

# Effects of satellite transmitters on survival in Snowy Owls *Bubo scandiacus*

Oddvar Heggøy<sup>1\*</sup>, Tomas Aarvak<sup>1</sup>, Ingar Jostein Øien<sup>1</sup>, Karl-Otto Jacobsen<sup>2</sup>, Roar Solheim<sup>3</sup>, Dan Zazelenchuk<sup>4</sup>, Marten Stoffel<sup>5</sup>, Oddmund Kleven<sup>6</sup>

<sup>1</sup>NOF-BirdLife Norway, Sandgata 30b, NO–7012 Trondheim, Norway

<sup>2</sup>Norwegian Institute for Nature Research (NINA), Fram Centre, P.O. Box 6606 Langnes, NO–9296 Tromsø, Norway

<sup>3</sup>Natural History Museum, Agder University, P.O. Box 422, NO–4604 Kristiansand, Norway

<sup>4</sup>P.O. Box 39, Kyle, Saskatchewan, S0L 1T0, Canada

<sup>5</sup>Department of Biology, University of Saskatchewan, Saskatoon, SK, S7N 5E2, Canada

<sup>6</sup>Norwegian Institute for Nature Research (NINA), P.O. Box 5685 Torgard, NO–7485 Trondheim, Norway

\*Correspondence: oddvar@birdlife.no

**Abstract.** The use of tracking devices to monitor birds is extensive, but the effects of such instruments on equipped individuals are still insufficiently taken into account. Here we evaluate potential effects of backpack-mounted satellite transmitters (platform terminal transmitters; PTTs) on survival of 28 Snowy Owls *Bubo scandiacus*. Six confirmed deaths were all probably related to natural and human-induced causes. Although PTT operational time was significantly shorter than expected lifetime of Snowy Owls, five owls were observed alive after transmissions ceased. Additionally four PTTs stopped due to low battery levels, indicating end of transmitter life and not owl mortality. We found no evidence of mortality caused by PTTs, but sample sizes are relatively low and detrimental effects on equipped Snowy Owls cannot be excluded. We recommend caution when instrumenting large owls.

**Key words:** Snowy Owl; satellite transmitters; survival; transmitter effects

## INTRODUCTION

Size and weight of satellite transmitters (platform terminal transmitters; PTTs) are steadily decreasing, but trade-offs between mass, solidity and operational time are still major challenges of this technology when used on birds and other wildlife (Tomkiewicz et al. 2010). Previous studies show that negative effects from such devices on wild animals should be taken seriously, and that they often have been given insufficient consideration in field studies (e.g. Barron et al. 2010, Vandenabeele et al. 2011). So far, tracking instruments have been associated with effects like increased energy use, impaired reproduction, higher stress levels, increased mortality rates and severe lesions in equipped individuals (Barron et al. 2010, Müller et al. 2011, Peniche et al. 2011, Vandenabeele et al. 2011).

Satellite telemetry is a very good method for tracking large bird species that are not easily recaptured, and which roam over vast and remote areas. One such species is the Snowy Owl *Bubo scandiacus* (Jacobsen et al. 2014, Potapov & Sale 2012), which has a circumpolar breeding distribution mainly confined to the arctic tundra. It is a nomadic and irruptive migrant, and the breeding distribution and frequency of breeding within

an area is closely related to food availability, mainly lemmings (*Lemmini* spp; Menyushina 1997, Fuller et al. 2003, Jacobsen et al. 2014). Based on population genetic analyses of birds sampled from three well separated geographical regions within the Snowy Owl breeding range, the long term effective population size for the global population was estimated at maximum 14000 Snowy Owl females (Marthinsen et al. 2008). The study found no phylogeographic structure among the sampled regions, indicating high levels of gene flow in the recent past and possibly still today.

Due to the nomadic nature of Snowy Owls, the Norwegian Snowy Owl project uses backpack-mounted PTTs programmed to cover a full microtine cycle (4–5 years; Korpimäki et al. 2004) to track seasonal movements, home ranges and habitat use of Snowy Owls. In this paper we investigate potential effects of PTTs on the species, by evaluating survival rates, causes of mortality and the interpretation of stationary PTT signals or cease of transmission.

