Effects of collar-attached transmitters on behaviour, pair bond and breeding success of snow geese Anser caerulescens atlanticus

Authors: Demers, Frédéric, Giroux, Jean-François, Gauthier, Gilles, and Bêty, Joël

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ORIGINAL ARTICLES

Effects of collar-attached transmitters on behaviour, pair bond and breeding success of snow geese *Anser caerulescens atlanticus*

Frédéric Demers, Jean-François Giroux, Gilles Gauthier & Joël Bêty

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There is growing evidence that harnesses may not be an effective technique to attach radio-transmitters on geese. The use of neck collars is an alternative, but studies on the effect of collars with or without radios on geese have reached divergent conclusions. As our objective was to determine if radio neck collars affect behaviour, pair bonds and breeding success of greater snow geese *Anser caerulescens atlanticus*, we fitted 230 females with radio neck collars during the 1995-1998 moulting periods on Bylot Island, Nunavut. Data were subsequently obtained for 159 birds on the staging and breeding grounds. Radios represented 2.5 ± 0.1% (± SE) of the birds' body mass. Unmarked geese and those fitted with conventional plastic collars served as controls. The behaviour of radio-collared geese was affected during the first fall after marking, but negative effects disappeared thereafter. Geese with conventional collars had similar behaviour as unmarked birds. Divorce rates were low for birds with conventional collars (0-4%), but were as great as 30% for radio-collared geese. We suggest that the modified behaviour of the radio-collared females promoted separation from the male. Apparent breeding propensity, nest initiation date, clutch size and nesting success of radio-marked birds were also negatively affected. Until better alternatives are developed, we recommend minimizing the mass of radio collars to < 2.5% of the birds' body mass and reducing the antenna length. This implies a trade-off between effects on birds and performance of the transmitters in terms of battery mass (longevity) and antenna length (range).

Key words: Anser caerulescens atlanticus, behaviour, greater snow geese, neck collar, radio-transmitter, reproduction, telemetry

Frédéric Demers & Jean-François Giroux, Département des sciences biologiques, Université du Québec à Montréal, C.P. 8888, Succursale Centre-ville Montréal, Québec, H3C 3P8, Canada - e-mail addresses: frederic_demers@yahoo.com (Frédéric Demers); giroux.jean-francois@uqam.ca (Jean-François Giroux) Gilles Gauthier & Joël Bêty, Département de Biologie and Centre d'Études Nordiques, Université Laval, Sainte-Foy, Québec, G1K 7P4, Canada - e-mail addresses: gilles.gauthier@bio.ulaval.ca (Gilles Gauthier); jbety@birdlover.com (Joël Bêty)*

**Present address: Atlantic Cooperative Wildlife Ecology Research Network, Department of Biology, University of New Brunswick, P.O. Box 45111, Fredericton, New Brunswick, E3B 6E1, Canada*

Corresponding author: Jean-François Giroux

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Radio telemetry plays a major role in studies of waterfowl ecology including the determination of space and habitat use (Giroux & Patterson 1995, Petrie & Rogers 1997), survival and harvest rates (Eberhardt, Anthony & Richard 1989, Longcore, McAuley, Clugston, Bunck, Giroux, Ouellet, Parker, Dupuis, Stotts & Goldsberry 2000), migration chronology (Reed, Stehn & Ward 1989, Petrie & Rogers 1997) and migration routes (Blouin, Giroux, Ferron, Gauthier & Doucet 1999). Researchers often assume that capturing, handling and marking birds with radio transmitters do not negatively affect their behaviour. However, if capture and/or radios have negative effects on marked individuals, the results of these studies may be biased.

