Wilson Bulletin, 110(1), 1998, pp. 56–64

EFFECTS OF MALE REMOVAL ON FEMALE REPRODUCTIVE BIOLOGY IN ROSS' AND LESSER SNOW GEESE

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ABSTRACT.—We studied effects of mate removal on nesting and hatching success, incubation behavior, body mass, and post-hatch dispersal distance of female Ross' (*Chen rossii*) and Lesser Snow Geese (*C. caerulescens caerulescens*) at Karrak Lake, N.W.T., Canada. Male geese were removed during early incubation (days 1–8), and widowed and paired control females were monitored through post-hatch dispersal. Nesting and hatching success did not differ between species or treatments (widowed vs paired) and averaged 77.5 ± 3.8% and 64.0 ± 3.6% (±SE), respectively. Paired females spent more time with their bills tucked (23.7 ± 3.3% vs 9.1 ± 4.0%) and less time alert (8.6 ± 2.9% vs 22.9 ± 3.5%) while on nests than did widowed females. Snow widowed females (31.1 ± 4.7%) and Ross' widowed females (20.6 ± 6.0%) generally spent more time each day in head-up alert than did Snow paired females (7.1 ± 3.8%), Snow paired males (11.8 ± 3.8%), Ross' paired females (9.4 ± 3.6%), and Ross' paired males (7.9 ± 3.6%). Body mass of paired and widowed female Ross' Geese did not differ at hatch or at time of post-hatch recapture; however, mean distance recaptured from the breeding colony was greater for paired (50.9 ± 6.1 km) than for widowed females (27.3 ± 6.6 km). Total mass gain (276 ± 19 g) and rate of mass gain (8.4 ± 0.5 g/day), from hatch until post-hatch recapture (33.1 ± 1.2 days), were similar for widowed and paired female Ross' Geese. Male removal experiments in monogamous, precocial species generally have produced few effects on female nesting success or incubation behavior. We suggest that male parental care in arctic-nesting geese is more critical during laying and the post-hatch period than during incubation. *Received 21 June 1996, accepted 29 June 1997.*

Swans and geese (Anserini), and whistling ducks (Dendrocygnini) form long-term pair-bonds in which both parents care for young. Perennial monogamy is associated with large body size, high probability of mate survival, lack of renesting opportunities, and obligate brood-rearing (Oring and Sayler 1992). Male geese defend territories and mates during incubation, and subsequently protect broods while females replenish nutrient reserves used during laying and incubation (Ryder 1975; Lazarus and Inglis 1978; Ankney 1977, 1979; Sedinger and Raveling 1990; Afton and Paulus 1992; Paine 1992). Arctic-nesting geese face ecological conditions that may favor extended male parental care, including colonial nesting, herbivory, and short breeding seasons (Martin et al. 1985, Gauthier and Tardif 1991, Oring and Sayler 1992). Although most geese pair for life, opportunities for extra-pair matings exist; thus, effective mate guarding and territorial defense by males should enhance their certainty of paternity and may deter predation. Consequently, mate loss, intrusion of other males, and costs of re-pairing reduce lifetime reproductive success (Owen et al. 1988, Forslund and Larsson 1990) and, therefore, could select for male attendance during incubation (Paine 1992).

Ross' (*Chen rossii*) and Lesser Snow Geese (*C. caerulescens caerulescens*; hereafter Snow Geese) nest sympatrically in the central Canadian Arctic, providing a unique opportunity for comparative studies of similar species. Ross' Geese are smaller than Snow Geese [mean body mass of nesting adults (sexes combined) = 1356 g and 2029 g, respectively; MacInnes et al. 1989]. Daily energy requirements, clutch size, and vulnerability to predation are influenced by body mass via stored nutrient reserves (Barbault 1986). Female geese generally feed little during egg-laying and incubation, relying primarily on endogenous reserves to complete their clutches (Ryder 1970a, Ankney and MacInnes 1978). However, small species of geese (e.g., Ross' Geese) cannot store as much endogenous reserves as large species (but see Bromley and

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Jarvis 1993); consequently small species generally take more recess time during incubation to feed than do large species (Aldrich and Raveling 1983; Thompson and Raveling 1987; Afton and Paulus 1992; Afton, unpubl. data).

