



Survival and Reproduction of Adult Snowy Owls Tracked by Satellite

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ABSTRACT Satellite telemetry can provide valuable information on spatial ecology of animals, especially in species inhabiting remote areas such as the Arctic. However, caution is always needed when selecting transmitter size and attachment methods because of the potential negative impact of the device itself on individuals. We determined survival and reproductive performance of adult female snowy owls (*Bubo scandiacus*) tracked by satellite to evaluate potential adverse effects of transmitters. In summer 2007, we captured 12 adult females on their nest in the Canadian Arctic, marked them with 30-g harness-mounted transmitters, and tracked their movement for up to 3 years. All marked birds resumed normal activities shortly (<60 min) after release and none deserted their nest. We had 2 known deaths and 2 transmitters that stopped moving over 3 years, yielding an annual survival rate between $85.2 \pm 7.0\%$ and $92.3 \pm 5.7\%$. Moreover, summer movement patterns, combined with ground checks in several cases, suggested that all successfully tracked birds initiated a nest every year after marking. Finally, laying date and clutch size of individuals did not differ before and after marking. Overall, our data indicate that life history traits of adult female snowy owls were not affected by satellite transmitters. © 2012 The Wildlife Society.

KEY WORDS Arctic, *Bubo scandiacus*, Canada, Nunavut, reproduction, satellite transmitter, snowy owl, survival.

Satellite telemetry greatly enhances our ability to study free-ranging wildlife and increases our understanding of the spatial ecology of animals (Fuller et al. 2005). This technique is especially useful for the study of highly mobile species such as birds and it can provide crucial information on movement and dispersion parameters, migration routes and chronology, demography, home range, and habitat use. Satellite telemetry is thus probably the most powerful tool available to obtain crucial ecological information that would be extremely difficult to document otherwise. However, potential adverse effects of those devices on the behavior and life history traits of studied organisms remain an ethical and scientific concern. Indeed, because species management and conservation are among the ultimate goals of most scientific studies involving the tracking of wild animals, detrimental effects on the studied organisms while gaining knowledge would be disturbing. Moreover, if transmitters adversely affect some life history traits, then researchers must take those into account before inferring to the whole population any scientific result obtained with the technique.

Although transmitters are now commercially available in highly compact sizes and aerodynamic shapes, fitting animals with such devices can still have negative consequences on them, and this is particularly true in flying organisms such as birds (reviewed by Barron et al. 2010). Negative effects of transmitters on birds can occur over short- (days) and long-term (months or years) time scales. Short-term effects, mostly due to handling stress and habituation to the device, can result in altered behaviors (Demers et al. 2003, Chipman et al. 2007) and clutch abandonment in reproductive birds (Barron et al. 2010). Long-term effects, often caused by the cumulative impact of a higher wing loading and increased drag leading to reduced flying and feeding efficiencies, can result in decreased body condition (Barron et al. 2010), reduced fecundity (Paton et al. 1991, Demers et al. 2003, Steenhof et al. 2006), or increased mortality (Burger et al. 1991, Paton et al. 1991, Gervais et al. 2006).

Potential adverse effects of transmitters can be minimized by limiting device weight. A transmitter weighing no more than 5% of the body mass is generally assumed to be acceptable, although this has never been experimentally tested in birds (but see Caccamise and Hedin 1985, Aldridge and Brigham 1988, Barron et al. 2010). Several methods have been developed to attach transmitters on birds (e.g., tail mounts, leg mounts, neck collars, and backpacks) but their suitability varies among species. In large-bodied birds such as

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raptors, the backpack method generally works well in the field (Snyder et al. 1989, Vekasy et al. 1996, McGrady et al. 2002) including with snowy owls (*Bubo scandiacus*; Fuller et al. 2003), although it has been associated with negative impacts on breeding and/or survival in golden eagles (*Aquila chrysaetos*; Gregory et al. 2003), burrowing owls (*Athene cunicularia*; Gervais et al. 2006), and prairie falcons (*Falco mexicanus*; Steenhof et al. 2006). Researchers should thus be careful when choosing an attachment method and transmitter size and, whenever possible, evaluate any potential negative impacts as these can vary depending of the body mass, habitat, behavior, and life history traits of the studied population.