There is growing evidence that harnesses may not be the best attachment technique for fitting radios to ducks and geese. They can affect their behaviour (Gilmer, Ball, Cowardin & Reichmann 1974, Pietz, Krapu, Greenwood & Lokemoen 1993, Blouin et al. 1999), induce feather wear, cause thickening of the skin beneath the tag and loss of bird's mass (Greenwood & Sargeant 1973). Additionally, harness-attached transmitters can interfere with established pair bonds (Pietz et al. 1993, Rotella, Howerter, Sankowski & Devries1993, Ward & Flint 1995). An alternative option for geese is to fix radio transmitters on neck collars (Blouin et al. 1999). However, results from studies on the effects of collars with or without transmitters are equivocal. Zicus, Schultz & Cooper (1983), Samuel, Rusch & Craven (1990), Castelli & Trost (1996), Schmutz & Morse (2000), and Alisauskas & Lindberg (2002) reported decreased survival of Canada geese *Branta canadensis*, emperor geese *Anser canagica* and white-fronted geese *Anser albifrons* fitted with neck collars, whereas Craven (1979) and Menu, Hestbeck, Gauthier & Reed (2000) did not detect differences in survival of Canada geese and greater snow geese *Anser caerulescens atlanticus*, respectively. Craven (1979) did not observe physical impairment such as feather wear or weight loss in neck-banded Canada geese. Lensink (1968), MacInnes & Dunn (1988) and Menu et al. (2000) found evidence that neck collars may affect breeding propensity and emigration of brant *Branta bernicla*, Canada geese and greater snow geese, respectively. Likewise, Schmutz & Morse (2000) detected smaller clutch size for emperor geese marked with either conventional or radio collars. The effects of neck collars, especially those with radios, clearly need further investigation.

In addition to potential negative consequences of putting radios on geese, captures may also adversely affect birds. The widespread technique for catching geese consists of encircling the birds during their moult and driving them towards a catching pen (Menu, Gauthier & Reed 2001). Mass captures (300-600 birds) could be a stressful event because of the time the birds spent in the enclosure (3-5 hours). Some evidence indicate that these operations may slightly affect survival of juveniles, but not of adults (Williams, Cooke, Cooch & Rockwell 1993, Menu et al. 2001). Scattering of individuals upon release may result in family and eventually pair breakups, but this has never been reported.

As part of a larger study of the migratory behaviour of greater snow geese, we sought to determine if fitting the birds with radio collars negatively affect behaviour, pair bonds and breeding success of birds. As birds were captured in family groups, we also examined if the behaviour of the family at release was a good predictor of pair-bond maintenance. Finally, some radio marked geese were recaptured a few days later during mass captures; this allowed us to determine if this method of capture further affected pair bonds.

Material and methods

Capture and marking

We captured greater snow goose families on Bylot Island (Nunavut) each August from 1995 to 1998. We fitted 230 adult females with a radio transmitter (20 in 1995, 60 in 1996, 71 in 1997 and 79 in 1998). We also recaptured and replaced the radio of 19 of these females. Beginning in 1996, we put conventional yellow plastic neck collars (Menu et al. 2000) onto males accompanying radio tagged females to facilitate determination of pair status. We ringed all captured birds with standard U. S. Fish and Wildlife Service metal leg bands.

Captures occurred after non-breeders and failed-breeders had regained flight capabilities (Reed, Bêty, Mainguy, Gauthier & Giroux 2003). Therefore, all moulting adults captured were breeders and were at least

two years old as snow geese do not breed as yearlings (Cooke, Rockwell & Lank 1995, Reed 2003). We captured geese by driving groups of 1-4 families (i.e. 3-20 birds) into corral traps (Menu et al. 2001). Juveniles were 25-35 days old during capture. Each capture lasted 15-60 minutes depending on the number of birds. The quality of the release was scored as grouped if all birds walked together or ungrouped if one or more birds immediately fled the group. We captured families approximately five days prior to initiation of the annual banding operation conducted at Bylot Island (Menu et al. 2001). We recaptured some families of geese during these drives and released them with other birds. Between 400 and 500 females were marked each year with conventional yellow plastic neck collars (Menu et al. 2000). These geese were used as controls to evaluate the effects of radio collars on pair bonds. Our marking and handling procedures were approved by the Université du Québec à Montréal Animal Care Committee.

Transmitters, provided by Holohil Systems Ltd (1995-1997) and Advanced Telemetry Systems Inc (1998), were fixed on rigid, green plastic neck collars 1.5-mm thick and 5.5-cm high, and engraved with individual alphanumeric codes. Together, the mass of the transmitter and collar was 59.3 ± 0.5 g (range: 46-72 g) and represented 2.5 ± 0.1% (range: 1.7-3.4%) of the female's body mass. In 1995, the 15-cm long antenna was coiled around the collar while in subsequent years, the antenna was protruding downwards when birds stood. This change was made to improve the signal range. In 1997 and 1998, a 3-cm long compressing spring was added around the antenna for support where it emerged from the transmitter. Longevity of the transmitters was 16-24 months. On staging areas, signals of transmitters with protruding antennas generally reached 1-3 km on the ground and 4-5 km in the air, but in the open arctic habitat they were audible from 5-10 km and 10-20 km, respectively. Yellow plastic neck collars were engraved with individual alphanumeric codes, measured 5.5-cm high and weighed 20 g, which represented < 1% of the bird's body mass (Menu et al. 2000). Both transmitters and conventional collars had folded rims at both ends that allowed the collar to slide along the neck without brushing up the feathers.