We investigated the importance of male Ross' and Snow Geese to nesting and hatching success, and to incubation behavior, body mass, and post-hatch dispersal of females. We predicted that widowed females would have lower nesting and hatching success than would paired females in both species. Snow Geese are larger and can store more nutrient reserves than can Ross' Geese; consequently, we reasoned that widowed Snow Geese would be capable of incubating for relatively longer periods and, therefore, should have greater success than should widowed Ross' Geese. We also predicted that behavior during incubation would differ between paired and widowed geese, if paired females benefit from mate-guarding. Benefits of male protection could include predator deterrence, reduced disturbance by neighboring females (i.e., nest parasitism), reduced harassment from males attempting forced extra-pair copulations, and increased foraging efficiency during incubation recesses. If male protection is beneficial during incubation, then paired females might be in better physiological condition at hatch than are widowed females. Finally, if parental care by male geese is important during brood rearing, then removing males at hatch should affect female condition, and gosling survival and growth. We predicted that if widowed females assumed sole responsibility for protecting their broods while concurrently replenishing nutrient reserves and molting, they would be in poorer condition than would paired females during the post-hatch period.

STUDY AREA AND METHODS

We studied Ross' and Snow Geese from 27 May to 9 August 1994 at Karrak Lake, N.W.T., Canada (67° 14′ N, 100° 16′ W). The area is typical tundra habitat with numerous shallow lakes and streams (Ryder 1972). Both species nest in areas of rock, heath, moss, or a mixture of these habitats located on islands or the mainland (McLandress 1983).

Nest selection.—We placed transects randomly through a 1-km^2 section of the colony located on the mainland and selected nests every 30 m along transects. We randomly selected species and direction from the transect (left or right) in which to select nests. A total of 120 nests (60 Ross', 60 Snow) were selected for the experiment and individually marked with small colored flags. We subsequently recorded final clutch size, embryo age (Weller 1956), and estimated first egg date (assuming a laying rate of 1 egg every 1.3 days for both species; Ryder 1970b). Each egg was numbered in several places and lines were drawn around the egg with a permanent marker to help determine hatching success (see below). Nests were observed every 3–5 days with a spotting scope to determine whether females were incubating their clutches. If a female was absent, we visited her nest immediately to determine condition of the clutch.

Nesting and hatching success.—After parents and broods left the colony, we estimated nesting and hatching success of all nests. A nest was classified as successful if at least 1 egg hatched. Hatching success was defined as percentage of eggs within a clutch that hatched. We classified an egg as hatched if any marked fragment (number or line) of eggshell, pieces of egg membrane, and/or gosling down were present in or near the nest.

Male removals.—Experimental nests were randomly assigned to one of two treatments: paired controls or widowed. Thirty-five nests of each species were allocated to control groups, and 25 nests of each species were assigned to widowed groups. Males assigned to the widow treatment were shot during early incubation (days 1–8) and used for other studies. We were unable to collect the entire sample of male Ross' Geese because of time constraints; consequently, we had 37 control and 23 widowed females for this species.

Incubation behavior.—We observed widowed and paired birds using focal-animal sampling techniques (Altmann 1974). We divided the day into 6 time periods: 00:01–04:00, 04:01–08:00, 08:01–12:00, 12:01–16:00, 16:01–20:00, and 20:01–24:00 CST. We randomly selected nests for observation during 2 of the 6 periods each day. We recorded activities of widowed females or paired females and their mates every 10 s during 15-min observation periods. Activities were categorized as alert (head-up or extreme head-up postures; Lazarus and Inglis 1978), foraging, walking, swimming, flying, comfort movements (preening, stretching, etc.; McKinney 1965), aggression (threats, calls, chases, and forced copulations), nest attendance (female only), and absent from territory. Behavior of females while on nests was subdivided into 4 categories: head-low (non-alert behavior; Lazarus and Inglis 1978), alert (head-up or extreme head-up), bill-tucked, and comfort movements.

