2	6.7	15	7.5	159	9.4	237	8.4	1634
3	5.5	120	8.2	658	9.4	844	9.0	2172
4	9.6	292	8.3	1737	8.4	1787	8.8	1924
5	8.6	255	9.0	1633	8.5	1426	9.9	905
6	5.3	57	8.5	374	10.3	330	11.4	114
7	19.2	52	17.4	115	9.5	63	9.5	42
Log-ratio χ^2	9.0		7.9		5.2		1.3	

NOTE.—Entries are percentages of fledged goslings recovered from nests of a particular clutch or brood size. Data are pooled over offspring sex and year. *N*, sample size. The degrees of freedom for each of the log-ratio χ^2 values is 6. None of the values is significant.

have been sufficient to increase this sort of post-fledging mortality. The reduced survival could also be related to parental behavior if parasitized parents are less vigilant during the laying period (Mineau 1978) and less attentive after fledging (see Lessells 1982).

Offspring Recruitment

Band recoveries examine only one type of mortality, that of hunter kill. Potentially, other causes of death may depend on the initial clutch or brood size. Since recruitment measures the probability that an individual returns to its natal colony to breed, it incorporates all sources of mortality as well as breeding propensity. Because the return of males to their natal colony is so low at La Perouse Bay, only female recruitment can be examined (Cooke and Rockwell 1988).

In these analyses, we consider whether recruitment depends on the size of the natal clutch (brood). A female gosling is considered recruited if she returned to the colony as a breeding adult at least 2 yr after her original banding date. Recruitments were contrasted with the number of fledged females that could have been recruited but were not, cross-classified according to natal clutch or brood size and year. We assume that our inability to detect a female actually present at the colony is independent of her natal clutch or brood size. For all measures of clutch (brood) size except TCL, there are no higher-order interactions involving years. Pooling over years, we find no significant dependence of recruitment rates on measures of clutch (brood) size (table 4). We conclude that the initial clutch (brood) size does not affect recruitment in this species.

Fecundity Selection: Integration of Components

The effects of clutch-size variation on various fitness components can be combined to produce an empirical estimate of the relative reproductive fitness of

TABLE 4

THE INFLUENCE OF FECUNDITY ON OFFSPRING RECRUITMENT IN LESSER SNOW GEESE

	FECUNDITY MEASURE							
	TOTAL CLUTCH LAID		CLUTCH SIZE AT HATCHING		GOSLINGS LEAVING NEST		BROOD SIZE AT FLEDGING	
CLUTCH OR BROOD SIZE	%	*N*	%	*N*	%	*N*	%	*N*
1	—	—	15.4	13	15.0	20	13.5	89
2	16.7	6	14.9	74	13.4	119	13.9	784
3	13.6	59	14.6	314	14.2	401	15.3	1064
4	12.6	151	14.6	869	16.3	889	16.7	980
5	23.5	119	19.6	771	18.0	718	18.3	438
6	18.5	27	21.3	212	23.4	158	20.0	55
7	27.6	29	19.2	52	23.1	26	35.7	14
Log-ratio χ^2	6.9		5.7		4.1		4.7	

NOTE.—Entries are percentages of fledged goslings recruited from the nests of a particular clutch or brood size. Data are pooled over years. *N*, sample size. The degrees of freedom for the log-ratio χ^2 of the total clutch laid is 5; all others are 6. None of the values is significant.

each clutch-size phenotype. Table 5 summarizes these components as a function of clutch size. The average number of female offspring recruited per breeding attempt for a clutch of size *i* is then calculated as $\theta_i = i(1 - \mathrm{TNF}_i)\mathrm{P}_{1i}\mathrm{P}_{2i}\mathrm{P}_{3i}(1 - \mathrm{TBL}_i)\mathrm{PR}_i$. As shown in figure 7, there is a monotonic (and linear) increase in θ_i over the interval $i = 1, \ldots, 6$. The lack of continued fitness increase in seven-egg clutches is related to problems associated with the disproportionately high rate of intraspecific nest parasitism (ISNP) in such nests. For those clutches in which the preponderance of eggs are laid by the attendant female, reproductive fitness increases with the number of eggs laid.

