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FITNESS CONSEQUENCES OF PARENTAL BEHAVIOR IN RELATION TO OFFSPRING NUMBER IN A PRECOICIAL SPECIES: THE LESSER SNOW GOOSE

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ABSTRACT.—We investigated the relationship between parental behavior and brood size, and the consequences of this relationship in terms of parental fitness (timing of molt and body mass at onset of molt in same year as breeding, and probability of return, timing of breeding, and clutch size in following year) in the precocial Lesser Snow Goose (*Chen caerulescens caerulescens*) at La Pérouse Bay, Manitoba. The percentage of time parent birds spent feeding decreased with increasing brood size, from greater than 90% for pairs without offspring to less than 80% for broods of seven and eight. The number of vigilant (head-up) postures per minute by parental birds increased up to brood size five and then decreased. Parental females also spent significantly less total time feeding and more time in alert behavior as brood size increased from one to five goslings. The relationship between parental behavior and brood size remained significant for small brood sizes even if pairs without goslings were excluded (range one to five goslings), and this relationship was independent of female age. Males (but not females) rearing larger broods molted later than those with smaller broods, although only by one to two days. This was directly related to rearing of offspring; in both sexes, birds that hatched four or more goslings and subsequently lost one or more goslings during brood-rearing molted significantly earlier than birds rearing all of their hatched goslings. There was no relationship, in either sex, between number of goslings reared and the adult mass five to six weeks posthatch (molt) in the same year, or probability of return or timing of breeding (laying date or hatch date) in the following year. Partners of males that reared the largest number of goslings laid significantly larger clutch sizes the following year, suggesting that these were "better-quality" pairs. Over the range of naturally observed brood sizes, the effect of increasing brood size on parental behavior does not appear to be associated with any negative effects on residual parental reproductive effort or fitness in this species. Received 24 June 1993, accepted 18 November 1993.

IN ALTRICIAL SPECIES, the evolutionary determination of clutch size and parental care are thought to be closely related; with increasing number of offspring there is a trade-off between benefits to the parent of increased inclusive fitness and costs of reduced residual reproductive value due to increased current reproductive effort (Perrins 1965, Williams 1966, Lack 1968, Trivers 1972, Drent and Daan 1980). The main form of parental care in altricial species is provision of food to the offspring. This form of parental care is considered to be "depreciable" (Altmann et al. 1977) or "shared" (Lazarus and Inglis 1986). The benefit of parental care per offspring declines with increasing number of offspring, and total parental expenditure is predicted to increase with increasing brood size (Lazarus and Inglis 1986). Numerous studies of altricial species have demonstrated costs of re-

production (decreased fecundity and/or survival) associated with increased parental effort in rearing experimentally enlarged broods (e.g. Nur 1984, Hegner and Wingfield 1987, see review in Partridge 1990).

In contrast to altricial species, the relationship between parental effort and number of offspring in precocial species is much less clear (Schindler and Lamprecht 1987). Precocial species do not feed their young and the main form of parental care (vigilance or brood-defense behavior) is generally assumed to be "nondepreciable" (Lazarus and Inglis 1986, Schindler and Lamprecht 1987), meaning that the total benefit of parental care is gained simultaneously by all offspring. In Southern Lapwings (*Vanellus chilensis*; Walters 1982), Bar-headed Geese (*Anser indicus*; Schindler and Lamprecht 1987), and Barnacle Geese (*Branta leucopsis*; Black and Owen

1989a, Forslund 1993), parents spent more time in vigilance behavior and less time foraging with increasing brood size, although no such relationship was found in Pink-footed Geese (*A. brachyrhynchus*; Lazurus and Inglis 1978) or in an earlier study of the Lesser Snow Goose (*Chen caerulescens caerulescens*; Lessells 1987). Schindler and Lamprecht (1987) suggested that in precocial species reduced foraging time of parent birds, associated with increasing brood size, may reduce parental fitness and, thus, represent a form of depreciable care. However, very few studies have considered actual fitness costs of rearing different numbers of offspring in precocial species. Parental care will only influence clutch size if the parent incurs such fitness costs, in terms of decreased future fecundity and/or survival. Otherwise, optimal clutch size should be infinite with respect to parental effort during brood rearing (Lessells 1987).