Snowy owls inhabit the Arctic tundra, one of the most remote and harshest environments on Earth, and are well known for their irruptive movements (Newton 2006). Satellite telemetry is thus an ideal technique to study migration and dispersal in this species (see Fuller et al. 2003 and Therrien et al. 2011 for recent applications). We evaluated annual survival and breeding performance (breeding probability, laying date, clutch size, and nesting success) of adult female snowy owls tracked by satellite for up to 3 years and investigated potential negative effects of transmitters.

STUDY AREA

Our study area covered approximately 400 km² of Arctic tundra in the southern portion of Bylot Island, Nunavut, Canada (73°N, 80°W). The landscape was constituted of gently rolling hills and river valleys. We searched a 100 km² area annually for nesting snowy owls and monitored the fate of all nests found (Gauthier et al. 2004).

METHODS

In 2007, we found 17 nests of snowy owls. From 27 June to 11 July, we captured 12 adult female snowy owls on their nest using a bow-net trap. We captured birds during the hatching period (on average, 3.6 young were present at the nest; range: 1–7) except for 2 birds where eggs had just started to crack. We weighed all birds to the nearest 10 g using a 3 kg or 5 kg spring scale (Pesola, Kapuskasing, Canada). During handling, we covered birds' heads with a cloth to minimize movements and struggling. We marked females with 30-g satellite transmitters (PTT-100; Microwave Telemetry Inc., Columbia, MD) attached with backpack harnesses made of Teflon ribbon (Bally Ribbons Mills, Bally, PA; Steenhof et al. 2006). The straps of the harness crossed the breast of the bird and were held in place with a 2-cm² leather pad. We knitted together the two strap ends of the harness in the back of the transmitters using 9.1-kg fishing line and applied a small amount of 5-minute epoxy glue on the fishing line knots. We fitted harnesses quickly (<10 min) and, after release, we observed the territory and the nest of the marked bird for up to 1 hour from a hidden vantage point to monitor its behavior.

Transmitters, including the harness, fishing line, and glue weighed approximately 39 g and represented 1.8% of the average body mass of the marked females (range: 1.6–2.1%; $n = 12$). Transmitters were programmed to transmit con-

tinuously for an average of 5 hours and then turned off for an average of 125 hours from marking through the first winter (up to Feb 2008). During the first spring and summer months (Mar–Jul 2008), the transmitters were programmed to transmit for 5 hours and then turned off for 49 hours. Finally, cycles of 4 hours on and 142 hours off were programmed for the remaining battery life of the transmitters. We received locations of marked owls on a regular basis via the Argos system (Collecte Localisation Satellites 2011). Each location was assigned to a class (0, 1, 2, 3, A, B, or Z) according to its estimated precision. The estimated accuracy of location classes 0, 1, 2, and 3 followed a normal distribution with a standard deviation of >1,000 m, <1,000 m, <350 m, and <150 m, respectively. Location classes A, B, and Z were considered to be of poorer accuracy by the system and we therefore only used locations with an accuracy class ≥ 1 for all analyses.

No birds returned to the marking site of Bylot Island the summer following manipulations. Nonetheless, between 25 June and 7 July 2008, we were able to visit by helicopter all the sites where satellite-tracked owls had settled with 1 exception, a bird that had settled in the western Canadian Arctic (>1,200 km away from Bylot Island). At each site, the helicopter circled briefly to detect any signs of owl presence before landing. On the ground, 1–3 persons searched the area for a few hours and scanned with a spotting scope in order to find the marked bird and determine if it was paired and nesting. When we found a nest (i.e., confirmed breeding), we checked its contents.

We defined clutch size as the maximum number of eggs (or chicks) recorded in a nest. We inferred laying date (defined as the date that the first egg was laid) from the nest contents assuming that 1 egg was laid every other day and that incubation lasts approximately 32 days (Parmelee 1992). For nests found when all eggs had hatched, we assessed hatching date based on the plumage development and size of young, assuming a normal chick growth curve as reported by Watson (1957). We compared laying dates and clutch sizes of marked birds among years (i.e., before and after marking) using paired t -tests. We also compared laying dates and clutch sizes of marked birds with unmarked birds breeding on Bylot Island in the same years using t -tests. We assessed nesting success (defined as the probability to fledge at least 1 chick) for nests that could be monitored until fledging (defined as when chicks are able to sustain flight). We compared nesting success of marked and unmarked birds on Bylot Island in 2007 using a Fisher's exact test.