Viability Selection: Adult Survival

Fitness-optimization arguments based on the theory of reproductive effort suggest a negative relationship between clutch (brood) size and adult survival. To assess this aspect of total fitness, we examined the relationship between clutch (brood) size in year *t* and the probability that an adult returned to the colony in any subsequent year $(t + 1), \ldots, 1984$. Because sample sizes were inadequate for individual years, cell counts were pooled over years, with any given individual appearing at most once in the pooled sample. The number of returning adults is contrasted to the number that could have returned but did not (or were not detected). Again, we assume that our inability to detect an individual that had returned is independent of the clutch (brood) size in year *t*.

The question is whether adult survival, indicated by return rate, depends on reproductive performance in a given year. Since the pattern of such dependence could differ between females and males, sex was included initially as a classification variable. It should be noted that we are not interested here in whether survival depends on sex per se. Rather, we are interested in whether any depen-

TABLE 5

COMPONENTS OF FITNESS AS A FUNCTION OF TOTAL CLUTCH LAID (TCL) FOR LESSER SNOW GEESE

TCL	Total Nest Failure	P_1	P_2	P_3	Total Brood Loss*	Recruitment
1	0.439 (.015)	1.000 (—)	1.000 (—)	1.000 (—)	0.158 (.033)	0.144 (.030)
2	0.235 (.006)	0.987 (.005)	0.942 (.010)	0.947 (.011)	0.123 (.036)	0.137 (.032)
3	0.125 (.004)	0.954 (.006)	0.931 (.008)	0.838 (.011)	0.101 (.041)	0.139 (.039)
4	0.083 (.002)	0.944 (.006)	0.929 (.007)	0.783 (.010)	0.081 (.038)	0.151 (.035)
5	0.081 (.003)	0.942 (.005)	0.917 (.007)	0.754 (.010)	0.066 (.047)	0.168 (.044)
6	0.091 (.004)	0.934 (.006)	0.875 (.008)	0.723 (.010)	0.057 (.055)	0.182 (.051)
7	0.087 (.010)	0.905 (.010)	0.786 (.011)	0.663 (.016)	0.056 (.088)	0.184 (.083)

NOTE.—Entries are means (and, in parentheses, 1 estimated standard-error unit). For TCL = 1, the values of P_1, P_2, and P_3 are 1 by definition and hence have no associated standard error. All other means and standard errors result from polynomial regressions involving the particular component (e.g., total nest failure) and total clutch laid.

* Calculations for total brood loss (TBL) and recruitment (PR) also used polynomial regressions involving goslings leaving the nest. Since both TBL and PR are based on resightings of goslings or adults (see the text), they are minimum estimates. Ancillary data indicate, however, that TBL and PR underestimate the real values by no more than 50%.

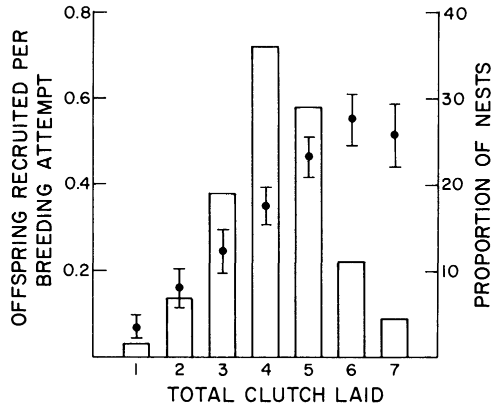

FIG. 7.—Reproductive fitness, measured as offspring recruited per breeding attempt, as a function of clutch size and the relative distribution of clutch-size classes for snow geese at La Perouse Bay. Reproductive fitness is plotted as the mean ± 2 standard errors.