In this paper we first analyze the relationship between parental behavior and brood size (decreased feeding performance and increased vigilance behavior) in the precocial Lesser Snow Goose. Second, as other parental traits (e.g. age or "quality") may be correlated both with the level of parental care and the number of offspring reared (Black and Owen 1989b, Clutton-Brock 1991), we investigate the effect of parental age on this relationship. Finally, correlational studies of parental behavior and brood size can be misleading because time (or energy) costs may not reflect fitness costs (Clutton-Brock 1991, Clutton-Brock and Godfray 1991). Therefore, we use data from a long-term population study of this species to investigate the relationship between number of offspring reared and five measures of residual parental fitness: (1) timing of molt and body mass at molt in the same year as brood rearing; and (2) probability of return, timing of breeding, and clutch size in the year following brood rearing.

METHODS

General methods and measures of parental fitness.—Data on the breeding biology of the Lesser Snow Goose have been collected at La Pérouse Bay, Manitoba (58°43'N 93°27'W) from 1968 to 1993. General field methods and details of the species' breeding biology are given in Cooke et al. (1985), Cooke and Rockwell (1988) and Cooch and Cooke (1991). In each year up to 2,000 nests were visited daily throughout hatch to obtain data on mean hatch date, the number of goslings leaving the nest (GLN), and the band numbers

of breeding adults. All hatching goslings were marked with individually numbered web tags. For a smaller sample of nests (those found at the one-egg stage and visited daily throughout egg laying), the date of clutch initiation (laying date) and total clutch laid (TCL) were also known. Since 1972, 4,000 to 7,000 adults and goslings have been banded annually prior to fledging of the goslings, five to six weeks after mean hatch date. During banding all birds were sexed by cloacal examination, each received a metal Canadian Wildlife Service band, and female goslings and all adults received a year-specific colored alphanumeric band. Only female goslings were color banded because this species shows highly female-biased philopatry; therefore, only known-age females were available for behavioral observations. The presence of web tags on goslings encountered at banding allowed the gosling's natal nest and parents to be identified, and the number of goslings reared (brood size at banding, BSB) to be determined. The timing of molt was determined for adults by measuring the length of the ninth primary at banding. To determine return rates any record of resightings (during nesting or brood rearing) and recaptures (during banding) of banded birds between 1973 and 1992 were used. As data were pooled over years, initial year of capture (the brood-rearing year for which BSB was known) was restricted to 1988 or earlier so that there were at least four potential re-encounter years (only 2% of birds were re-encountered five or more years after the brood-rearing year, $n = 3,466$). Adult body mass and ninth primary length at banding varied significantly with year and absolute date. Therefore, data were converted to residuals from predicted year and date values (using the GLM procedure; SAS Institute 1990) before analysis of the relationship with respect to brood size. Similarly, there was significant annual variation in mean laying date, hatch date, and clutch size. Therefore, all data were converted to residuals from annual means before being pooled over years. All data were restricted to older birds (five or more years of age) for which age and fecundity are statistically independent in this population.

Data on foraging behavior were collected in 1985, 1986, and 1992, and general activity budgets were recorded in 1991 and 1992 during the brood-rearing period. All observations were made between hatch and banding from a permanent, 5-m-high tower situated on intertidal feeding flats (Randy's Flats) adjacent to the nesting area. For all pairs from which data were obtained, at least one adult was banded (and, therefore, of known sex) and, whenever possible, pairs with known-age females were chosen. Observations were made throughout daylight hours, from 0500–2200 CST, with a minimum of 24 records obtained for each hourly interval. Due to disturbance from other researchers on the feeding flats, more observations were made in the early morning (0500–0900, 48%) than during the later part of the day, but

time of observation was not biased with respect to brood size.