## MATERIAL AND METHODS

We carried out field work in the years 2007–2013 in Northern Norway (summer) and in the Canadian

provinces of Saskatchewan and Alberta (winter). On Norwegian breeding grounds, Snowy Owls ( $n = 15$ ) were captured close to nests containing small to medium-sized chicks using a remotely triggered bownet or a self-made «noose board» (a «board» of large-meshed wire (appr. 50x50 cm) with 50–100 nylon fish-line nooses on it). To reduce thermal loss, nests and nestlings were covered with an insulating piece of wool clothing during mounting of traps and handling of adults. In Canadian wintering areas, Snowy Owls ( $n = 13$ ) were lured with a bait (mice or pigeons) to the trap (bownet or a cage with external fish-line nooses [«Bal Chatri Trap»], both self-made). Snowy Owls in Canada were brought indoors when mounting the PTTs and released on the capture site within a couple of hours. All birds were weighed to the nearest 5 g. PTTs were attached as backpacks with a Teflon ribbon harness (0.25 inch tubular Teflon tape, Bally Ribbon Mills Inc., USA). Four different kinds of PTTs were used for which the type and transmission cycle are given in Table 1. Total mass of harness (10 g) and PTT (30–35 g) constituted 2.5–2.8 % and 2.0–2.3 % of male and female body mass, respectively (mean  $\pm$  SE males:  $1599 \pm 36$  g,  $n = 17$ ; females:  $2000 \pm 53$  g,  $n = 11$ ). When possible, PTTs with stationary signals were searched for in the field. Causes of death were investigated in retrieved owls (at external veterinary laboratories), and PTT diagnostics (temperature, activity, battery level) were examined to reveal causes of transmission stops. Necropsy was performed on one individual. Relationships between mortality and body mass, sex and geography were investigated, as well as the relationships between these variables and PTT operational time. No data were available on natural survival rates in Snowy Owls, although an estimate was made on a small sample of PTT-equipped birds in another telemetry study (Therrien et al. 2012). To calculate expected lifetime, and compare this with PTT operational time, fifteen years of mark-recapture data from a Canadian Snowy Owl program (excluding yearlings and non-aged birds; marked birds:  $n = 360$ ; recoveries:  $n = 16$ ) was used to estimate a crude survival rate using MARK v. 8.0 (MARK 2014). A Life Table (van der Meulen 2012) was constructed to calculate expected lifetime based on population data

on reproduction (clutch size, proportion of breeding Snowy Owls in the population) and survival, assuming that emigration and immigration did not significantly influence population trajectory. Reproductive parameters were taken from a six-year study on Wrangel Island, Russia (Menyushina 1997). Statistical tests were performed using SPSS v.21.0 (SPSS 2012). All t-tests were two-tailed and results were considered significant at  $p \leq 0.05$ . Means and parameter estimates are given with standard error ( $\pm$  SE).

## RESULTS

Of the totally 28 Snowy Owls tagged with PTTs, six were located and confirmed dead following instrument deployment (four in Norway, two in Canada), but we found no evidence that mortality was caused by the devices (Table 2). One PTT located in Norway without harness and with no signs of the carcass nearby strongly suggests poaching (Table 2, 3). Observations of Snowy Owls alive confirmed that three owls in Canada removed their harness (probably by tearing it off with their beak) and lost their PTT. Additionally, two owls were seen in the field with the PTT still well positioned on the back after transmissions ceased (Table 2, 3).

We found no difference in body mass at the time of instrument deployment between owls confirmed dead ( $n = 6$ ) and the remaining Snowy Owls equipped with PTTs ( $t = -0.58$ ,  $p = 0.57$ ,  $n = 22$ ), or between owls confirmed dead and those confirmed alive ( $n = 5$ ) after losing their PTT or transmission stopped ( $t = 0.85$ ,  $p = 0.42$ ). No relationship was found between sex and mortality ( $\chi^2 = 0.05$ ,  $p = 0.82$ ).

Mean operational time for PTTs on equipped Snowy Owls was  $1.63 \pm 0.23$  years (range: 0.08–3.72 years,  $n = 28$ ), and all battery powered PTTs stopped transmitting before the theoretical operational time was completed (Table 2). The operational time of PTTs on owls confirmed dead was significantly lower than that of remaining PTTs ( $t = -4.47$ ,  $p < 0.001$ ,  $df = 19$ ). No difference in PTT operational time was found between PTTs deployed in winter in Canada and in summer in Norway ( $t = 0.49$ ,  $p = 0.63$ ,  $df = 26$ ), but there was a significant relationship between operational

Table 1. Numbers and types of satellite transmitters (PTTs) deployed on Snowy Owls in the Norwegian Snowy Owl project in 2007–2013. Intervals between each plotting cycle in summer (10 May–31 August) and winter (1 September–9 May) are given, as well as theoretical operational time (Th.op.t.) of battery powered PTTs.