TABLE 6

REPRODUCTIVE EFFORT AND ADULT SURVIVAL IN LESSER SNOW GEESE

	FECUNDITY MEASURE							
	TOTAL CLUTCH LAID		CLUTCH SIZE AT HATCHING		GOSLINGS LEAVING NEST		BROOD SIZE AT FLEDGING	
CLUTCH OR BROOD SIZE	%	N	%	N	%	N	%	N
1	33.3	3	22.7	22	52.6	78	63.6	121
2	61.1	18	59.4	165	47.6	254	57.8	265
3	52.6	97	53.1	608	50.6	700	53.3	257
4	41.8	237	49.6	1283	50.5	1080	57.3	178
5	49.7	161	49.2	921	49.9	633	62.1	66
6	57.1	49	45.6	270	45.1	153	72.7	11
7	48.1	27	50.0	80	45.5	33	0.0	3
Log-ratio χ^2	2.6		17.3**		2.6		9.4	

NOTE.—Entries are percentages of adults with a given clutch or brood size in a given year; these adults were resighted or subsequently recaptured at La Perouse Bay. N, sample size. The degrees of freedom for each log-ratio χ^2 is 6.

** $P < 0.01$.

dence of return rate on clutch (brood) size itself depends on sex. Since the relevant third-order terms in the multidimensional contingency analyses did not approach significance for any of the fecundity variables, indicating that any dependence of survival on clutch (brood) size is independent of sex, we present the data and analyses for the data pooled over sex.

There is no indication that adult survival depends on any of the fecundity measures examined except CSH (table 6). In this case, the effect arises almost entirely from the reduced proportion of returning adults whose clutch size at hatching was one (22.7% vs. 50.6%, $G = 7.18$, df $= 1$, $P < 0.01$). Since clutches with one egg present at hatching are most often laid by young, inexperienced breeders (Rockwell et al. 1983) and since there is some indication of increased mortality of younger birds (Cooke and Rockwell 1988), this effect is probably related to parental age or experience rather than clutch size per se. In general, clutch (brood) size does not influence subsequent adult survival.

We also examine the effect of TNF, PCL, PBL, and TBL on adult return rates. Analyses of these data, again pooled over sex, indicate that return rates, and hence adult survival, do not depend on reproductive performance.

Viability Selection: Male Survival and Mate Change

Pair-bond breakage occurs in this species primarily as a result of death (Cooke and Sulzbach 1978). Thus, if a female returns to the colony with a new mate, it is almost always a consequence of the death of her previous mate. The rate of mate change by females is thus a measure of the mortality of their mates in the time interval between breeding attempts. Individually marked pairs are scored on the basis of all measures of reproductive success. For each measure, the number of

TABLE 7

Reproductive Success and Mate Change

	Fecundity Measure							
	TOTAL CLUTCH LAID		CLUTCH SIZE AT HATCHING		GOSLINGS LEAVING NEST		BROOD SIZE AT FLEDGING	
Clutch or Brood Size	%	*N*	%	*N*	%	*N*	%	*N*
1	100.0	1[a]	0.0	1	80.0	5	80.0	15
2			85.7	14	83.3	24	69.0	42
3	64.3	14	68.4	57	68.9	74	65.6	32
4	73.7	38	65.2	161	64.3	143	71.4	21
5	80.0	20	70.7	133	70.2	84	57.1	14
6	85.7	7	74.4	43	75.0	28	66.7	3[b]
7	100.0	4	83.3	12	83.3	6		
Log-ratio χ^2	4.4		7.6		5.5		2.0	

Note.—Entries are percentages of females that had a given clutch or brood size in a particular year and were subsequently resighted with the same mate. *N*, sample size. The degrees of freedom for total clutch laid and brood size at fledging are each 5; the others are 6. None of the values is significant.

[a] Clutches of 1 and 2 were pooled.

[b] Broods of 6 and 7 were pooled.

females that had the same mate when they were resighted is contrasted to the number of females that were resighted with a different mate (table 7). Each female is included only once in the sample. Although sample sizes are low, mate change, and thus male mortality, does not appear to depend on reproductive performance.