Body mass and dispersal distance of female Ross' Geese.—We trapped a random sample of paired control females (N = 16) at the end of incubation (days 21–23) to compare body mass with that of widowed females. Females were captured using remote-controlled, modified bow-net traps (B. M. Grand, pers. comm.). Widowed females (N = 10) were shot at days 22–23 of incubation and used for other studies. All trapped and collected geese were weighed (±1 g) and measured (mid-wing, tarsus bone, and head length; ±0.1 mm; Dzubin and Cooch 1992).

We attached radio transmitters to random samples of paired control females ($n = 16$) and paired females whose mates subsequently were removed at hatch ($n = 13$) to obtain post-hatch dispersal distances. Transmitters weighed an average of 26 g and were attached using a modified backpack harness (Dwyer 1972). Captured females also were fitted with neck collars and standard leg bands. Goslings ($n = 33$ of paired control females, $n = 32$ of females widowed at hatch) were web-tagged through the eggshell during the pipping stage (Alliston 1975) or at hatch using metal web-tags to allow comparisons of gosling growth and survival rates. Geese were relocated 29–42 days after hatch using telemetry; aerial antennae were mounted on a helicopter, and flightless geese were captured by driving them into a portable net corral. Females and web-tagged goslings were banded, collared, weighed and measured. Recapture distance from the breeding colony was determined using a Global Positioning System. As a result of time, permit and funding constraints, we were unable to trap, radio track or collect female Snow Geese for analysis of body mass and dispersal distance.

Statistical analysis.—We used analysis of variance (ANOVA) to test for differences in first egg date, clutch size, predicted hatch date, and hatching success between species, treatments, and their interaction (Proc GLM, SAS Institute 1990). We compared least-square means (LSM) using t-tests when sample sizes were unequal (PDIFF option, SAS Institute 1990) and used Tukey's studentized range test to compare unadjusted means when sample sizes were equal (Sokal and Rohlf 1981). Because of time constraints, we were unable to accurately estimate first egg date for 18 of the 120 experimental nests. These included four paired Ross', five widowed Ross', three paired Snow, and six widowed Snow Goose nests. Accordingly, these nests were excluded from analyses of first egg date and predicted hatch date.

We tested whether nest success differed between species, treatments, and their interaction using maximum-likelihood ANOVA (Proc CATMOD, SAS Institute 1990). We present apparent nest success (number of successful nests/total nests) because we began monitoring all nests during early laying. We also used maximum-likelihood ANOVA to test whether number of nests that had partial clutch reduction during incubation (but still hatched ≥ 1 egg) differed between species, treatments or their interaction.

We computed proportion of time spent in various behavioral activities by dividing the frequency that each behavior was recorded by the maximum number of behaviors possible per 15-min sampling period ($n = 90$). We analyzed raw and arcsine square-root transformed proportions (Sokal and Rohlf 1981) using multivariate analysis of variance (MANOVA) to examine differences in overall time-activity budgets by species, treatment, stage of incubation, and associated interactions. Stage of incubation was divided into 3 categories: early (days 1–8), mid (days 9–15), and late (days 16–23). We used means of behavioral observations for the few nests that were observed more than once. Significant explanatory variables from MANOVA were used in ANOVAs to examine effects on individual behaviors. For females, four behaviors were used in the analysis: nest attendance (i.e., incubation constancy), foraging, absent from territory, and alert posture (while off nests). These behaviors accounted for more than 98% of female activities. We further analyzed head posture of females while on nests (head-low, comfort movements, bill-tucked, and alert). In addition, we compared time spent alert (head-up or extreme head-up) each day among experimental female groups ($k = 4$ groups) and male geese ($k = 2$). We compared LSMs in behavioral analyses because of unbalanced designs (PDIFF option, SAS Institute 1990). Analyses of raw and transformed proportion data yielded similar results in final models; therefore, we report results from analyses of raw data (LSM ± SE).

Because body mass often is related to structural size and body size is positively correlated with post-hatch dispersal distance in Ross' Geese (Slattery 1994), we indexed female body size using Principal Components Analysis (PCA; Proc PRINCOMP, SAS Institute 1990). Body size was defined as the first principal component (PC1) computed from the correlation matrix of mid-wing, tarsus bone, and head length measurements. We ran separate PCAs to estimate body size for females at hatch and during post-hatch dispersal; all loadings were positive and explained 80–84% of the original cumulative variance.