Activity budget

Activity budgets were determined during the 1998 spring and fall staging periods for females tagged in 1997 and 1998 with radio and conventional collars and for unmarked females (control). Focal observations (Altman 1974) were conducted and data recorded in continuous mode with a hand-held computer. During 30-minute observation periods we recorded seven activities: 1) feeding (head below horizontal, including drinking, grazing, grubbing or searching for food), 2) manipulating the collar (preening feathers near the collar, pecking at the radio or collar or pulling the antenna), 3) comfort (all comfort activities excluding those associated directly with the collar and radio), 4) resting (sleeping or loafing with closed eyes or head tucked under feathers), 5) alert (head-up standing still on land or water), 6) locomotion (walking head up, swimming or flying) and 7) social interactions (pecking or chasing other birds or being pecked at or chased).

Radio marked birds were randomly chosen among those present at a site. Once an observation bout was completed, the nearest conventional neck-collared female in the flock was selected and a new bout started. This was followed by the observation of a randomly selected unmarked paired female (with or without young) differentiated from the male by her size and behaviour (Cooke et al. 1995). It was not always possible to complete all observation bouts as birds were often scared away by disturbances; we therefore retained bouts that lasted at least 15 minutes. We also tried to balance the number of observation bouts for each type of female between morning and afternoon and among the main habitat types (hayfields, cornfields, marshes and open water). Only females marked in the previous summer were used to evaluate the effect of the radio and conventional collars. Each observer avoided doing repeated observations of the same female during a given season to avoid pseudo-replication.

Social status

Social status of the marked birds was determined each time they were observed during the fall and spring staging periods in southern Quebec and during the subsequent breeding seasons on Bylot Island. Five to seven persons tracked the geese daily throughout the staging grounds while two persons observed the birds on the breeding grounds. We determined status changes between seasons and years. The status in year i+1 after marking was based on observations conducted both during the spring staging period in Quebec (end of March - end of May) and the breeding period on Bylot Island (early June - mid August). We pooled observations for these two periods because few separations occurred between spring and summer (one case in 36 instances). The median observation date for the two periods corresponded to mid June. Therefore, we considered that the status in year i+1 and i+2 was established 10 and 22 months, respectively, after banding. A radio-marked female could be paired with its original mate (male with a conventional neck collar

and/or a leg band), alone or paired with a new partner (uncollared and unringed). Similarly, females with conventional collars could be paired with their original mate (male with a leg band), alone or paired with a new partner (unringed). We assumed that the original mate of a neck-collared female was wearing a leg band because both members of a pair are caught and ringed during mass captures. We also assumed that in the event of mate change, it was unlikely that a female's new mate would also be ringed because of the low frequency (< 2%) of ringed birds in the population. Two observations during the same season were required to establish that a collared female was alone or with a new male whereas a single observation of a female associated with its original marked male was sufficient to establish that no status change had occurred.

Breeding parameters

Radio marked geese were monitored for one or two years following initial marking to determine their reproductive output. Apparent breeding propensity (the proportion of females present in the population that initiated a nest on Bylot Island), nest initiation date (date of first egg laid), clutch size and nesting success (proportion of nests where at least one egg hatched successfully) of radio marked birds were recorded in 1997 and 1998. Most nests were found during laying or early incubation. Nests of unmarked geese monitored within the colony during the same year served as controls (Bêty, Gauthier, Giroux & Korpimäki 2001). Finally, brood success (proportion of females with at least one young) was established during the second fall after marking and the following spring on the staging grounds in southern Quebec.