DISCUSSION

Theories of clutch-size evolution generally predict that the most productive clutch size in a population will be smaller than the largest that can be produced. Thus, most theories suggest that clutch size and fitness will be related in an inverted U fashion, reflecting some form of stabilizing selection. This is clearly not the case for fecundity selection in lesser snow geese breeding at La Perouse Bay. Though there are trade-offs involving some components of fecundity (e.g., fledging success is inversely related to clutch size), the effects are not sufficient to offset initial clutch-size differences. Thus, larger clutches have higher fitness (fig. 7). This effect is nearly linear for clutch sizes of one to six, the range in which the preponderance of eggs are laid by the attendant female. Clutches larger than six are primarily the result of ISNP. As explained earlier, the lack of further fitness increases in parasitized clutches probably reflects more on the developmental asynchrony of parasitic eggs than on the ability of host females to handle them. Overall, the relationship between clutch size and reproductive fitness is consistent with fecundity selection being directional rather than stabilizing in this species.

In contrast, we find no evidence of any pattern of viability selection related to clutch-size differences in this species, in that the return rates of females and males were independent of their reproductive performance. There is need for some caution, however, since our analyses may not have detected small differences in annual survival. In long-lived species, such differences could accrue over time and result in clutch-size-dependent differences in viability (see Charlesworth 1980). Until substantially more data are collected on this point, we must conclude that an individual's survival is independent of its reproductive performance. This is consistent with a growing number of studies (Perrins 1965; De Steven 1980; Loman 1980; Roskaft 1985; Lessells 1986) that have failed to find trade-offs between fecundity and viability in the determination of total fitness.

Given our results for fecundity and viability selection, the overall relationship between clutch size and total relative fitness is that depicted in figure 7. This curve indicates that individuals producing large clutches are more fit than those producing small ones, but it does not imply that all females currently breeding at La Perouse Bay would be more successful if they laid additional eggs. The fitness of an individual results from the integrated action of traits spanning its life from birth (as a fertilized egg) through the recruitment of its offspring into the breeding population (Rockwell, in press). The set of traits possessed by an individual (its strategy) may be coadapted to operate most efficiently around a particular clutch size, such that any departure from that clutch size would reduce the individual's total fitness (e.g., Perrins and Birkhead 1983). As Lessells (1986) pointed out, only manipulation experiments would indicate whether the clutch-size strategies in a population operate in this fashion. However, regardless of whether clutch-size strategies extant in a wild population are coadapted in this fashion or not, strategies with higher fitnesses will increase in frequency assuming that the observed phenotypic variation has some genetic basis.

The pattern of directional selection demonstrated here leaves us with two unresolved issues, highlighted when the frequency distribution of clutch sizes at La Perouse Bay is superimposed on the graph relating relative fitness to clutch size (fig. 7). Simply put, if selection is indeed favoring those birds that lay the largest clutches, why is the mean clutch size smaller than the most productive size, and why is there variation in clutch size? Of the numerous explanations that could be advanced, we present three (not mutually exclusive ones) that are most consistent with the natural history of this species. (1) Directional selection is acting on a population that was at a different fitness equilibrium. (2) Directional selection at La Perouse Bay is balanced by gene flow from populations affected by different selection regimes. (3) Temporal and spatial variability in the environmental factors affecting egg production constrains clutch size below its maximum.

There have been many recent changes in both the distribution and color-phase composition of the Hudson Bay snow goose populations (Geramita et al. 1982; Cooke and Rockwell, in press). Not only have distinct blue and white populations merged during the present century, but there has been an expansion of breeding colonies in the southern part of the breeding range, including the establishment of the colony at La Perouse Bay. Thus, the current mean clutch size and level of variation may reflect historical selection regimes that are no longer present. Given the present directional selection and a genetic component to the clutch-size variation, the population should shift toward a new equilibrium with a higher mean clutch size and reduced variance.