Foraging behavior.—Foraging behavior was recorded continuously. Observations started once the bird adopted the head-down feeding posture and ended after 5 (1992) or 10 (1985, 1986) min, or when the bird changed to nonforaging behavior (preening, sleeping, or drinking). The following were recorded: (1) total observation time; (2) total time spent feeding (in head-down position); (3) number of feeding bouts, delimited by the bird stopping feeding and adopting the head-up posture while either stationary or moving; and (4) number of steps during feeding bouts. In addition, peck rates were measured at the beginning or end of each observation by counting the time taken for 50 pecks during bouts of continuous foraging (i.e. with no interruptions by head-up postures; Sedinger and Raveling 1988). Using these data the following additional variables were calculated: (1) number of pecks per minute during continuous feeding; (2) percentage of time spent feeding (feeding time/total study time); (3) number of vigilant, head-up postures per minute; and (4) number of steps per minute feeding. Sex, brood size, and band information also were recorded for all individuals.

Foraging behavior in relation to brood size was analyzed by multiple regression using the GLIM statistical package (Numerical Algorithms Group 1987), correcting for variation in adult sex, days since mean hatch, and year. Dependent variables were transformed to improve the distribution of the residuals: percentage time feeding (arcsine transformed), number of head-ups, and steps per minute feeding (both square-root transformed). Models were constructed using a stepwise procedure including both linear and quadratic terms for the independent variables. Tests for inclusion of independent variables were based on an *F*-distribution of the change in deviance per degree of freedom, when the variable was dropped from the model, divided by the deviance per degree of freedom in the full model. Brood size, days since mean hatch date, year, and sex were included as independent variables, and year and sex were entered as factors.

Activity budgets.—Activity budgets were recorded, in addition to detailed feeding behavior, to test the possibility that differences in foraging behavior in relation to brood size might be compensated for by changes in other behaviors. These were obtained using a scan-sampling technique, activity being recorded at 5-s intervals over 4-min periods ($n = 48$ records). In all cases activity of both birds of a pair was recorded consecutively. The following activities were distinguished: feeding (head-down), alert or vigilant (head-up plus extreme head-up of Lazarus and Inglis 1978), motor (swimming or walking, and not feeding), comfort (preening, stretching or resting), drinking, and social (usually inter- or intrabrood interactions). Birds brooding goslings were excluded from observations.

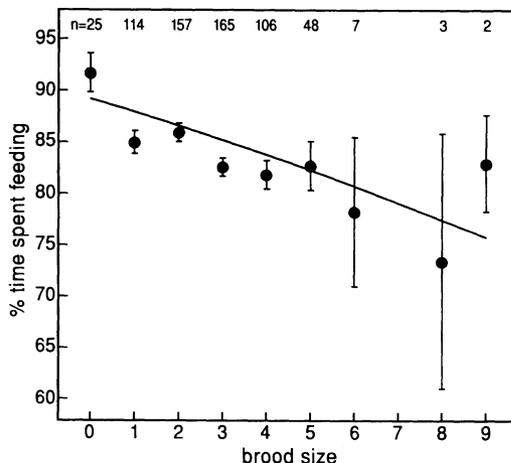


FIG. 1. Relationship between percentage of time spent feeding and brood size in Lesser Snow Geese. $\bar{x} \pm SE$, with sample sizes above points. Equation for line is $Y = 1.237 - 0.0202X$, where X is brood size.

We assumed that the proportion of total 5-s activity records spent in each activity reflected the actual proportion of time spent in each activity (following Eberhardt et al. 1989). Contingency table analysis and Spearman rank correlations were used to analyze activity budgets in relation to sex, year, brood size, or female age. All analyses were carried out using SAS (SAS Institute 1990).

RESULTS

Foraging behavior.—The percentage time spent feeding by parental birds decreased linearly with increasing brood size (Fig. 1; $F = 15.79$, $df = 1$ and 608 , $P < 0.001$) from greater than 90% for zero brood sizes to less than 80% for brood sizes of seven and eight. The number of alert (head-up) postures per min by parents also varied significantly with brood size (Fig. 2; $F = 12.41$, $df = 2$ and 617 , $P < 0.001$), increasing for brood sizes from one to five and then decreasing for larger broods. The relationships between these two behavioral variables and brood size were not significantly different in male and female birds (ANCOVA, sex \times brood interaction; feeding, $F = 1.78$; head-ups, $F = 0.12$). There was no significant relationship between number of pecks or number of steps per minute feeding and brood size ($P > 0.05$). Trends in parental behavior with brood size have often been reported to be dependent on inclusion of pairs without offspring (e.g. Sedinger and Raveling 1990). Therefore, data were reanalyzed for