Transmitter	Summer	Winter	Th.op.t.	Norway	Canada
35 g Solar PTT, Microwave Telemetry, Inc., USA	3 days	7 days	-	2	-
35 g Battery Powered PTT, Microwave Telemetry, Inc., USA	9 days	9 days	3.8 yrs	1	2
30 g Solar Argos/GPS PTT, Microwave Telemetry, Inc., USA	3 days	7 days	-	3	2
30 g PTT, North Star Science and Technology, LLC, USA	8 days	8 days	4.9 yrs	9	9

Table 2. Summary of diagnostics and operational time (Op.t.; days) for 28 Snowy Owl satellite transmitters (PTTs). PTT diagnostics at, or shortly after, the time when signals became stationary/transmission stopped are given. Dashed horizontal line separates owls caught in Norway (above) and Canada (below). Age: Ad: Adult, 1cy: 1st calendar year, 2cy: 2nd calendar year, etc. Temperatures (Temp) are given as body/ambient (Amb.) temperature. Active: “Yes” – PTT in active movement until cease of transmission, transmission ended abruptly; “No” – PTT stopped moving but continued transmitting (i.e. PTT lost or bearer dead). Battery: battery voltage status.

Name	Sex	Age	PTT type	Date (dd.mm.yy)	Op.t.	Temp	Active	Battery	Likely cause of stop
Høst	F	Ad	35 g solar	13.07.07	794	Body	Yes	Normal	Unknown
Albertine	F	Ad	35 g solar	13.07.07	1010	Amb.	No	Normal	Unknown
Yngvar	M	Ad	35 g battery	15.07.07	1356	Body	Yes	Low	Low battery (obs. alive)
Hedwig	F	Ad	30 g battery	26.06.11	419	Body	Yes	Normal	Unknown
Marna	F	Ad	30 g battery	30.06.11	551	Amb.	No	Normal	Starvation
Irina	F	Ad	30 g battery	01.07.11	62	Amb.	No	Normal	Unknown
Herman	M	Ad	30 g battery	02.07.11	100	Amb.	No	Normal	Predated
Edvard	M	Ad	30 g battery	03.07.11	104	Amb.	No	Normal	Predated
Eira	F	Ad	30 g battery	03.07.11	1034	Body	Yes	Normal	Unknown
Espa	F	Ad	30 g battery	04.07.11	78	Amb.	No	Normal	Predated
Noarsa	F	Ad	30 g battery	04.07.11	969	Body	Yes	Normal	PTT failure (obs. alive)
Gabba	F	Ad	30 g battery	05.07.11	794	Body	Yes	Low	Low battery
Kengu	F	Ad	30 g solar GPS	07.07.11	55	Amb.	No	Normal	Poaching
Gary	M	Ad	30 g solar GPS	07.07.11	1113	Amb.	No	Normal	Unknown
Olava	F	Ad	30 g solar GPS	10.07.11	1058	Amb.	No	Normal	Unknown
Kyle1	M	Ad	30 g battery	16.03.10	100	Amb.	No	Normal	PTT lost (obs. alive)
Sovereign	M	Ad	30 g battery	02.04.10	616	Amb.	No	Normal	Unknown
Kyle2	M	Ad	30 g battery	29.12.10	790	Body	Yes	Normal	Unknown
Prime	M	1cy	35 g battery	21.12.11	29	Amb.	No	Normal	Poisoned
Elrose	M	2cy	30 g battery	21.12.11	354	Body	Yes	Low	Low battery
Hardy	M	Ad	30 g battery	18.01.13	462	Body	Yes	Normal	PTT lost (obs. alive)
Hilltop	M	Ad	30 g battery	27.01.13	168	Amb.	No	Normal	Killed in collision
Sam	M	3cy	35 g battery	06.02.13	643	Body	Yes	Low	Low battery
Dan	M	Ad	30 g solar GPS	02.03.13	369	Amb.	No	Normal	PTT lost (obs. alive)
Milden	M	4cy	30 g battery	07.03.13	821	Body	Yes	Normal	Unknown
Marten	M	Ad	30 g battery	10.03.13	168	Amb.	No	Normal	Unknown
Mike	M	4cy	30 g battery	02.02.13	969	Amb.	No	Low	Low battery
Whitelaw	M	3cy	30 g solar GPS	16.03.13	1640	-	-	-	Still transm. (11.09.17)