Data analysis

We used the time spent on the various activities during a bout to calculate the percentage of time allocated to each activity and applied an angular transformation to these data (Sokal & Rohlf 1995). We used a factorial multivariate analysis of variance (MANOVA) with collar types (radio, conventional, none) and status (paired, unpaired) as factors for each season. Tukey's tests were conducted to determine which activities differed among collar types. Because different observers located the same marked birds at different sites, some birds were observed more than once. A maximum of four bouts were recorded for radio-marked females and two for neck-collared females. For these birds, we used the mean of the repeated observations to ensure that each female contributed a single value to the analysis. For control females, it is unlikely that the same birds were chosen more than once because of the large number of birds in the observed flocks (1,000-40,000).

The probability of observing a marked female with its original mate at time i+1 (θ, θ = 1 - separation rate) is the combined probability of two independent events: the probability for the mate to survive from i to i+1 (S) and the probability that the two partners are still together (τ, τ = 1 - divorce rate) given that the male survives, thus $\tau = \theta/S$. If we know the survival rate of the mate (S), it is thus possible to calculate the divorce rate. Annual survival has been estimated with precision for adult female greater snow geese but not for males (Gauthier, Pradel, Menu & Lebreton 2001). Because there is little difference between male and female survival rate in adult snow geese (Francis & Cooke 1992, Menu, Gauthier & Reed 2002), we used the 83% value established by Gauthier et al (2001) for females. We ignored variations in survival rate during a year because they are small (Gauthier et al. 2001) and calculated a survival rate for 10 and 22 months as follows:

$$S_{10\ \text{months}} = S_{\text{annual}}^{(10/12)} = 0.83^{(10/12)} = 0.856$$
$$S_{22\ \text{months}} = S_{\text{annual}}^{(22/12)} = 0.83^{(22/12)} = 0.711.$$

For separation rate, nesting success and proportion of females with new partners or with young, we assumed a binomial distribution and calculated standard error (SE) and 95% CI using traditional formulas based on a normal approximation (Sokal & Rohlf 1995). SE associated to annual survival has been established at 0.048 (Gauthier et al. 2001). SE for a 10- and 22-month period can then be calculated using the delta method of Seber (1994):

$$SE_{10\ \text{months}} = \sqrt{\left[(10/12)S^{((10/12)-1)^2}\right] * SE^2} = 0.041$$
$$SE_{22\ \text{months}} = \sqrt{\left[(22/12)S^{((22/12)-1)^2}\right] * SE^2} = 0.075.$$

When we divide θ by S, we have an error associated with each term and both have to be taken into account to calculate the error on the estimated divorce rate. We can again use the delta method to compute:

$$SE_\tau = \sqrt{\left[\left(\frac{\theta}{S^2}\right)^2 * SE_S^2\right] + \left[\left(\frac{1}{S}\right)^2 * SE_\theta^2\right]}$$

for each period and then estimate the respective 95% CI.

We used Pearson chi-square tests to compare the pro-

portion of females separated from their original mate 10 and 22 months after banding between those fitted with radios and conventional collars. We used a t-test to compare the mean percentage of the female body mass represented by the radio collar between females paired with their original male 10 months after marking and those that were separated. We also used chi-square tests to compare nest success and brood success between females with radios and conventional collars and to compare the proportion of females separated from their original mate 10 months after marking between 1) birds with grouped and ungrouped releases and 2) birds recaptured and those not recaptured during mass captures. Finally, we used a median test, a Wilcoxon rank sum test and a chi-square test to respectively compare nest initiation dates, clutch size and nesting success between radio marked and unmarked females.

Results

Activity budget

We completed 32 observation bouts on radio-marked birds, 27 on geese marked with conventional collars and 58 on unmarked females for a total of 57 hours of focal observation. In the first fall, about two months after marking, activity budgets of paired females differed among those fitted with radios, conventional collars or no collar ($F_{14,48} = 3.22$, $P = 0.001$; Fig. 1), and between lone females marked with radio or conventional collars ($F_{7,3} = 11.30$, $P = 0.036$). Our sampling procedure precluded the observation of unmarked lone females. Paired females with radios manipulated their collar seven times more than those with conventional collars, and their time spent resting was doubled. Although it was not significantly different, radio-marked females, either alone ($F_{1,9} = 2.56$, $P = 0.144$) or paired ($F_{2,30} = 2.77$, $P = 0.079$), tended to spend 2-3 times less time in foraging activities than females with conventional collars. Finally, lone females with a radio collar spent much more time in comfort activities than females with conventional collars ($F_{1,9} = 11.32$, $P = 0.008$).