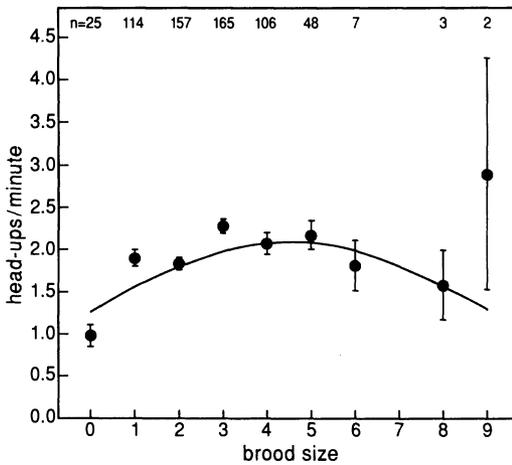


FIG. 2. Relationship between number of head-up postures per minute and brood size in Lesser Snow Geese. $\bar{x} \pm SE$, with sample sizes above points. Equation for line is $Y = 1.050 + 0.1418X - 0.0156X^2$, where X is brood size.

brood sizes of one to five only. For this restricted data set, both behavioral parameters were still significantly related to brood size (percentage time spent feeding, $F = 7.65$, $df = 1$ and 575 , $P < 0.01$, number of head-ups per minute, $F = 3.72$, $df = 2$ and 580 , $P < 0.05$).

Activity budgets.—There were significant differences in activity budgets between sexes ($X^2 = 246.8$, $df = 5$, $P < 0.001$, data pooled across years) so males and females were analyzed separately. Males spent more time alert and less time feeding than females (Table 1). The proportion of time spent in different behaviors did not vary between years in either sex (males, $X^2 = 0.215$; females, $X^2 = 0.616$; comfort, drinking, and social behaviors accounted for less than 5% of the total time, so these behaviors were pooled

TABLE 2. Activity budgets of male and female Lesser Snow Geese in relation to brood size.

Brood size	n	Percent time spent in each activity			
		Feeding	Alert	Motor	Other
Female					
1	37	85.2	3.3	6.4	5.1
2	64	87.8	6.0	4.8	1.4
3	72	83.8	5.2	5.8	5.2
4	48	87.9	5.2	5.3	1.6
5	12	75.7	8.5	8.5	7.3
Male					
1	37	81.2	8.6	6.6	3.6
2	64	82.9	10.6	5.7	0.9
3	72	78.9	11.3	6.3	3.5
4	48	79.5	12.2	6.0	2.2
5	12	79.2	10.4	8.7	1.7

with motor behavior). Therefore, data were pooled across years.

In females, for brood sizes of one or more, the proportion of total time spent alert and time spent feeding were positively ($r = 0.14$, $n = 239$, $P < 0.05$) and negatively ($r = -0.11$, $n = 239$, $P = 0.07$) correlated with brood size, respectively (Table 2). Time spent in motor or other activities was not related to brood size ($P > 0.50$). Females without goslings spent significantly more time feeding and less time in alert and other behaviors than females with one or more goslings (Table 1; $X^2 = 49.8$, $df = 2$, $P < 0.001$). With pairs without offspring included, the time spent alert and time spent feeding were more highly positively ($r = 0.22$, $n = 253$, $P < 0.001$) and negatively ($r = -0.18$, $n = 253$, $P < 0.01$) correlated with brood size, respectively. For individuals with goslings, the proportion of time spent alert was negatively correlated with time spent feeding ($r = -0.535$, $P < 0.0001$),

TABLE 1. Activity budgets of male and female Lesser Snow Geese with and without broods. Values are percentages of total number of observations.