time and country where signals became stationary, or transmission stopped ( $F = 3.82$ ,  $p = 0.036$ ,  $df = 2$ ). The post hoc test confirmed that the operational time of PTTs on owls located in Russia was significantly longer than for owls located in Norway or Canada/USA at cease of transmission (LSD,  $p < 0.05$ ). The percentage of PTTs that became stationary or stopped transmitting in Norway during late summer and autumn (July-September;  $n = 8$ ) differed significantly from the expected 25 % (Binomial test;  $p = 0.017$ ).

Based on mark-recapture data from the Canadian Snowy Owl program, annual survival was calculated to  $70.4 \pm 8.6\%$ , and discoverability (catchability) to  $2.7 \pm 1.0\%$  (QAICc = 221.4; adjusted for overdispersion,  $\hat{c} = 0.80$ ). Data on first year survival was missing. Menyushina (1997) calculated mean clutch size of Snowy Owls on Wrangel Island to 2.6 chicks and mean reproductive success (proportion of successful

pairs) to 55.0%. Adjusted for the age distribution in the population, generation time (mean age of reproducing females) was calculated to 4.7 years and expected further lifetime of Snowy Owls older than one year to approximately 2.7 years when first year survival was set at 50%. A population with these properties decreases by 3.8% annually. A first-year survival of 60% produced an expected further lifetime of 3.0 years, and an approximately stable population trend (0.3% annual increase). Analysing data from all marked Snowy Owls in Canada regardless of age (including young and non-aged birds,  $n = 418$ ), produced an annual survival estimate of  $65.0 \pm 9.6\%$  and a catchability of  $3.4 \pm 1.4\%$ . The 5.4% lower survival estimate supports a first year survival rate closer to 60% as a much lower first year survival rate would have resulted in a similar lower annual survival estimate irrespective of age.

Mean operational time for PTTs on equipped Snowy

Table 3. Likely causes of stationary signals/cease of transmission from satellite transmitters (PTTs) deployed on 28 Snowy Owls in the Norwegian Snowy Owl project 2007–2013. Mean PTT operational time is given for each group.

Assumed cause of stop	Number of cases	Mean # days
Low battery/PTT failure	6	848
PTT lost	3	310
Still transmitting (11.09.2017)	1	1640
Natural (predation/starvation)	4	208
Collision (with human construction)	1	168
Poaching and poisoning	2	42
Unknown	11	717
Total	28	594

Owls was significantly lower than expected further lifetime from catching date of an adult Snowy Owl of any age (> 1 year) calculated from the Canadian mark-recapture material (2.7–3.0 years;  $t = -4.62/-5.92$ ,  $p < 0.001$ ,  $df = 27$ ).

## DISCUSSION

The present study was undertaken because of shorter than expected operational time of PTTs deployed on Snowy Owls, which could be due to instrumental effects on survival of equipped individuals. We found no evidence of mortality caused by the PTT devices in the present study, but the operational time of PTTs was significantly shorter than the expected lifetime of adult Snowy Owls when caught, indicating technical problems and other independent causes. Although a lowered survival rate of equipped Snowy Owls cannot be excluded based on available data, actual lifetime was in many cases higher than the operational time of PTTs. Five owls observed alive after transmission stopped and additionally four PTTs with low battery levels prior to cease of transmission demonstrates this.

Operational time of PTTs on owls located in Russia was significantly longer than for owls located in Norway or Canada/USA at cease of transmission. Whether this indicates a higher survival rate in Russian areas is unknown. Nevertheless, Snowy Owls tracked in Russia are generally found in remote areas with little human settlement as compared to those tracked in Norway and in the winter areas in Canada. Thus, fewer or less serious threats may be expected in the Russian areas. Further investigations are however required to confirm such a relationship.

Little is known about natural mortality of wild Snowy Owls. Therrien et al. (2012) calculated an annual survival rate between  $85.2 \pm 7.0\%$  and  $92.3 \pm 5.7\%$  based on survival of 12 Snowy Owl females equipped with PTTs. Based on the Life Table analyses in the present study, this corresponds to a first year survival rate of 25%, given a stable population trend.