We assessed average daily locations of the marked owls using all locations of a given date. We defined settlement on a potential breeding site when movements between 2 successive locations were less than 5 km (settlement date was the midway point between these 2 dates; Ganusevich et al. 2004). Similarly, we inferred departure from the breeding site as the first time that birds were located 5 km away from the nest site (or the center of the cluster of summer locations when the exact position of the nest site was unknown). The departure date was the midway point between this date and the date of the previous location (Ganusevich et al.

2004). We calculated the daily distance moved (as the distance between average daily locations divided by the number of days separating them) and the home range size (100% minimum convex polygon) recorded between the settlement and departure dates. We used this information to infer breeding for birds that could not be visited on the ground during summer 2008, 2009, and 2010. We inferred that a bird was breeding if its locations fulfilled 3 criteria. First, the length of time between settlement and departure date had to be at least 46 days, the minimum length of time recorded for a confirmed breeding bird (Table 1). Second, the mean daily movements needed to be within 1 standard deviation of the mean daily movements of confirmed breeders (confirmed breeding birds moved 0.67 ± 0.32 km per day on average, mean \pm SD, $n = 19$). Third, summer home range size needed to be within 1 standard deviation of the mean size observed in confirmed breeding birds (i.e., 18.2 ± 15.2 km², $n = 19$). This was a conservative approach to infer reproduction because only 14 of 19 confirmed breeding attempts fulfilled those 3 criteria (Table 1).

During the study period, 4 transmitters stopped moving and generated stationary signals. We were able to visit 2 sites from which stationary signals had been received for >20 weeks. We conducted a thorough search on the ground for the transmitter and/or for any evidence of an owl carcass around the position provided by the satellite.

We estimated monthly survival rate over a 36-month period using a Kaplan–Meier model for known fate individuals using the program MARK (version 4.3; White and Burnham 1999). One transmitter stopped sending signals while the bird was still moving normally (after 14 months of tracking or 550 hr of transmission time). We assumed that this was because of transmitter failure because the battery had reached 73% of its life expectancy (i.e., 750 hr of total transmission time). Consequently, we assigned an unknown status to this individual after the transmitter failure for the survival analysis. We transformed monthly survival estimates (S_m) into annual survival (S_a) as follows: $S_a = (S_m)^{12}$.

We performed spatial analyses with ArcGIS 9.2 software (ESRI Inc., Redlands, CA) and statistical analyses with SAS

Table 1. Breeding parameters of twelve adult female snowy owls marked with satellite transmitters on Bylot Island, Nunavut, Canada in 2007 and tracked for up to 3 years. Empty cells indicate that information was unknown.