Year	Sex	n	Activity					
			Feeding	Alert	Comfort	Motor	Drink	Social
With brood								
1991	M	147	80.1	10.7	1.6	6.2	1.2	0.2
1991	F	147	84.2	5.6	3.1	5.5	1.5	0.1
1992	M	92	81.5	11.1	0.3	6.0	1.1	<0.1
1992	F	92	87.4	5.5	0.4	5.6	1.0	<0.1
Without brood								
1992	M	14	92.3	2.2	0.0	5.5	0.0	0.0
1992	F	14	94.9	0.9	0.0	4.0	0.2	0.0

TABLE 3. Adult mass and timing of molt (indicated by ninth-primary length) in relation to brood size at banding (BSB, 5–6 weeks posthatch), and timing of molt in relation to brood loss (number of goslings reared compared to number leaving the nest, GLN-BSB). Values are mean residuals (to correct for variation with year and date), with standard error and sample size.

Adult mass (g)		Ninth-primary length (mm)			
BSB	$\bar{x} \pm SE (n)$	BSB	$\bar{x} \pm SE (n)$	Loss	$\bar{x} \pm SE (n)$
Females					
0	$-7.8 \pm 10.9 (93)$	0	$3.25 \pm 2.92 (64)$	0	$-1.55 \pm 2.86 (73)$
1	$12.7 \pm 11.2 (151)$	1	$1.23 \pm 2.50 (108)$	1	$-2.33 \pm 2.36 (109)$
2	$-4.4 \pm 8.6 (230)$	2	$0.86 \pm 1.78 (135)$	2	$2.34 \pm 2.55 (65)$
3	$-7.8 \pm 6.7 (303)$	3	$-1.83 \pm 1.79 (172)$	3	$2.07 \pm 3.88 (38)$
4	$8.5 \pm 9.7 (207)$	4	$-2.14 \pm 2.39 (111)$	4	$5.78 \pm 4.17 (25)$
5	$5.1 \pm 12.7 (85)$	5	$3.05 \pm 3.87 (31)$		
Males					
0	$9.3 \pm 26.6 (24)$	0	$15.53 \pm 4.55 (15)$	0	$-3.49 \pm 3.76 (39)$
1	$17.1 \pm 26.6 (48)$	1	$10.19 \pm 4.27 (35)$	1	$-4.80 \pm 2.77 (45)$
2	$-12.1 \pm 16.9 (96)$	2	$-1.33 \pm 2.80 (60)$	2	$-4.75 \pm 4.35 (34)$
3	$4.6 \pm 11.6 (133)$	3	$-2.99 \pm 2.75 (71)$	3	$7.37 \pm 5.59 (16)$
4	$-9.5 \pm 15.0 (107)$	4	$-4.12 \pm 2.37 (63)$	4	$12.61 \pm 5.13 (12)$
5	$11.7 \pm 24.0 (45)$	5	$-2.92 \pm 7.88 (13)$		

but not with time spent in other behaviors ($P > 0.30$).

In males, for brood sizes of one or more, there was no correlation between brood size and either proportion of total time spent alert or time spent feeding (Spearman rank, $r = 0.09$, $n = 239$ and $r = -0.06$, $n = 239$, respectively; Table 2). Similarly, time spent in motor or other activities was not related to brood size ($P > 0.50$). However, as for females, males without goslings spent significantly more time feeding and less time in alert and other behaviors than males with one or more goslings (Table 1; $X^2 = 62.7$, $df = 2$, $P < 0.001$). If these pairs without offspring were included, time spent alert and time spent feeding were significantly positively ($r = 0.18$, $n = 253$, $P < 0.01$) and negatively ($r = -0.14$, $n = 253$, $P < 0.05$) correlated with brood size, respectively. For individuals with goslings, the proportion of time spent alert was negatively correlated with time spent feeding ($r = -0.658$, $n = 239$, $P < 0.0001$), but not with time spent in other behaviors ($P > 0.20$).

Effect of female age on behavior.—For known-age females, using data on foraging behavior, there was no significant relationship between female age and either percentage time spent feeding ($F = 0.07$) or number of head-ups per minute ($F = 0.13$). If the foraging-behavior data were restricted only to known-age females, and female age was included as a variable in the model, both the behavioral variables were still

significantly related to brood size (percentage time spent feeding, $F = 5.19$, $df = 1,263$, $P < 0.05$; number of head-ups per minute, $F = 9.56$, $df = 1,269$, $P < 0.01$).