An annual survival rate of 85.2% produces an expected further lifetime in owls older than one year of 5.8 years, i.e. much higher than calculated in the present study. This demonstrates how sensitive the expected further lifetime estimate is to survival rates. More data, especially on first-year survival, are therefore needed to provide better survival estimates of wild Snowy Owls.

Eight out of totally fifteen PTTs deployed on Snowy Owls in Norway in the present study stopped in July–September, and additionally one stopped in early October. Three of these cases were confirmed to be caused by the deaths of the equipped owls, which was probably related to predation from raptors. All of these individuals were equipped the same year as they were found dead. Early autumn is usually the time of year when young Gyrfalcons *Falco rusticolus* disperse from their hatching area (McIntyre et al. 2009, Nielsen 2003), which perhaps could explain some of the higher mortality of equipped Snowy Owls in Norway during this period. In Canada PTTs are mounted during wintertime, and the Snowy Owls have more time to habituate to the devices before the young Gyrfalcons disperse. Nevertheless, no published documentation confirms that this dispersion phase involves a general increase in predation pressure. Natural mortality has, however, been found to increase in Willow Ptarmigan *Lagopus lagopus*, an important Gyrfalcon prey, during this period in autumn which coincides with the most intense human Willow Ptarmigan hunting season (Sandercock et al. 2011). PTTs may have caused increased preening activity and more time spent biting the harness and transmitter in Snowy Owls, thus making them more vulnerable to predation, as observed in other owls (Chipman et al. 2007, Gervais et al. 2006).

Although reduced vigilance or other negative effects such as lower hunting efficiency, higher energy consumption during movement or higher stress levels cannot be ruled out in the present study, we have no evidence of higher mortality caused by PTTs. It is also evident that PTT operational time is not a reliable parameter to determine lifetime of equipped birds. Nevertheless, instrument deployment on wild birds

necessarily involves at least some minor effects, connected to the trapping procedure, handling or the instrument attachment itself. For instance, a short-term increase in levels of stress hormones related to the trapping procedure cannot be avoided in most cases (Romero & Romero 2002), and usually there will be some degree of behavioural effects, or increased energy expenditure due to the mass load or drag of an instrument (Barron et al. 2010, Bowlin et al. 2010, Passos et al. 2010). To secure animal welfare and reliable results, it is important to mitigate these effects as much as possible. We therefore, with support from the present study, recommend caution when using harness-mounted devices on large owls, as well as when interpreting results from such studies.

*Acknowledgments.* We thank The Norwegian Nature Inspectorate (SNO) in Finnmark, Norway for their help in locating used PTTs and breeding Snowy Owls. Thanks also to Paul Shimmings for helpful comments and corrections to the manuscript. We are indebted to Mike Blom, Mike Russell and Erhard Pletz for catching and instrumenting three of the Snowy Owls in Alberta, Canada. Funding was provided by the Norwegian Environment Agency, County Governors of Finnmark, Troms, Nordland, Nord-Trøndelag, Sør-Trøndelag, Oppland, Telemark, Hordaland and Buskerud, as well as NOF-BirdLife Norway's Snowy Owl foundation. Permissions to deploy PTTs on Snowy Owls were completed by the Norwegian Animal Research Authority (ref. FOTS ID 3346), as well as the Norwegian Environment Agency (ref. 2011, 3906 ART-VI-ORD). The Animal Care Committee for the Province of Saskatchewan and the Canadian Federal Banding Office (ref. AUP# 20090025) approved the attachment of PTTs on Snowy Owls in Canada.