The effect of radio collars on behaviour decreased with time. In the spring following marking, there was still a significant difference among the paired females of the three groups ($F_{14,92} = 3.89$, $P = 0.001$; see Fig. 1) but not for lone females ($F_{7,9} = 1.83$, $P = 0.197$). The only significant difference occurred with the collar-related activ-

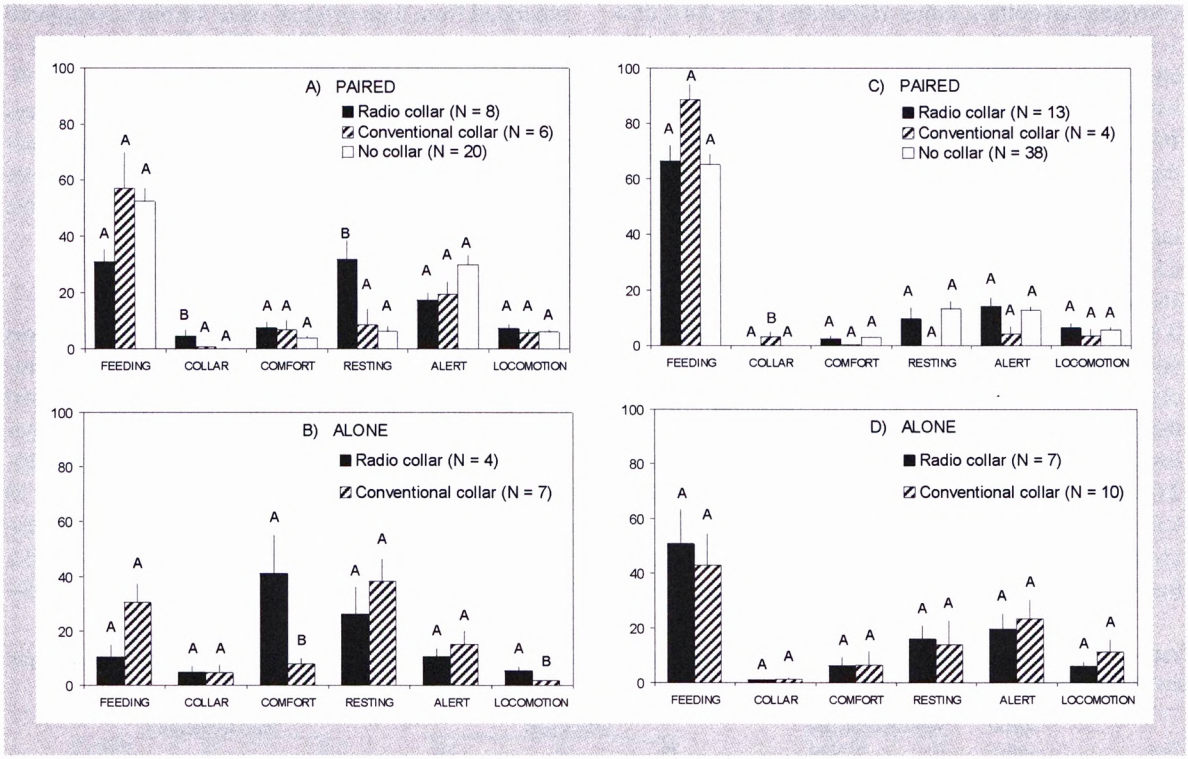

Figure 1. Activity budget of paired and lone female greater snow geese fitted with radio or conventional collars, or with no collar (control), during the fall (A, B) and spring (C, D) following the marking of the radio-marked birds. Vertical lines represent 1 SE and bars with the same letter (above the bar) do not differ significantly among groups for either activity (Tukey's test: $P < 0.05$). The activity COLLAR refers to manipulation of the collar by geese and include the attached radio and antenna.

Table 1. Percentage of female greater snow geese fitted with radio and conventional collars that were separated and divorced from their original mate 10 and 22 months after banding, 1995-1998.