Parental fitness and brood size.—Adult body mass at banding did not vary significantly with number of offspring reared (BSB) in either males or females, either with pairs without offspring included (Table 3) or excluded ($P > 0.70$ in all cases). Similarly, adult mass was not related to brood loss (GLN-BSB) in either sex ($P > 0.70$ in all cases).

There was no significant difference in the number of days between hatch and banding for different brood sizes (BSB), so we did not explicitly control for this in subsequent analyses. Ninth-primary length decreased significantly with increasing BSB (for all brood sizes) in males ($F = 13.41$, $P < 0.001$) by an average 3.96 mm for each additional gosling (i.e. males with larger broods molted significantly later; Table 3). Primary length also decreased in females, by 0.91 mm per additional gosling, but this was not significant ($F = 1.74$; Table 3). This relationship remained significant in males if data were restricted to broods of one or more (3.51 mm per gosling; $F = 7.65$, $P = 0.006$). For birds hatching four or more goslings, ninth-primary length increased significantly with increasing brood loss in males (4.01 mm per gosling lost, $F = 6.28$, $P = 0.013$), and this relationship approached significance in females (2.27 mm per

TABLE 4. Effect of brood size at banding (BSB) on laying date, hatch date, clutch size, and probability of being re-encountered in the following year. Laying date, hatch date, and clutch size given as residuals from annual means and pooled over years; $\bar{x} \pm SE$ (n).

	Laying date	Hatch date	Clutch size	Percent re-encountered ^a
Females				
1	0.47 ± 0.39 (17)	-0.18 ± 0.28 (62)	0.17 ± 0.14 (62)	68.1 (160)
2	-0.19 ± 0.45 (18)	-0.27 ± 0.21 (93)	0.09 ± 0.12 (93)	68.5 (276)
3	-0.44 ± 0.37 (27)	-0.23 ± 0.19 (78)	0.31 ± 0.14 (78)	65.0 (257)
4	-0.03 ± 0.57 (16)	-0.50 ± 0.27 (56)	0.56 ± 0.17 (56)	64.6 (192)
5 ^b	-0.71 ± 0.80 (8)	0.35 ± 0.40 (28)	0.27 ± 0.19 (28)	73.0 (74)
6 ^b	—	—	—	83.3 (12)
Males				
1	—	-0.84 ± 0.43 (24)	0.00 ± 0.80 (24)	68.1 (47)
2	—	-0.32 ± 0.37 (33)	0.08 ± 0.17 (33)	71.7 (92)
3	—	-0.20 ± 0.30 (29)	0.17 ± 0.24 (29)	64.1 (92)
4	—	-0.30 ± 0.40 (28)	0.80 ± 0.23 (28)	70.4 (81)
5 ^b	—	0.16 ± 0.72 (8)	0.52 ± 0.33 (8)	80.5 (41)

^a n in parentheses.

^b Brood sizes 5 and 6 pooled for laying date, hatch date, and clutch size, as well as for return rate in males.

gosling lost, $F = 3.23$, $P = 0.071$; Table 3); birds that had the greatest reduction in brood size molted significantly earlier.

There was no significant difference in laying date (in females), or hatch date (in both sexes) in the following year, relative to the number of offspring reared the previous year ($P > 0.20$ in all cases; Table 4). Residual mean clutch size increased with number of goslings reared the previous year in males ($b = 0.22$, $F = 7.12$, $P = 0.009$); males rearing larger broods bred with females that laid larger clutches the following year. The relationship between clutch size and number of goslings reared was also positive in females ($b = 0.09$), but this relationship was not significant ($F = 2.90$, $P = 0.09$; Table 4).

The probability of birds being re-encountered in any subsequent year, up to four years after BSB, did not vary with number of goslings (BSB) reared in either males ($X^2 = 3.15$, $df = 4$, $P > 0.50$) or females ($X^2 = 6.10$, $df = 5$, $P > 0.30$; Table 4). Similarly, among those birds which were subsequently reencountered there was no difference in the probability of the bird being seen in the year following BSB compared to two or more years later, relative to BSB (males, $X^2 = 3.79$, $df = 4$, $P > 0.40$, females, $X^2 = 3.98$, $df = 5$, $P > 0.50$); that is, there was no evidence that birds rearing larger broods were more likely to skip a breeding attempt.