We used analysis of covariance (ANCOVA) to test for differences in body mass and post-hatch dispersal distance between treatments, with PC1 (i.e., body size) used as a covariate in models. We used ANCOVA to test for differences in mass change (from hatch to post-hatch recapture) between treatments, with days elapsed since hatch, recapture distance, and PC1 as covariates. We also used ANCOVA to test for differences in rate of mass change between treatments, with recapture distance and PC1 as covariates. Pearson correlation coefficients (r) were used to describe relationships between PC1 and various response variables (Proc CORR, SAS Institute 1990). Finally, we tested for statistical significance of the combined results of ours and other goose studies, to determine whether nest success of widows was lower than that of controls, using Fisher's inverse χ^2 method (Hedges and Olkin 1985:37).

RESULTS

First egg date, clutch size, and predicted hatch date.—First egg date did not differ between species ($F = 2.82$; df = 1, 98; $P > 0.05$) or treatments ($F = 0.62$; df = 1, 98; $P > 0.05$); the species-by-treatment interaction also was not significant ($F = 0.52$; df = 1, 98; $P > 0.05$). Modal first egg date for Ross'

TABLE 1. Fate of experimental nests at Karrak Lake, N.W.T., Canada, 1994.

	Ross' Geese				Snow Geese			
	Control		Widow		Control		Widow	
Fate of nest	n	%	n	%	n	%	n	%
Unsuccessful[a]	7	18.9	8	34.8	6	17.1	6	24.0
Successful	30	81.1	15	65.2	29	82.9	19	76.0
Clutch reduction[b]	8	21.6	3	13.0	9	25.7	6	24.0
Total nests[c]	37		23		35		25	

[a] Nests abandoned, or preyed upon and entire clutch lost.
[b] Reduction occurred during incubation, but ≥1 egg hatched in nest.
[c] Unsuccessful + successful nests.

(39% of 51 nests) and Snow Geese (41% of 51 nests) was 31 May.

Mean clutch size of Snow Geese (3.95 ± 0.08; $n = 60$) was larger ($F = 16.64$; df = 1, 116; $P < 0.001$) than that of Ross' Geese (3.43 ± 0.08; $n = 60$), but the treatment main effect ($F = 0.14$; df = 1, 116; $P > 0.05$) and treatment-by-species interaction were not significant ($F = 0.64$; df = 1, 116; $P > 0.05$).

Predicted hatch date did not differ between species ($F = 0.01$; df = 1, 98; $P > 0.05$) or treatments ($F = 1.25$; df = 1, 98; $P > 0.05$), and the species-by-treatment interaction also was not significant ($F = 0.18$; df = 1, 98; $P > 0.05$). Modal predicted hatch date for Ross' (55% of 51 nests) and Snow Geese (45% of 51 nests) was 27 June. First egg and predicted hatch dates were 8–16 days earlier in 1994 as compared to previous years (1991–1993) at Karrak Lake (Slattery and Alisauskas 1993).

Nesting and hatching success.—Nesting success did not differ between species ($\chi^2 = 0.53$, df = 1, $P > 0.05$) or treatments ($\chi^2 = 1.98$, df = 1, $P > 0.05$); the species-by-treatment interaction also was not significant ($\chi^2 = 0.21$, df = 1, $P > 0.05$; Table 1). Nesting success for both species combined was 77.5 ± 3.8% (N = 120). Nests with partial clutch reduction did not vary by species ($\chi^2 = 1.04$, df = 1, $P > 0.05$) or treatments ($\chi^2 = 0.54$, df = 1, $P > 0.05$), and the species-by-treatment interaction was not significant ($\chi^2 = 0.29$, df = 1, $P > 0.05$; Table 1).

Hatching success did not differ between species ($F = 0.12$, df = 1, 116, $P > 0.05$) or treatments ($F = 0.12$, df = 1, 116, $P > 0.05$); the species-by-treatment interaction also was not significant ($F = 0.10$, df = 1, 116, $P > 0.05$). Hatching success for both species combined averaged 64.0 ± 3.6% (N = 120).