| Year | Owl ID | Settlement date | Laying date | Departure date | Time spent on breeding site (days) | Distance (km) traveled daily | | | Home range (km ²) | Breeding attempt | | Nesting success | |
|------|--------|-----------------|-------------|----------------|------------------------------------|------------------------------|------|------|-------------------------------|-----------------------|------------------------|-----------------|--|
| | | | | | | \bar{x} | SD | n | | Inferred ^a | Confirmed ^b | | |
| 2007 | F1 | | 25 May | 6 Sep | 104 | 0.58 | 0.50 | 5 | 11.61 | Yes | Yes | Yes | |
| | F2 | | 2 Jun | 22 Sep | 112 | 1.25 | 1.93 | 8 | 35.65 | No | Yes | No | |
| | F3 | | 25 May | 15 Sep | 113 | 0.20 | 0.21 | 10 | 2.42 | Yes | Yes | Yes | |
| | F4 | | 30 May | 10 Aug | 72 | 0.25 | 0.14 | 3 | 0.40 | Yes | Yes | Yes | |
| | F5 | | 20 May | 5 Jul | 46 | | | 1 | | | Yes | No | |
| | F6 | | 23 May | 11 Aug | 80 | 0.48 | 0.32 | 6 | 8.09 | Yes | Yes | Yes | |
| | F7 | | 29 May | 9 Sep | 103 | 0.45 | 0.34 | 7 | 21.59 | Yes | Yes | No | |
| | F8 | | 4 Jun | 26 Jul | 52 | 0.81 | 0.22 | 3 | 3.84 | Yes | Yes | No | |
| | F9 | | 26 May | 16 Sep | 113 | 0.94 | 0.89 | 13 | 40.91 | No | Yes | Yes | |
| | F10 | | 24 May | 18 Sep | 117 | 1.07 | 0.72 | 7 | 49.43 | No | Yes | | |
| | F11 | | 12 Jun | 7 Sep | 87 | 0.23 | 0.37 | 8 | 1.21 | Yes | Yes | Yes | |
| | F12 | | 7 Jun | 9 Sep | 94 | 0.36 | 0.53 | 8 | 4.01 | Yes | Yes | Yes | |
| 2008 | F1 | 23 Apr | 08 May | 21 Sep | 151 | 0.97 | 0.91 | 54 | 37.79 | No | Yes | | |
| | F2 | 23 May | 29 May | 21 Aug | 90 | 1.08 | 0.68 | 20 | 32.64 | No | Yes | | |
| | F3 | 13 May | 19 May | 18 Jul | 66 | 0.36 | 0.37 | 24 | 3.56 | Yes | Yes | | |
| | F6 | 2 May | 23 May | 23 Aug | 113 | 0.93 | 0.90 | 36 | 25.34 | Yes | Yes | | |
| | F8 | 5 May | | 10 Aug | 97 | 0.56 | 0.44 | 30 | 18.19 | Yes | No | | |
| | F9 | 1 Apr | 11 May | 08 Aug | 129 | 0.79 | 0.63 | 48 | 23.19 | Yes | Yes | | |
| | F10 | 9 May | 21 May | — ^c | — ^c | 0.91 | 0.91 | 32 | 12.78 | Yes | Yes | | |
| | F11 | 13 May | 19 May | 24 Aug | 103 | 0.62 | 0.56 | 42 | 12.37 | Yes | Yes | | |
| | F12 | 11 Jun | | 21 Aug | 71 | 0.81 | 0.48 | 30 | 10.88 | Yes | | | |
| | 2009 | F1 | 11 Apr | | 03 Aug | 114 | 0.47 | 0.31 | 15 | 30.34 | Yes | | |
| | | F3 | 21 May | | 04 Sep | 106 | 0.21 | 0.14 | 14 | 10.33 | Yes | | |
| | | F6 | 14 May | | 31 Jul | 78 | 0.29 | 0.18 | 8 | 9.23 | Yes | | |
| F8 | | 25 Jun | | 27 Aug | 63 | 0.47 | 0.29 | 9 | 11.38 | Yes | | | |
| F9 | | 9 May | | 17 Aug | 100 | 0.48 | 0.25 | 16 | 23.19 | Yes | | | |
| F11 | | 21 Jun | | 25 Aug | 65 | 0.40 | 0.38 | 9 | 8.31 | Yes | | | |
| 2010 | F12 | 25 Jun | | 31 Aug | 67 | 0.46 | 0.29 | 9 | 33.09 | Yes | | | |
| | F1 | 27 Apr | | 2 Oct | 159 | 0.29 | 0.14 | 16 | 17.82 | Yes | | | |
| | F3 | 27 Apr | | 12 Nov | 199 | 0.21 | 0.26 | 32 | 10.71 | Yes | | | |
| | F6 | 3 May | 30 May | — ^d | — ^d | 0.53 | 0.31 | 9 | 18.05 | Yes | Yes | | |
| | F8 | 23 Apr | | — ^c | — ^c | 0.25 | 0.20 | 7 | 24.81 | Yes | | | |
| | F9 | 4 May | | — ^c | — ^c | 0.29 | 0.21 | 14 | 15.66 | Yes | | | |
| | F11 | 6 May | | 11 Sep | 128 | 0.28 | 0.28 | 10 | 15.72 | Yes | | | |
| | F12 | 19 May | | 13 Sep | 118 | 0.51 | 0.68 | 14 | 29.54 | Yes | | | |

^a Breeding status inferred from movement parameters (see Methods section).

^b Breeding status confirmed with ground check.

^c Transmission stopped before the end of the breeding period.