DISCUSSION

Male and female Lesser Snow Geese had significantly different overall activity budgets dur-

ing brood rearing at La Pérouse Bay; males spent more time alert and less time feeding compared to females (although both sexes showed the same trends in behavior with respect to brood size). This sex difference in behavior clearly was related to the presence or absence of offspring. In pairs without goslings, activity budgets did not differ between sexes. Several other studies similarly have shown that female geese spend more time feeding than males during brood rearing (Harwood 1977, Lazarus and Inglis 1978, Lessells 1987) and that males spend more time in the alert, head-up posture (Black and Owen 1989a, b, Sedinger and Raveling 1990). Sedinger and Raveling (1990) suggested that male Canada Geese (*Branta canadensis*) perform more brood defense and vigilance behavior so that their mates can spend more time feeding in order to recover body reserves lost during egg laying and incubation (Raveling 1979). Male Lesser Snow Geese spent more time in alert (vigilance) behavior than did females for each brood size (Table 1). This suggests that the role of male Lesser Snow Geese may actually be more important than that of females in brood defense and vigilance behavior. Martin et al. (1985) reported a rapid reduction in brood size of single parent females, and decreased gosling survival (in one year) in broods where the male was experimentally removed, compared to biparental families.

Foraging behavior of Lesser Snow Geese was significantly related to brood size in both sexes; birds adopted the alert (vigilant) posture more frequently with increasing brood size up to five

goslings and spent less time feeding with increasing brood size up to seven to eight goslings. We did not manipulate brood size to create experimentally enlarged broods; however, 99.8% ($n = 3,466$) of broods encountered at banding comprised six or fewer goslings. In addition, the relationship between parental behavior and number of offspring existed over a limited range of smaller brood sizes (from one to five goslings). Data from overall activity budgets also were consistent with this result for females, although not significantly so for males. Females spent a greater proportion of total time alert and a lesser proportion of time feeding as brood size increased from one to five goslings. In males, although activity budgets did not vary significantly with number of goslings, the trends for male behavior and brood size were in the same direction as those for females. Rockwell et al. (1993) showed that older Lesser Snow Geese (seven or more years of age) had lower reproductive success and that this was partly due to increased rates of total brood failure. However, we found no difference in mean female age relative to brood size in our sample. In addition, among known-age birds there was still a significant positive relationship between vigilance behavior and brood size, and a significant negative relationship between feeding behavior and brood size, controlling for female age. Schindler and Lamprecht (1987) similarly concluded that variation in parental behavior with increasing brood size was independent of female age in Bar-headed Geese.

In females (and in males considering all individuals), there was an inverse relationship between time spent alert and time spent feeding, but there was no systematic change in the amount of time spent in other activities. Increases in the time spent in vigilance behavior, with increasing brood size, therefore, are not compensated for by changes in other nonfeeding behaviors. Movement (walking and swimming) and drinking comprised between 70 and 95% of these other behaviors in male and female Lesser Snow Geese, respectively. Continuous movement is an integral part of the foraging strategy of geese because birds rapidly deplete food patches (Prop and Loonen 1988) and have to find new areas to graze. Regular drinking may also be essential in order to maintain water balance in this species which forages mainly on salt-marsh plants. Lesser Snow Geese, therefore, may be unable to further reduce the amount of time they spend in these other activities, even

though this would allow an increase in vigilance behavior while maintaining time spent feeding.