Months after marking	Cohort	Radio collar N	Radio collar Separated %	Radio collar Separated 95% CI	Radio collar Divorced[a] %	Radio collar Divorced[a] 95% CI	Conventional collar N	Conventional collar Separated %	Conventional collar Separated 95% CI	Conventional collar Divorced[a] %	Conventional collar Divorced[a] 95% CI
10	1995	12	33	7 - 60	22	0 - 54	-	-	-	-	-
	1996	42	40	26 - 55	30	12 - 49	-	-	-	-	-
	1997	37	35	20 - 51	24	5 - 44	40	23	10 - 35	9	0 - 27
	1998	21	29	9 - 48	17	0 - 40	78	15	7 - 23	1	0 - 14
	Total	112	36	27 -	25	12 - 37	118	18	11 - 25	4	0 - 16
22	1995	6	83	54 - 100	77	34 - 100	-	-	-	-	-
	1996	21	43	22 - 64	20	0 - 54	47	21	10 - 33	0	0 - 18
	1997	11	45	16 - 75	23	0 - 68	75	27	17 - 37	0	0 - 22
	Total	38	50	34 - 66	30	3 - 56	122	25	17 - 32	0	0 - 18

[a] Male survival taken into account; see section Methods for details.

ity of paired females with conventional neck collars. This slight difference did not influence other important activities like foraging, resting or alert.

Pairing

No difference in the probability of separation occurred among years for females with radios ($\chi^2 = 0.92$, df = 3, P = 0.821) and conventional collars ($\chi^2 = 0.92$, df = 1, P = 0.339). We therefore pooled the data of the different cohorts (Table 1). Probability of separation was twice as high for radio-marked geese than for those with conventional collars, either 10 months ($\chi^2 = 9.47$, df = 1, P = 0.002) or 22 months ($\chi^2 = 8.81$, df = 1, P = 0.003) after marking. After having corrected for male survival, we obtained similar divorce rates for females with radios 10 and 22 months after marking (25-30%). Few divorces occurred for females with conventional collars (0-4%).

Among separated females marked with radio collars, 45% (95% CI = 30-60%, N = 40) and 53% (95% CI = 30-75%, N = 19) were paired with a new partner 10 and 22 months after marking, respectively ($\chi^2 = 0.30$, df = 1, P = 0.583). Of the 12 radio-marked females observed with a new mate during the first spring six were observed alone the following fall or spring. Among the females marked with conventional collars which had lost their original mate, 48% (95% CI = 26-67%, N = 21) and 57% (95% CI = 39-74%, N = 30) were paired with a new mate 10 and 22 months after marking, respectively ($\chi^2 = 0.41$, df = 1, P = 0.524). The proportion of females alone or paired with a new partner was not significantly different between birds with radio and conventional collars either 10 ($\chi^2 = 0.04$, df = 1, P = 0.845) or 22 months ($\chi^2 = 0.08$, df = 1, P = 0.782) after marking.

Radio-marked geese had a similar separation rate regardless of the quality of the release ($\chi^2 = 0.93$, df = 1, P = 0.334). We observed 36% (95% CI = 26-45%, N = 88) of separation among geese that remained as a group and 25% (95% CI = 6-44%, N = 20) for those that scattered when released. There was no difference ($\chi^2 = 0.05$, df = 1, P = 0.819) in the proportion of females that separated from their original mate for birds recaptured during mass banding (33%; 95% CI =13-54%, N = 21) compared to those that were not recaptured (31%; 95% CI = 21-40%, N = 91). Finally, the relative mass of the radio collars of females that remained with their original male (2.4 ± 0.1%, N = 72) did not differ from that of females that were separated from their mate (2.3 ± 0.1%, N = 40; t = 0.274, P = 0.785).

Reproductive parameters

Apparent breeding propensity of radio-marked birds was 54% (20/37) in 1997 and 47% (28/59) in 1998. This proportion was not available for conventional neck-collared geese. In 1998, females marked with radio collars either 10 or 22 months before had similar median nest initiation dates (10 months: 11 June, N = 18; 22 months: 10 June, N = 10; Z = -0.50, P = 0.618). Clutch size was also similar 10 (2.83 ± 0.19, N = 18) and 22 months (3.20 ± 0.20, N = 10) after marking (Z = 1.24, P = 0.215).

Table 2. Nest initiation date, clutch size and nesting success of female greater snow geese marked with radio collars and unmarked control geese, 1997-1998.