^d Transmitter was removed from the bird when recaptured.

9.1.3 software (SAS Institute, Cary, NC). We captured and handled all birds according to the animal care committee of Université Laval (CPAUL permit #84921). Results are presented as mean \pm SE unless otherwise stated.

RESULTS

Short-Term Effects

No young were hurt and no eggs were broken during capture at the nest. All marked females returned rapidly to their nest after marking (mean = 12 min, range = 3–57 min), and quickly resumed normal activities (i.e., they all incubated the eggs and brooded their chicks).

Average nesting success of snowy owls breeding on Bylot Island was relatively low in 2007 (60%, $n = 15$). However, nesting success did not differ between females that were captured and marked (64%, $n = 11$) and those that were not manipulated (67%, $n = 3$, Fisher's exact test = 0.77, $P = 0.79$); this comparison excludes 1 nest abandoned during laying and for which the female was therefore not available for marking.

Long-Term Effects

We found an owl carcass at each of the 2 visited locations where transmitters were sending stationary signals. Based on the cessation of movement, those birds died approximately 6 weeks and 17 months after marking. Carcasses did not provide any evidence of entanglement with the harness and the transmitters were still well positioned on the birds' backs, without any scars on the skin. For the 2 sites with stationary signals that could not be visited, transmitters stopped moving 1.5 months and 5 months after marking. We thus performed the survival analyses with 2 scenarios. We first assumed that all stationary transmitters were associated to dead birds (worst case scenario). We also ran the analyses assuming that the 2 stationary transmitters that we were unable to visit were lost by live birds. Based on the first scenario, monthly survival rate calculated over a 36-month period was 0.987 ± 0.007 , or 0.852 ± 0.070 on an annual basis. However, if we consider that only 2 birds died (best scenario based on confirmed mortalities), monthly survival estimates was 0.993 ± 0.005 or 0.923 ± 0.057 on an annual basis.

In 2008, 1 year after marking, all successfully tracked birds settled in confined areas. At all 8 sites where we conducted ground visits, marked birds were resighted and appeared healthy. Transmitters were hidden in the plumage and observations of the antennas sticking out at the back suggested that transmitters were still well positioned on the birds. In all cases, the radio-marked females were paired with a male and no other pair was observed in the vicinity. For 7 of these 8 birds, we found a nest within the cluster of positions provided by the satellites where the bird had settled. Although movement parameters strongly suggest that female F8 was also breeding (see Table 1), we failed to find its nest. This likely resulted from limited searching effort because of logistic and climatic constraints (the only opportunity we had to visit the area was on a foggy and rainy day, which restricted visibility and time spent on the ground) or perhaps a failed nesting attempt. In 2009 and 2010, all successfully

tracked birds settled again in confined areas for extended periods of time and, based on the 3 criteria defined from movement patterns of confirmed breeders (see Methods section), we inferred that all of them initiated a nest, which was confirmed in 1 case in 2010 (Table 1).

Mean clutch size tended to be greater 1 year after the initial capture than before marking (2007: 6.1 ± 0.6 ; 2008: 7.1 ± 0.8 ; $t_{1,7} = 1.87$, $P = 0.11$). In 2008, clutch size of marked birds did not differ from unmarked birds breeding on Bylot Island (unmarked birds: 7.0 ± 0.3 ; $t_{1,24} = 0.19$, $P = 0.85$). Moreover, the only marked breeding bird that was visited in 2010 (the bird returned to our study area 3 years after marking) had a clutch of 7 (compared to 3 in 2007). Mean clutch size of unmarked breeding snowy owls on Bylot Island in 2010 was 6.9 ± 0.3 . Finally, females started laying on average 10 days earlier during their first post-marking breeding season (2007: 28 May \pm 3 days; 2008: 18 May \pm 3 days; $t_{1,7} = 2.65$, $P = 0.04$; Table 1). In 2008, laying date of marked birds did not differ from unmarked birds breeding on Bylot Island (unmarked birds: 16 May \pm 1 days; $t_{1,23} = 1.45$, $P = 0.19$). In 2010, the laying date recorded for the only visited marked female was 30 May (compared to 23 May in 2007). Average laying date of unmarked breeding birds on Bylot Island in 2010 was 23 May \pm 2 days.