In contrast to the present study, Lessells (1987) found no relationship between time spent feeding and brood size in Lesser Snow Geese at La Pérouse Bay in an earlier year (1979). This difference may reflect the long-term decrease in food availability (by up to 75%) that has occurred at La Pérouse Bay over the last decade (Williams et al. 1993; although there were also some methodological and analytical differences between the two studies; C. M. Lessells pers. comm.). Parental behavior may now be constrained by food availability and the adults own food requirements (Loonen et al. in prep.). Schindler and Lamprecht (1987) also found an increase in vigilance behavior and a decrease in time spent feeding in female Bar-headed Geese, but they found no such relationship in males. In contrast, for Canada Geese the percentage of foraging periods spent in the alert posture was greater in males than females, and the proportional increase in vigilance behavior with increasing brood size was twofold greater in males. If pairs without offspring were excluded, time spent alert increased with brood size in males but not in females (Sedinger and Raveling 1990). Several studies of precocial species, therefore, have now demonstrated a reduction in time spent feeding by parental birds, usually as a consequence of increased vigilance behavior, with increasing brood size (see also Madsen 1981, Walters 1982, Schindler and Lamprecht 1987, Forslund 1993).

Schindler and Lamprecht (1987) suggested that reduced feeding time in female Bar-headed Geese, with increasing brood size, might induce a slower, or incomplete, recovery of body condition following incubation, thus reducing female fitness. However, the only studies to date that have investigated fitness consequences of brood size in precocial species are those of Rohwer (1985), Lessells (1986), and Rohwer and Heusmann (1991). Female Canada Geese that reared experimentally enlarged broods had lower body mass at the end of the brood-rearing period, molted later, and laid eggs later the following year, compared to those with smaller broods. However, there was no effect of brood size on overwinter survival or on clutch size in the following year (Lessells 1986). Rohwer (1985) found no relationship between female mass at the end of the rearing period and brood size in Blue-winged Teals (*Anas discors*), and adult fe-

male survival was not related to brood size in the Wood Duck (*Aix sponsa*; Rohwer and Heusmann 1991). In Lesser Snow Geese, there was no correlation between brood size and adult mass five to six weeks posthatch, but males rearing larger broods molted later than those with small broods. The fact that birds (of both sexes) that lost goslings during brood rearing had significantly more advanced molt, compared to birds losing no goslings, suggests that delayed molt was directly related to the rearing of large broods. Forslund (1993) showed that in Barnacle Geese parents responded immediately to a decrease in brood size by decreasing their vigilance time. Delayed onset of, or slower, molt may be disadvantageous in arctic-nesting geese because it reduces the length of the final feeding phase, between completion of molt and departure from the breeding grounds. This period may be critical in achieving the condition necessary to successfully complete migration (Prop et al. 1984, Owen and Black 1989). Nevertheless, male Lesser Snow Geese with brood sizes of five had ninth primaries that on average were only 13 mm shorter than those with brood sizes of one. As primary feathers grow at a rate of 7 to 8 mm per day in Lesser Snow Geese (Hanson and Jones 1976), the delay in completion of molt would only have been of the order of one to two days. This relatively small effect is consistent with the fact that we found no evidence for a negative effect of increasing brood size on the probability of return in the following year or any residual effect on timing of breeding the following year. In contrast, birds that reared the largest number of goslings laid significantly larger clutches the following year, suggesting that birds rearing the largest number of goslings were, in fact, "better-quality" birds. This is supported by the fact that the trends in return rate and timing of breeding with brood size also were positive rather than negative. Several previous studies have suggested that larger brood sizes may actually be advantageous in geese (Lamprecht 1986, Gregoire and Ankney 1990, Williams in press). For example, in most species, family groups are maintained during the winter. Offspring contribute increasingly to vigilance behavior and assist in conflicts with neighbors throughout the winter, allowing an increase in adult feeding time (Black and Owen 1989a, b). Thus, large brood sizes may enhance, rather than decrease, overwinter survival. Similarly, Prop et al. (1984) showed that larger

broods were more dominant and tended to feed in the areas of highest food availability on the breeding grounds.

In conclusion, parental behavior was significantly related to the number of offspring reared in Lesser Snow Geese at La Pérouse Bay; parents of larger broods spent less time feeding and more time in vigilance behavior. However, over the range of naturally observed brood sizes we found no evidence that this was negatively related to parental fitness or future reproductive effort in this precocial species. We are aware of the difficulties of detecting true costs of reproduction (sensu Lessells 1991); additional studies of parent-offspring behavior are required for precocial species, but these should measure both changes in parental behavior and the consequences of these changes to parental fitness.

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