Female behavior during incubation.—We collected focal-animal samples from 44 female Ross' ($n = 27$ control, 17 widow) and 46 female Snow Geese ($n = 27$ control, 19 widow) during incubation. Overall percent time spent in nest attendance, alert (off nest), absent from territory, and foraging by females did not differ between species ($F = 0.50$; df = 4, 129; $P > 0.05$) or treatments ($F = 1.38$; df = 4, 129; $P > 0.05$), or among incubation stages ($F = 1.60$; df = 8, 258; $P > 0.05$; Table 2); none of the interactions of various main effects were significant (all $P > 0.05$). Nest attendance for both species combined averaged 91.8 ± 3.0%.

Head postures of incubating females differed between treatments ($F = 4.72$; df = 4, 130; $P < 0.002$) and among incubation stages ($F = 3.09$; df = 8, 260; $P < 0.003$), but were similar between species ($F = 0.80$; df = 4, 122; $P > 0.05$); none of the interactions were significant (all $P > 0.05$). Paired females spent more time with their bills tucked ($F = 8.32$; df = 1, 133; $P < 0.005$), and less time alert while on nests than did widows ($F = 10.62$; df = 1, 133; $P < 0.002$; Table 2). Time spent with bill tucked under the wing differed among incubation stages ($F = 9.32$, df = 2, 133, $P < 0.001$). Females spent more time with bill tucked during late incubation than during early or mid incubation (Table 2).

Alert behavior of males and females.—Overall time spent alert each day differed among control Ross' females, widowed Ross' females, control Snow females, widowed Snow females, Ross' males, and Snow Goose males ($F = 3.08$; df = 10, 390; $P < 0.001$); however, stage of incubation ($F = 0.96$; df = 4, 390; $P > 0.05$) and stage-by-group interaction were not significant ($F = 0.99$; df =

TABLE 2. Percent time spent in various behaviors (least-square means ± SE) by species, treatment, and incubation stage for female geese at Karrak Lake, N.W.T., Canada, 1994.

		Analysis of on-nest behaviors				Analysis of off-nest behaviors		
Category	n	Head-low	Alert	Bill-tucked	Comfort	Feeding	Absent	Alert
Species								
Ross'	44	59.8 ± 4.8A[a]	13.5 ± 3.2A	15.0 ± 3.6A	0.6 ± 0.1A	1.3 ± 0.7A	6.4 ± 2.6A	0.5 ± 0.4A
Snow	46	57.4 ± 4.7A	17.9 ± 3.1A	17.7 ± 3.6A	0.5 ± 0.1A	0.3 ± 0.6A	4.3 ± 2.5A	0.5 ± 0.4A
Treatment								
Control	54	59.4 ± 4.3A	8.6 ± 2.9B	23.7 ± 3.3A	0.4 ± 0.1A	1.5 ± 0.6A	3.7 ± 2.3A	0.7 ± 0.4A
Widow	36	57.7 ± 5.2A	22.9 ± 3.5A	9.1 ± 4.0B	0.7 ± 0.2A	0.2 ± 0.2A	7.0 ± 2.8A	0.4 ± 0.5A
Stage								
Early	26	55.4 ± 7.4A	17.9 ± 4.9A	13.6 ± 5.7B	0.8 ± 0.2A	0.2 ± 1.1A	7.5 ± 4.0A	0.2 ± 0.2AB
Mid	63	66.2 ± 4.7A	15.2 ± 3.1A	5.9 ± 3.6B	0.3 ± 0.1A	0.8 ± 0.7A	8.7 ± 2.5A	1.2 ± 0.5A
Late	47	54.0 ± 5.4A	14.2 ± 3.6A	29.7 ± 4.2A	0.5 ± 0.2A	1.4 ± 1.1A	4.6 ± 2.9A	0.1 ± 0.1B

[a] Within an analysis, least-square means with different letters within a category and behavior are significantly different ($P < 0.05$).

TABLE 3. Percent time spent in head-up alert (least-square means ± SE) during incubation by experimental group at Karrak Lake, N.W.T., Canada, 1994.