That shift would be related to the phenotypic selection operating on the parents (the selection differential, *SD*) and the heritability of the trait (Falconer 1981). The selection differential is simply calculated as the mean clutch size of the parents subtracted from a weighted mean of those parents, with the weights being the relative fitnesses of the clutch sizes. Formally, $SD = \Sigma i f_i w_i / \Sigma f_i w_i - \Sigma i f_i$, where i is the clutch size, f_i is its frequency, and w_i is its relative fitness. The latter variables are obtained from figure 7. Considering only clutch sizes of 1 to 6, the selection differential for this population is 0.33.

The response to selection (R) is estimated as $R = SDh^2$, where h^2 is the heritability of the trait (Falconer 1981), and will be seen as an increase in the mean clutch size of the offspring over that of their parents. Given the selection differential of 0.33 and an h^2 of clutch size of 0.20 (Findlay and Cooke 1987), the expected increase for the offspring cohort will be 0.066 eggs. Since the population has overlapping generations, the effect of this selection on the population mean will be less than on the mean of the selected offspring cohort because selected cohorts are only gradually incorporated into the population's age structure. Assuming that the selection regime does not change and the intensity of selection does not destabilize the age distribution, a new equilibrium clutch size, based on the cumulative selection differential and the total additive genetic variance of clutch size, will be approached asymptotically (Charlesworth 1980). Granted these assumptions and a generation time of approximately 5 yr (Geramita et al. 1982), we would expect to see an increase in mean clutch size of approximately 0.2 eggs over the course of this study. The available data show no such trend (fig. 2), but in view of the amount of annual clutch-size variation (Rockwell et al. 1983), such a trend would be difficult to detect.

Lesser snow geese nest at a number of breeding colonies throughout the Hudson Bay–Foxe Basin region of arctic Canada. Possibly one or more of the components affecting fitness varies among those colonies in response to habitat or, perhaps, predator differences. Thus, the colonies may be under the influence of different selection regimes, which could lead to differences in mean clutch size. Cooch (1958), for example, reported that colonies in the high Arctic had clutch sizes below what we have found at La Perouse Bay. Almost all reproductively mature males at La Perouse Bay were hatched elsewhere, primarily in more-northern colonies (Cooke et al. 1975). This influx of breeding males results in a gene-flow estimate of 0.49 per generation, once age-specific fecundity and viability are taken into account (Rockwell and Barrowclough, in press). Such gene flow prevents fine-level local adaptation (Rockwell and Cooke 1977) and, if the males are from colonies with lower mean clutch sizes, it would certainly oppose the directional selection for increased clutch size that we have found at La Perouse Bay.

Neither the selection nor the selection–gene flow explanation suggests specific proximate factors that determine or limit the size of an individual's initial clutch. Lack (1967) argued that clutch size in nidifugous species depends on nutrient acquisition during laying. Ryder (1970) suggested that for arctic geese such acquisition occurred south of the breeding grounds in both the wintering areas and, more importantly, the staging areas associated with northern migration. Ankney and MacInnes (1978) provided support for this view by showing that clutch size and the nutrient reserves of females arriving at the breeding grounds were positively related. Although identification of such proximate factors increases our understanding of the situation, it does not of itself resolve the problems of clutch-size mean and variance in relation to the relative-fitness curve. For example, the strategy of individuals having six eggs in a clutch may enable them to acquire the most nutrient, transport it to the north, and subsequently lay, hatch, fledge, and recruit the most young. Given our fitness results and a genetic component to variation in such acquisition, such higher-clutch-size strategies should increase in frequency unless the selection is countered by gene flow.

The importance of nutrient acquisition in determining initial clutch size leads to our third explanation. Acquisition depends not only on food-gathering ability but also on food availability. The latter changes from year to year (e.g., Davies and Cooke 1983) and varies spatially within years (Frederick and Klaas 1982; Cooch, pers. comm.). If individuals can produce their maximum clutch size only when they have reached some minimum nutritional level (Ryder 1970; Ankney and MacInnes 1978; Findlay and Cooke 1983; Hamann et al. 1986), then yearly differences in food availability will prevent individuals from consistently achieving their maximum output. Similarly, if individuals are randomly distributed with respect to a patchy food supply in a particular year, then some can achieve their maximum clutch while others produce a reduced one. Over its life span, then, we expect an individual's average annual clutch size to be below the maximum possible and, moreover, generally less than that associated with maximum fitness. Averaging across individuals, it is therefore not surprising to find that the population's mean clutch size is lower than the most productive one.