Year	Radio collar	Nest initiation date N	Nest initiation date Median	Clutch size N	Clutch size $\bar{x}$	Clutch size SE	Nest success (%) N	Nest success (%) $\bar{x}$	Nest success (%) 95% CI
1997	Yes	20	14 June	20	2.75	0.27	20	50	28-72
	No	326	10 June	289	4.27	0.10	317	83	79-87
1998	Yes	28	10 June	28	2.96	0.14	29	55	37-73
	No	339	7 June	299	4.1	0.1	333	79	75-84

Finally, nesting success did not differ between females with a radio for 10 (53%; N = 19, 95% CI = 30-75) and 22 months (60%; N = 10, 95% CI = 30-90; $\chi^2 = 0.14$, df = 1, P = 0.705). We therefore pooled these data for subsequent analyses.

Geese fitted with a radio initiated their nests 3-4 days later than the rest of the population both in 1997 (Z = 3.49, P < 0.001) and 1998 (Z = 6.45, P < 0.001; Table 2). Furthermore, they laid 1.1 and 1.5 eggs less than the control population in 1997 (Z = -5.04, P < 0.001) and 1998 (Z = -5.75, P < 0.001), respectively. Finally, nesting success was about 1.5 times lower for radio-marked geese than for the overall population (1997: $\chi^2 = 13.29$, df = 1, P < 0.001; 1998: $\chi^2 = 8.85$, df = 1, P = 0.003).

During the second fall following marking, the proportion of females accompanied by at least one young tended to be lower for birds marked with radio collars (15%; N = 20, 95% CI = 0-31) than for females marked with conventional neck collars (31%; N = 49, 95% CI = 18-44), but the difference was not significant (Fisher's exact test: P = 0.235). The same trend was observed during the following spring when the proportion of the radio-marked females with at least one young was 7% (N = 15, 95% CI = 0-19) and 19% (N = 47, 95% CI = 8-30) for the birds with conventional collars (Fisher's exact test: P = 0.427).

Discussion

Activities of female greater snow geese marked with conventional neck collars were minimally or not affected, whereas the behaviour of radio-collared birds seemed negatively affected, especially during the first 2-3 months after being marked. Ely (1990) suggested that conventional neck collars mostly affected behaviour of white-fronted geese immediately after capture. The largest amount of time spent manipulating the collars and in comfort activities by greater snow geese fitted with radio collars may be explained by the presence of the antenna extending downward into the breast feathers. When geese were preening their breast feathers, they often seemed to be disturbed by the antenna. Although this activity was recorded as comfort movements, it was indirectly related to the radio. The birds frequently started with normal comfort movements (preening breast or back feathers) then switched to collar related activities (pecking the radio or pulling the antenna). Radio collars also induced short-term abnormal behaviours such as backward walks by females (F. Demers & J-F. Giroux, pers. obs.). However, these effects disappeared the following spring possibly because of habituation and/or because several females had cut the antenna by that time.

The annual rate of pair separation has been established at 10-20% in Anserini (Owen, Black & Liber 1988, Raveling 1988, Forslund & Larsson 1991). These values roughly correspond to the annual mortality rates, which means that divorces are rare. Indeed, Black, Choudhury & Owen (1996) reported an average probability of divorce of 3% for several species of geese, and this is consistent with our observations on female greater snow geese fitted with conventional neck collars. If neck collars do not promote divorces, then adding a radio increased the probability to 25% in the first year after marking. Because the divorce rate showed little increase in the second year after marking, we suggest that the females that did not habituate to their radio collar lost their mate rapidly because of changes in their behaviour. Nevertheless, divorce rates for radio-collared greater snow geese were much lower than the 90% recorded by Ward & Flint (1995) for brant fitted with harnesses. Comparison of divorce rates between radio and conventional neck collars assumes that neck collars did not enhance the mortality rate of males accompanying radio-marked females. Menu et al. (2000) found that conventional neck collars did not affect survival in female greater snow geese.

Prevett & MacInnes (1980) observed that 11-22% of paired adults had not reunited a week after their capture and banding. Our results, however, indicate that mass captures and ungrouped releases had no effect on pair bond 10-22 months later. Pairs that split up during an ungrouped release may have either reunified, and those released together may eventually have divorced resulting in a similar percentage of separation. Moreover, not all pairs may have split during an ungrouped release. Because the birds move rapidly, we were unable to get detailed information for each pair. Nevertheless, our results provide no evidence that high separation rates of radio-marked geese was a consequence of the captures themselves.