## REFERENCES

- Barron, D.G., Brawn, J.D. & Weatherhead, P.J. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods in Ecology and Evolution* 1: 180–187.
- Bowlin, M.S., Henningsson, P., Muijres, F.T., Vleugels, R.H.E., Liechti, F. & Hedenström, A. 2010. The effects of geolocator drag and weight on the flight ranges of small migrants. *Methods in Ecology and Evolution*. DOI: 10.1111/j.2041-210X.2010.00043.x.
- Chipman, E.D., McIntyre, N.E., Ray, J.D., Wallace, M.C. & Boal, C.W. 2007. Effects of radiotransmitter necklaces on behaviors of adult male Western Burrowing Owls. *Journal of Wildlife Management* 71: 1662–1668.
- Fuller, M., Holt, D. & Schueck, L. 2003. Snowy Owl movements: variation on the migration theme. Pp. 359–366 in: Berthold, P., Gwinner, E. & Sonnenschein, E. (eds.). *Avian Migration*. Springer-Verlag, Berlin.
- Gervais, J.A., Catlin, D.H., Chelgren, N.D. & Rosenberg, D.K. 2006. Radiotransmitter mount type affects Burrowing Owl survival. *Journal of Wildlife Management* 70: 872–876.
- Jacobsen, K.-O., Øien, I.J., Solheim, R. & Aarvak, T. 2014. Present knowledge and threats to Snowy Owl *Bubo scandiacus* in Norway. NINA Report 727: 1–69. (In Norwegian with English summary)
- Korpimäki, E., Brown, P.R., Jacob, J. & Pech, R.P. 2004. The puzzles of population cycles and outbreaks of small mammals solved? *BioScience* 54: 1071–1079.
- MARK 2014. Program MARK for Windows, version 8.0. Colorado State University, Fort Collins.
- Marthinsen, G., Wennerberg, L., Solheim, R. & Lifjeld, J.T. 2008. No phylogeographic structure in the circumpolar Snowy Owls (*Bubo scandiacus*). *Conservation Genetics* 10: 923–933.
- McIntyre, C.L., Douglas, D.C. & Adams, L.G. 2009. Movements of juvenile Gyrfalcons from western and interior Alaska following departure from their natal areas. *Journal of Raptor Research* 43: 99–109.
- Menyushina, I.E. 1997. Snowy Owl (*Nyctea scandiaca*) reproduction on relation to lemming population cycles on Wrangel Island. Pp. 572–582 in: Duncan, J.R., Johnson, D.H. & Nicholls, T.H. (eds.). *Biology and conservation of owls of the Northern Hemisphere: 2nd International Symposium*. USDA Forest Services Gen. Tech. Rep. NC-190, St. Paul, MN.
- Müller, C., Jenni-Eiermann, S. & Jenni, L. 2011. Heterophils/Lymphocytes-ratio and circulating corticosterone do not indicate the same stress imposed on Eurasian kestrel nestlings. *Functional Ecology* 25: 566–576.
- Nielsen, Ó.K. 2003. The impact of food availability on Gyrfalcon (*Falco rusticolus*) diet and timing of breeding. Pp. 283–302 in: Thompson, D.B.A., Redpath, S.M., Fielding, A.H., Marquiss, M. & Galbraith, C.A. (Eds.). *Birds of prey in a changing environment*. Scottish Natural Heritage, Edinburgh.
- Passos, C., Navarro, J., Giudici, A. & González-Solís, J. 2010. Effects of extra mass on the pelagic behaviour of a seabird. *The Auk* 127: 100–107.
- Peniche, G., Vaughan-Higgins, R., Carter, I., Pocknell, A., Simpson, D. & Sainsbury, A. 2011. Long-term health effects of harness-mounted radio transmitters in red kites (*Milvus milvus*) in England. *Veterinary Record*: 10.1136/vr.d4600.
- Potapov, E. & Sale, R. 2012. *The Snowy Owl*. T & AD Poyser, London.
- Romero, L.M. & Romero, R.C. 2002. Corticosterone responses in wild birds: the importance of rapid initial sampling. *The Condor* 104: 129–135.
- Sandercock, B.K., Nilsen, E.B., Brøseth, H. & Pedersen, H.C. 2011. Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of Willow Ptarmigan. *Journal of Animal Ecology* 80: 244–258.
- SPSS 2012. IBM SPSS statistics for Windows, version 21.0. IBM Corporation, Armon.
- Therrien, J.-F., Gauthier, G. & Béty, J. 2012. Survival and reproduction of adult Snowy Owls tracked by satellite. *Journal of Wildlife Management* 76: 1562–1567.
- Tomkiewicz, S.M., Fuller, M.R., Kie, J.G. & Bates, K.K.

2010. Global positioning system and associated technologies in animal behaviour and ecological research. *Philosophical Transactions of the Royal Society B* 365: 2163–2176.

Vandenabeele, S.P., Wilson, R.P. & Grogan, A. 2011. Tags on seabirds: How seriously are instrument-induced

behaviours considered? *Animal Welfare* 20: 559–571.

van der Meulen, A. 2012. Life tables and survival analysis. *Statistic methods*. Statistics Netherlands, The Hague/Heerlen, Rotterdam.

*Received 4 April 2017. Accepted 6 September 2017*