We recaptured the marked owl that returned to our study area 3 years after the initial capture and removed its transmitter. The transmitter and the harness were both well positioned on the bird and we observed no sign of injury apart a small amount of feather abrasion under the transmitter. The body mass recorded during the early chick rearing period for the recaptured female varied little from 2007 (2.325 kg) to 2010 (2.175 kg; a 6% decline).

DISCUSSION

We did not find any significant negative effect of satellite transmitters on several key life history traits of snowy owls tracked for up to 3 years. We thus conclude that methods used to capture and mark the birds were safe and well adapted to the study species (see also Fuller et al. 2003). However, the limited sample size and the lack of adequate control (unmarked) groups for some comparisons could have reduced our ability to detect subtle effects.

Nesting success of snowy owls breeding on Bylot Island in 2007, the year of initial capture and marking, was relatively low (60%) compared to other years when nesting owls were found (average annual nesting success = $96 \pm 3\%$, range: 85–100%, $n = 5$ years; J.-F. Therrien, Université Laval, unpublished data). However, nesting success did not differ between marked and unmarked females, indicating that capture and marking was not the cause of the low overall success. The abundance of both collared (*Dicrostonyx groenlandicus*) and brown (*Lemmus trimucronatus*) lemmings, the primary prey of owls, was relatively low on Bylot Island in 2007 compared to other years when owls nested at our study area (0.32 lemmings/ha in 2007 compared to 5.7 ± 2.1 in other years; J.-F. Therrien, unpublished data). Since lemming abundance is a strong determinant of reproductive success of snowy owls (Parmelee 1992, Gauthier et al.

2004), the low nesting success recorded in 2007 was probably a result of low prey abundance.

Although we could not ascertain the reason of death in the 2 retrieved owl carcasses, the transmitter did not appear to be a direct cause as judged by its position on the bird. Also, the female recaptured in 2010 did not show any sign of injury related to the transmitter or the harness, and was still flying with ease. Based on the 2 confirmed deaths, the maximum estimates of annual survival rate was 92.3% for our 12 owls. Fuller et al. (2003) also reported the death of 1 individual out of 5 radio-marked females tracked for up to 2 years. Although no published survival rates exist for snowy owls in the wild, our estimate is relatively high considering the range of values reported in comparable species. Indeed, annual survival of closely related and similar size species, such as the great horned owl (*Bubo virginianus*), is usually within the range of 80–90% (90.5% for owls with radio-transmitters in Yukon, Rohner 1996; 81–88% for ring recovered owls in Saskatchewan, Houston and Francis 1995). Similar survival estimates have also been reported for smaller owls (e.g., 80–88% in color-banded spotted owls [*Strix occidentalis*]; Foster et al. 1992, Van Deusen et al. 1998, Seamans et al. 2002, Zimmerman et al. 2007). We thus conclude that the tracking of marked snowy owls for up to 3 years does not provide evidence that transmitters impaired their survival.

One of our marked owls died 6 weeks after marking and 2 transmitters became stationary during the first winter for unknown reasons. This could be interpreted as evidence that a few individuals did not adapt well to wearing a transmitter. However, we do not know if the latter 2 transmitters became stationary because the birds died or because they freed themselves of the transmitter. Harnesses used to attach transmitters are made of resistant material but they still need to be smooth and flexible to prevent any harm to the bird. Raptors have previously been observed removing their harness and dropping their transmitter (Buehler et al. 1995, Reynolds et al. 2004, Steenhof et al. 2006). Moreover, these 2 birds had moved over long distances (over 1,000 km each) and for periods of 1.5–5 months before the signals became stationary suggesting that they were able to fly with ease while wearing the transmitter. However, if we assume, under the worst case scenario, that all stationary transmitters were associated to dead birds, this would bring the annual survival of our marked owls to 85.2%, a value that is still within the range of values reported in comparable species (see above).