Reproduction of radio-marked geese was first impaired by an increase in separation rates attributed to divorces. This resulted in < 55% of the radio-marked birds that attempted to nest. The radio-marked geese were ≥ 3 years old during the year following their marking, and we therefore expected a breeding propensity of > 75% as established for leg-banded greater snow geese during the same years of our study (Reed 2003). Similarly, Sedinger, Lindberg & Chelgren (2001) estimated a breeding probability of ≥ 68% for ≥ 3-year-old female black brant. Although our percentage of non-nesters may include birds that have attempted to breed and failed early, the difference between radio-marked females and leg-band-

ed birds indicates that radio collars had a direct impact on breeding propensity, which also has been observed for emperor geese (Schmutz & Morse 2000).

The presence of radio collars negatively influenced all reproductive parameters even during the second season after marking. Schmutz & Morse (2000) also observed a decline of about one egg for emperor geese marked with radio and conventional collars. Radio-marked greater snow geese initiated their nest 3-4 days later and laid 1.1 to 1.5 eggs less than the rest of the population. Based on the Lepage, Gauthier & Menu (2000) estimate of 0.2 egg of reduction for each day of laying delay, we should have observed a diminution of 0.6-0.8 egg attributed to this delay. This indicates that radio collars had a direct effect on both laying date and clutch size, and these effects may be related to a reduction of the birds' condition.

Fat accumulation in spring plays a major role in the reproduction of geese (Ankney & MacInnes 1978, Choinière & Gauthier 1995). In spring, radio-marked geese fed at similar rates as did neck-collared and unmarked geese and should therefore not have been disadvantaged in accumulating fat reserves. Moreover, there was no evidence that radio-marked geese were using sub-optimal habitats during their spring staging period in Quebec (A. Béchet, Université du Québec à Montréal, pers. comm.). Gessaman & Nagy (1988) and Obrecht, Pennycuick & Fuller (1988) reported that radio transmitters fixed with harnesses on the back of pigeons and snow geese increased the aerodynamic drag. Geese marked with radio collars might also be impacted by aerodynamic drag and may thus have to expend extra efforts on flying, resulting in depletion of more fat reserves to complete their spring migration (Gauthier, Giroux & Bédard 1992). The additional mass associated with the radio collar, when geese are at the maximum body mass in their annual cycle, may also contribute to the depletion of energy reserves during migration. Consequently, radio neck-collared females may have had fewer reserves upon arrival, and Bêty, Gauthier & Giroux (2003) have shown a direct link between body reserves, nest initiation date and clutch size. Reed (2003) found a smaller clutch size reduction than we found and no significant nest initiation delay for greater snow geese fitted with conventional collars, and this indicates that the additional drag and/or mass of the radio collars further impacted the breeding performance of the birds.

Conclusions

Radio collars should be used with caution to assess demographic parameters of geese because they modify their behaviour, promote divorces and depress reproductive success. Similar effects have been reported for harness-attached transmitters. In addition, harnesses are difficult to adjust during the moulting period because they cannot be fitted too tightly to account for future expansion of the atrophied breast muscles and cannot be fitted too loosely as a bird can get its foot entangled (J-F. Giroux, pers. obs.). Implants with either internal or external antennas are becoming standard for ducks (Rotella et al. 1993, Esler, Mulcahy & Jarvis 2000, Garrettson, Rohwer & Moser 2000). Although there are no published tests, implants may not be a good option for geese because some species may pull at the external antenna with their strong bill, causing injuries. Also, internal antennas may not provide sufficient range to track their long-distance movements. Until better alternatives are developed, we consider that fixing radios on neck collars remains the best option for tracking movements of geese. Kenward (1987) and Cochran (1980) recommended that markers should not represent more than 2-5% of a bird body mass. For birds of the size of a greater snow goose, we recommend that the weight of a radio neck collar should be < 2.5% of the body mass. Having the whole antenna coiled around the collar may reduce behavioural modifications, but this design results in significant range reduction as we found with our 1995 sample of birds. We nevertheless recommend shortening the protruding part of the antenna, and in recent years we have used a 7-cm long antenna completely embedded in a flexible spring. Researchers should always remain alert to the potential effects of their marking technique. For telemetry, one needs to compromise between the potential negative effects of a transmitter and its performance in terms of battery mass (longevity) and antenna length (range).

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