Group	n	Head-up
Ross' widow females	28	20.6 ± 6.0AB[a]
Snow widow females	32	31.1 ± 4.7A
Ross' paired females	40	9.4 ± 3.6C
Snow paired females	37	7.1 ± 3.8C
Ross' paired males	40	7.9 ± 3.6C
Snow paired males	37	11.8 ± 3.8BC

[a] Least-square means with different letters are significantly different ($P < 0.05$).

20, 390; $P > 0.05$). Time spent head-up alert each day differed among groups ($F = 4.42$; df = 5, 196; $P < 0.001$), whereas time spent in extreme head-up alert was similar among groups ($F = 1.40$; df = 5, 196; $P > 0.05$) and averaged 0.9 ± 0.2%. Widowed Ross' and Snow Goose females generally spent more time in head-up alert than did geese in other groups (Table 3).

Body mass and post-hatch dispersal distance of female Ross' Geese.—Body mass at hatch was positively ($r = 0.54$) related to PC1 ($F = 9.48$; df = 1, 23; $P < 0.006$), but mass did not differ ($F = 0.01$; df = 1, 23; $P > 0.05$) between paired (995 ± 18 g, $n = 16$) and widowed females (997 ± 23 g, $n = 10$). Overall mean mass at hatch, unadjusted for size, was 996 ± 16 g ($n = 26$).

Because of limited helicopter time, we captured only 13 radio-tagged females (5 paired controls, 8 widowed at hatch). Only one female (paired control) recovered in banding drives had web-tagged goslings ($n = 2$ out of 4 goslings hatched); one other control female escaped before being weighed. Body mass at recapture was positively ($r = 0.82$) related to PC1 ($F = 19.22$; df = 1, 9; $P < 0.002$), but mass did not differ ($F = 0.07$; df = 1, 9; $P > 0.05$) between paired (1266 ± 40 g; $n = 4$) and widowed females (1279 ± 28 g; $n = 8$). Overall mean mass at recapture was 1275 ± 37 g ($n = 12$).

Mass change of females was not related to days elapsed since hatch (33.1 ± 1.2 days, Range = 29–42 days, $n = 12$; $F = 0.20$; df = 1, 7; $P > 0.05$), recapture distance ($F = 0.01$; df = 1, 7; $P > 0.05$) or PC1 ($F = 0.75$; df = 1, 7; $P > 0.05$), and mass change did

TABLE 4. Summary of studies investigating the influence of male removals on reproductive parameters in precocial birds.

	Impact of Male-removal				
Species (Citation)	Nest success	Brood survival	Brood growth	Female survival	Female body mass
Lesser Snow Geese (Martin et al. 1985)	Varied[a]	Varied[b]	—[c]	—	Decline
Bar-headed Geese (Schneider and Lamprecht 1990)	—	Decline	NS[d]	—	—
Canada Geese (Paine 1992)	NS	Decline	—	—	NS
Wood Duck (Hipes and Hepp 1993)	NS	—	—	—	—
Willow Ptarmigan (Hannon 1984)	Varied[e]	NS	—	Decline	—
Willow Ptarmigan (Martin 1984)	—	—	—	NS	Increase
Willow Ptarmigan (Martin and Cooke 1987)	NS	NS	—	NS	Varied[f]
Western Sandpiper (Erckmann 1983)	Decline	—	—	—	—
Ross' Geese (This study)	NS	—	—	—	NS
Lesser Snow Geese (This study)	NS	—	—	—	—

[a] At Boas River, paired females had higher ($P < 0.001$) nest success than did widows whose mates were removed during early laying, but nest success was similar when males were removed during late laying ($P > 0.051$) and during incubation ($P > 0.056$). At La Perouse Bay, nest success was similar for paired females and widows whose males were removed in early incubation ($P > 0.05$).

[b] Suggested decline at La Perouse Bay in 1983, but no difference in 1984.

[c] Data not collected.

[d] Data not significant.

[e] Nest success declined in 1981, but did not differ in 1979 and 1980.