Even when transmitters do not cause mortality, more subtle effects are still possible. For instance, transmitters may reduce flight performance or feeding efficiency, leading to poor body condition (Barron et al. 2010) or cause pair bond breakage and interfere with pairing (Demers et al. 2003). When animals are disturbed or weakened, one of the first activities that they curtailed is breeding (Barron et al. 2010). If radio-transmitters have negative effects on owls, we would expect marked individuals to have a reduced clutch size, delay laying, or in the worst case, be unpaired and completely forego breeding. We found that all our successfully tracked birds apparently bred every year during the study period (up to 3 years following marking) and this was confirmed for 8 of

the 9 cases where ground checks were possible. Moreover, during the breeding season following the initial capture, all marked birds were paired and bred, laid earlier, and had similar clutches on average to the year before. Their clutch size and laying date did not differ from that of unmarked birds breeding on Bylot Island in the same year although the power of this comparison is weakened by the fact that all marked birds settled >200 km from Bylot Island in 2008. These results therefore strongly suggest that transmitters had no detrimental long-term effects on female snowy owls, as found in several other raptors species (Snyder et al. 1989, Sodhi et al. 1991, Hiraldo et al. 1994, Reynolds et al. 2004).

MANAGEMENT IMPLICATIONS

We conclude that harness-mounted satellite transmitters can be safely used on snowy owls in the wild. Their use is likely to provide reliable long-term information on movements, habitat use, reproduction, and survival of this elusive predator that would be otherwise virtually impossible to obtain using conventional techniques. To our knowledge, this study provides the first survival and multi-annual individual reproduction estimates in wild snowy owls. With the anticipated climate changes, especially in Arctic regions, such information on key players of the food webs are of prime importance for management decisions and conservation of the integrity of the tundra ecosystem.