A requirement of this explanation is that some portion of the clutch-size variation must be environmental in origin. This condition is certainly met since the heritability of clutch size is only 20%, leaving at least 80% of the phenotypic variance to be explained by factors other than additive genetic ones (Findlay and Cooke 1983, 1987). As suggested by Ankney and MacInnes (1978) and Davies and Cooke (1983), a substantial portion of that variation may derive from proximate factors related to food acquisition. Since the response to selection is proportional to heritability, the high proportion of environmental variance retards the increase in mean clutch size expected from the selection differential alone, as indicated above.

The increase in mean clutch size would be slowed even further if the calculated heritability overestimated the true proportion of additive genetic variance. Indeed, there is no response if the true heritability is zero. Our estimate is based on mother-daughter regression, a technique known to be sensitive to contamination from environmental variance common to mother and daughter (Findlay and Cooke 1983). Lesser snow goose families often remain together for nearly 2 yr, migrating north and south together (Prevett and MacInnes 1980). As such, daughters share feeding areas with mothers and may even learn their locations from them (Healey et al. 1980). Raveling (1970) has suggested that larger families, perhaps by virtue of their size alone, are able to outcompete smaller families for the best feeding areas. Under such conditions, we might expect common environmental effects to operate in the same direction as the fitness curve; daughters in large families would occupy prime feeding sites that would allow maximal nutrient acquisition and, in turn, could result in the production of a large clutch. Although such a cultural transmission of environmental effects would result in a true heritability of zero being overestimated by mother-daughter regression, it would not necessarily reduce the rate of evolution. As long as density-dependent factors did not reduce the feeding-area advantage of larger families, cultural transmission of traits required to find, defend, or use prime feeding sites would facilitate a phenotypic response to the selection differential given above (Cavalli-Sforza and Feldman 1981).

Natural selection is expected to produce sets of coadapted traits (strategies) that maximize an individual's lifetime reproductive fitness (Stearns 1976). For snow geese, the initial clutch size is one of the important components of such strategies (Rockwell, in press). Most theories of clutch-size evolution predict that in a constant environment the relationship between clutch size and total fitness will be consistent with a pattern of stabilizing selection. This is not the case for lesser snow geese, for which there is a clear pattern of directional selection favoring strategies with larger clutch sizes. Our results join those of a growing number of studies (e.g., review in Lessells 1986) that have used different approaches but have failed to support the notion of fitness trade-offs leading to a negative correlation between life history traits (see also van Noordwijk and de Jong 1986). Our view is that a comprehensive theory of clutch-size evolution must account for such discrepancies. Although we agree with Lack's notion (see Lessells 1986) that some of the requisite information can be obtained from manipulation studies, much can be gained by following Endler's (1986) charge to study selection in wild populations.

SUMMARY

We examined the relationship between clutch size and total fitness in the lesser snow goose (*Anser caerulescens*) employed a life-cycle model in which successive life stages are used to estimate fitness components. Though there are trade-offs involving some components of fecundity, the effects are not sufficient to offset initial differences in clutch size. Further, there is no evidence that viability depends on reproductive performance. Overall, there is a positive relationship between clutch size and total fitness consistent with directional selection favoring larger clutches. This contrasts with many theories of clutch-size evolution, which predict a relationship more consistent with stabilizing selection. The pattern of directional selection raises the twin questions of why the mean clutch size of the population is smaller than the most productive clutch size, and why there is variation about that mean. We offer three resolutions that incorporate the influence of a recent shift in the selection regime, gene flow, spatiotemporal variation in nutrients, and cultural transmission of behaviors associated with feeding.

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