[f] Widows were heavier than paired females at hatch in 1982; trends in 1981 and 1983 were similar, but not significantly different. Widows lost more weight than did paired females in the post-hatch period.

not differ ($F = 0.31$; df = 1,7; $P > 0.05$) between paired (282 ± 58 g; $n = 4$) and widowed females (273 ± 12 g; $n = 8$). Mass change averaged 276 ± 19 g (Range = 192–448 g; $n = 12$) for all females combined. Rate of mass change was not related to recapture distance ($F = 0.03$; df = 1, 8; $P > 0.05$) or PC1 ($F = 1.18$; df = 1, 8; $P > 0.05$), and did not differ between paired (7.5 ± 1.2 g/day; $n = 4$) and widowed females (8.8 ± 0.7 g/day; $n = 8$; $F = 0.75$; df = 1, 8; $P > 0.05$). Overall rate of mass gain averaged 8.4 ± 0.5 g/day (Range = 5.1–10.7 g/day; $n = 12$). Distance recaptured from the colony was not related to PC1 ($F = 1.42$; df = 1, 10; $P > 0.05$), but paired female Ross' Geese (50.9 ± 6.1 km; $n = 5$) were recaptured further ($F = 7.54$; df = 1, 10; $P < 0.021$) from the colony than were widowed females (27.3 ± 6.6 km; $n = 8$).

DISCUSSION

Female reproductive success.—We predicted that removal of male Ross' and Snow Geese during early incubation would negatively affect several components of female reproductive success. However, we did not detect statistically significant differences in nesting or hatching success between treatments, although nest success varied in the predicted directions for both species (Table 1). Simulation modeling indicated that sample size would have to be doubled (i.e., 120 nests for each species) in order for observed estimates of nest success to be statistically different ($P < 0.05$). Other male removal studies in precocial species also detected little or no differences in nest success between widowed and paired females (Table 4). However, among the 6 statistical tests on geese, nest success varied in the predicted direction in 4 tests and was significantly different in 1 test. Meta-analysis of combined P-values from the 6 tests indicated a significant overall difference between treatments ($\chi^2 = 23.11$, df = 12, $P = 0.0268$); however, when the P-value from the single significant test was excluded, the combined analysis was not significant ($\chi^2 = 9.30$, df = 10, $P > 0.05$). Martin et al. (1985) also reported that rates of egg loss or intraspecific nest parasitism did not differ between widowed and paired Snow Geese breeding at a smaller sub-arctic colony.

Several factors may explain why male removals during incubation have little or no effect on nest success in colonial geese. By early incubation, territories have been established, laying is completed, and females can no longer be fertilized via extra-pair copulations (EPCs). Accordingly, forced EPCs rarely occurred during incubation at Karrak Lake (LeSchack, unpubl. data; Afton, unpubl. data;

but see Mineau and Cooke 1979). Paine (1992) rejected the hypothesis that non-colonial Canada Goose females benefit from male protection against predators; however, he questioned his results because nest success was high (>82%) and many males frequently were away from their nests.

We found that early snow melt at Karrak Lake did not result in increased overall nest success. Although egg-laying began 8–16 days earlier than in the previous three years, nest success of Ross' (75%) and Snow Geese (80%) were similar to rates recorded at Karrak Lake in 1993 (82% Ross', 76% Snow; Slattery and Alisauskas 1993). Adverse weather conditions upon arrival at breeding grounds delay reproduction and reduces clutch size. Atlantic Brant (*Branta bernicla hrota*) expended more energy searching for nest sites and food resources, and had lower productivity when nesting was delayed by late snow melt (Barry 1962). We suggest, that during a delayed breeding season, widowed females might have significantly lower nest success than do paired females as a result of declines in physiological condition caused by an increase in energy expenditure. Widows also might take more or longer incubation recesses than would paired females during late breeding seasons to search for food, thereby increasing the risk of both nest predation and a lengthened incubation period (Aldrich and Raveling 1983, Madsen et al. 1989). We observed that time spent off nests by widowed and paired females of both species, although not statistically different, varied in the predicted direction even though it was an early breeding season. We suspect that our sampling effort was not adequate to detect small differences in reproductive success that could impinge on fitness differences between treatment groups.