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LITERATURE CITED

- Aldridge H. D. J. N., and R. M. Brigham. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. *Journal of Mammalogy* 69:379–382.
- Barron, D. G., J. D. Brawn, and P. J. Weatherhead. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution* 1:180–187.
- Buehler, D. A., J. D. Fraser, M. R. Fuller, L. S. McAllister, and J. K. D. Seegar. 1995. Captive and field-tested radio transmitter attachments for bald eagles. *Journal of Field Ornithology* 66:173–180.
- Burger, L. W. Jr., M. R. Ryan, D. P. Jones, and A. P. Wywiałowski. 1991. Radio transmitters bias estimation of movements and survival. *Journal of Wildlife Management* 55:693–697.
- Caccamise, D. F., and R. S. Hedin. 1985. An aerodynamic basis for selecting transmitter loads in birds. *Wilson Bulletin* 97:306–318.
- Chipman, E. D., N. E. McIntyre, J. D. Ray, M. C. Wallace, and C. W. Boal. 2007. Effects of radiotransmitter necklaces on behaviors of adult male western burrowing owls. *Journal of Wildlife Management* 71:1662–1668.
- Collecte Localisation Satellites. 2011. Argos user's manual. CLS America Inc., Largo, Maryland, USA.
- Demers, F., J.-F. Giroux, G. Gauthier, and J. Bêty. 2003. Effects of collar-attached transmitters on behaviour, pair bond, and breeding success of snow geese *Anser caerulescens atlanticus*. *Wildlife Biology* 9:161–170.
- Foster, C. C., E. D. Forsman, E. C. Meslow, G. S. Miller, J. A. Reid, F. F. Wagner, A. B. Carey, and J. B. Lint. 1992. Survival and reproduction of radio-marked adult spotted owls. *Journal of Wildlife Management* 56: 91–95.
- Fuller, M., D. Holt, and L. Schueck. 2003. Snowy owl movements: variation on the migration theme. Pages 359–366 in P. Berthold E. Gwinner and E. Sonnenschein, editors. *Avian migration*. Springer-Verlag, Berlin, Germany.
- Fuller, M. R., J. J. Millsbaugh, K. E. Church, and R. E. Kenward. 2005. Wildlife radiotelemetry. Pages 377–417 in C. E. Braun, editor. *Techniques for wildlife investigations and management*. Sixth edition. The Wildlife Society, Bethesda, Maryland, USA.
- Ganusevich, S. A., T. L. Macchtle, W. S. Seegar, M. A. Yates, M. J. McGrady, M. Fuller, L. Schueck, J. Dayton, and C. J. Henny. 2004. Autumn migration and wintering areas of peregrine falcons *Falco peregrinus* nesting on the Kola Peninsula, northern Russia. *Ibis* 146:291–297.
- Gauthier, G., J. Bety, J. F. Giroux, and L. Rochefort. 2004. Trophic interactions in a high arctic snow goose colony. *Integrative and Comparative Biology* 44:119–129.
- Gervais, J. A., D. H. Catlin, N. D. Chelgren, and D. K. Rosenberg. 2006. Radiotransmitter mount type affects burrowing owl survival. *Journal of Wildlife Management* 70:872–876.
- Gregory, M. J. P., A. G. Gordon, and R. Moss. 2003. Impact of nest-trapping and radio-tagging on breeding golden eagles *Aquila chrysaetos* in Argyll, Scotland. *Ibis* 145:113–119.
- Hiraldo, F., J. A. Donazar, and J. J. Negro. 1994. Effects of tail-mounted radio-tags on adult lesser kestrels. *Journal of Field Ornithology* 65: 466–471.
- Houston, C. S., and C. M. Francis. 1995. Survival of great horned owls in relation to the snowshoe hare cycle. *Auk* 112:44–59.
- McGrady, M. J., T. L. Macchtle, J. J. Vargas, W. S. Seegar, and M. C. P. Peña. 2002. Migration and ranging of peregrine falcons wintering on the Gulf of Mexico coast, Tamaulipas, Mexico. *Condor* 104:39–48.
- Newton, I. 2006. Advances in the study of irruptive migration. *Ardea* 94:433–460.
- Parmelee, D. F. 1992. Snowy owl. Pages 1–20 in A. Poole P. Stettenheim and F. Gill, editors. *The birds of North America*, The American Ornithologists' Union, Washington, D.C., USA.
- Paton, P. W. C., C. J. Zabel, D. L. Neal, G. N. Steger, N. G. Tilghman, and B. R. Noon. 1991. Effects of radio tags on spotted owls. *Journal of Wildlife Management* 55:617–622.
- Reynolds, R. T., G. C. White, S. M. Joy, and R. W. Mannan. 2004. Effects of radiotransmitters on northern goshawks: do tailmounts lower survival of breeding males? *Journal of Wildlife Management* 68:25–32.
- Rohner, C. 1996. The numerical response of great horned owls to the snowshoe hare cycle: consequences of non-territorial 'floaters' on demography. *Journal of Animal Ecology* 65:359–370.
- Seamans, M. E., R. J. Gutiérrez, and C. A. May. 2002. Mexican spotted owl (*Strix occidentalis*) population dynamics: influence of climatic variation on survival and reproduction. *Auk* 119:321–334.
- Snyder, N. F. R., S. R. Beissinger, and M. R. Fuller. 1989. Solar radio-transmitters on snail kites in Florida. *Journal of Field Ornithology* 60:171–177.
- Sodhi, N. S., I. G. Warkentin, P. C. James, and L. W. Oliphant. 1991. Effects of radiotagging on breeding merlins. *Journal of Wildlife Management* 55:613–616.
- Steenhof, K., K. K. Bates, M. R. Fuller, M. N. Kochert, J. O. McKinley, and P. M. Lukacs. 2006. Effects of radiomarking on prairie falcons: attachments failures provide insights about survival. *Wildlife Society Bulletin* 34:116–126.
- Therrien, J. F., G. Gauthier, and J. Bêty. 2011. An avian terrestrial predator of the Arctic relies on the marine ecosystem during winter. *Journal of Avian Biology* 42:363–369.
- Van Deusen, P. C., L. L. Irwin, and T. L. Fleming. 1998. Survival estimates for the northern spotted owl. *Canadian Journal of Forest Research* 28: 1681–1685.
- Vekasy, M. S., J. M. Marzluff, M. N. Kochert, R. N. Lehman, and K. Steenhof. 1996. Influence of radio transmitters on prairie falcons. *Journal of Field Ornithology* 67:680–690.
- Watson, A. 1957. The behaviour, breeding, and food-ecology of the snowy owl *Nyctea scandiaca*. *Ibis* 99:419–462.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:S120–S139.
- Zimmerman, G. S., R. J. Gutiérrez, and W. S. Lahaye. 2007. Finite study areas and vital rates: sampling effects on estimates of spotted owl survival and population trends. *Journal of Applied Ecology* 44:963–971.

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