Incubation behavior, body mass and post-hatch dispersal distance.—In our study, nest attendance of Ross' and Snow Geese during early incubation was similar to that recorded in June 1993 at Karrak Lake (Afton, unpubl. data). Others who did male removal experiments in Snow Geese (Martin et al. 1985) and Canada Geese (Paine 1992) reported no differences in incubation constancy between widowed and paired geese. However, widows were harassed and displaced more often than paired females (Martin et al. 1985, Schneider and Lamprecht 1990). We also found that nest attendance was similar between widowed and paired females, although the trend was in the predicted direction. Similar trends also were reported for Snow Geese (Martin et al. 1985) and Canada Geese (Paine 1992).

We found that presence of their mates resulted in paired females spending more time with their bills tucked and less time alert while on nests than did widowed females. Widowed female Snow Geese spent twice as much time in the extreme head-up posture while incubating compared to paired individuals (Martin et al. 1985). A similar observation was reported for widowed Canada Geese (Paine 1992). Martin et al. (1985) suggested that an increase in alert behavior might result in an energy cost (i.e., decrease in body mass) to widowed birds. We did not detect a significant difference in body mass at hatch between paired and widowed female Ross' Geese, although the trend was in the predicted direction; however, our sample size was small. Body mass of widowed ptarmigan also did not differ from that of paired females at the end of incubation (Martin 1984).

Our study is the first to examine effects of male removal on post-hatch dispersal distance. Paired Ross' females were recaptured nearly twice as far from the breeding colony as were widowed females. We suggest that paired females are able to travel further and to better brood-rearing areas than are widowed females because of presence of their mates; however, this hypothesis needs to be tested. Slattery (1994) found that body size of Ross' Geese varied positively with recapture distance from the breeding colony at Karrak Lake; however, we found no relationship between body size and recapture distance. Thus, pair status appears more important than body size in determining post-hatch dispersal from the colony.

Role of male geese in biparental care.—Male removal experiments in monogamous, precocial species generally have produced few effects on nest success or female incubation behavior. In our study, widowed female geese spent increased time alert while on nests, but this apparently did not entail major physiological costs because body mass at hatch was similar for paired and widowed females.

We suggest that male parental care in Arctic-nesting geese is more critical during laying than during incubation. Removal of males during laying may cause many females to abandon nests because of increased sexual and physical harassment (e.g., forced EPCs) from conspecifics. Nest success differed between widowed and paired Snow Geese in a subarctic colony when males were removed during early laying (eggs 1–2; Martin et al. 1985). Lone Snow Goose females were subjected to frequent harassment from neighboring males (Martin et al. 1985); however, these authors did not determine whether this directly caused nest failure.

We also suggest that male parental care is more critical after hatch than during incubation because males are primary providers of brood defense while females replenish nutrient reserves utilized during laying and incubation (Ankney 1977, 1979; Lazarus and Inglis 1978; Sedinger and Raveling 1990; Afton and Paulus 1992). Female geese lose 11–32% of their body mass during incubation (Ankney and MacInnes 1978, Aldrich and Raveling 1983, Thompson and Raveling 1987, Afton and Paulus 1992). Brood survival generally is reduced by male removal (Table 4). For example, Schneider and Lamprecht (1990) reported higher gosling feeding and survival rates and fewer interruptions of brooding for paired females than for widows in a semicaptive flock of Bar-headed Geese (*Anser indicus*). We conclude that, under normal breeding conditions, male removal during incubation is not greatly detrimental to nest success or female body condition; however, effects of male removal during incubation in a late nesting season should be studied. Finally, we believe that future research should focus on the importance of biparental care during the laying and post-hatch periods.

ACKNOWLEDGMENTS

Our project received financial and logistical support from the Canadian Wildlife Service (CWS), Arctic Goose Joint Venture, California Dept. of Fish and Game, Polar Continental Shelf Project, Louisiana Cooperative Fish and Wildlife Research Unit, Louisiana Dept. of Wildlife and Fisheries, School of Forestry, Wildlife and Fisheries at Louisiana State Univ. (LSU), and NSF/LaSER Grant (1993)-HRD-01. Geese were captured and collected under LSU Institutional Animal Care and Use Permit #A94-16 and CWS Permit #WSNWT-04/93. We thank S. L. Koch and R. Bon for assistance in data collection, and C. F. Bryan, P. O. Dunn, P. A. Gowaty, G. R. Hepp, K. G. McCracken, and an anonymous reviewer for providing helpful comments on the manuscript.

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