JOURNAL OF
AVIAN BIOLOGY

Article

Survival probability in a small shorebird decreases with the time an individual carries a tracking device

Veli-Matti Pakanen, Nelli Rönkä, Robert Leslie Thomson, Donald Blomqvist and Kari Koivula

V.-M. Pakanen (https://orcid.org/0000-0003-4838-9927) ✉ (velimatti.pakanen@gmail.com) and D. Blomqvist, Dept of Biological and Environmental Sciences, Univ. of Gothenburg, Gothenburg, Sweden. – V.-M. P. N. Rönkä and K. Koivula, Ecology and Genetics Research Unit, Univ. of Oulu, Oulu, Finland. – R. L. Thomson, FitzPatrick Inst. of African Ornithology, DST-NRF Centre of Excellence, Univ. of Cape Town, Cape Town, South Africa.

Journal of Avian Biology
2020: e02555
doi: 10.1111/jav.02555

Subject Editor: Anders P. Tøttrup
Editor-in-Chief: Thomas Alerstam
Accepted 27 July 2020

Effects of tracking devices on survival are generally considered to be small. However, most studies to date have been conducted over a time-period of only one year, neglecting the possible accumulation of negative effects and consequently stronger negative impacts on survival when the individuals have carried the tracking devices for longer periods. We studied the effects of geolocators in a closely monitored and colour-ringed southern dunlin *Calidris alpina schinzii* population breeding in Finland. Our capture–recapture data spans 2002–2018 and includes individual histories of 338 colour-ringed breeding adult dunlins (the term 'recapture' includes resightings of colour-ringed and individually recognizable birds). These data include 53 adults that were fitted with leg-flag mounted geolocators in 2013–2014. We followed their fates together with other colour-ringed birds not equipped with geolocators until 2018. Geolocators were removed within 1–2 years of attachment or were not removed at all, which allowed us to examine whether carrying a geolocator reduces survival and whether the reduction in survival becomes stronger when geolocators are carried for more than one year. We fit multi-state open population capture–recapture models to the encounter history data. When assessing geolocator effects, we accounted for recapture probabilities, time since marking, and sex and year effects on survival. We found that carrying a geolocator reduced survival, which contrasts with many studies that examined return rates after one year. Importantly, survival declined with the time the individual had carried a geolocator, suggesting that the negative effects accumulate over time. Hence, the longer monitoring of birds carrying a geolocator may explain the difference from previous studies. Despite their larger mass, females tended to be more strongly affected by geolocators than males. Our results warrant caution in conducting tracking studies and suggest that short-term studies examining return rates may not reveal all possible effects of tracking devices on survival.

Keywords: capture–recapture, geolocator, migration, survival, wader

Introduction

Technological advances have resulted in multiple types of tracking devices and a multitude of movement studies (McKinnon and Love 2018, Geen et al. 2019). There may be negative consequences for survival, reproduction and future population growth for individuals carrying these devices (Barron et al. 2010, Saraux et al. 2011, Costantini and Møller 2013, Weiser et al. 2016), However, recent meta-analyses suggest these consequences are small (Bodey et al. 2018, Brlík et al. 2019). Nevertheless, relatively few studies have examined the effects of tracking devices with capture–recapture methods or across periods longer than one year (van Wijk et al. 2015, Morganti et al. 2018, Taff et al. 2018). This leaves a major gap in our understanding as the negative effects may accumulate and survival may be impacted more severely when the individuals have carried the tracking devices for longer periods (Wilson and McMahon 2006, Saraux et al. 2011). Furthermore, effects may be dependent on sex or traits such as body size. Indeed, smaller and aerial species are most vulnerable to tracking devices (Bridge et al. 2013, Weiser et al. 2016, Morganti et al. 2018, Brlík et al. 2019), warranting more detailed studies of such species.

Geolocators are the main tracking devices for studying migration of smaller species (Briedis et al. 2018, Procházka et al. 2018). We deployed geolocators in 2013–2014 to document migration of a southern dunlin *Calidris alpina schinzii* population that has been studied in detail since 2002 (Pakanen et al. 2011, 2015, 2018). Our previous analyses found no strong effects on return rates or reproduction in the year after deployment in this long-distance migratory shorebird (Pakanen et al. 2015, Weiser et al. 2016). Here, we use capture–recapture methods and long-term data collected since the start of the study until 2018 to re-examine the effect of geolocators on adult survival and to further test whether the effect of geolocators on survival increases when birds have carried them for longer than one year.

Material and methods

Our study population of the southern dunlin breeds on eight coastal meadows in the Bothnian Bay in Finland (64°50′N, 25°00′E). Due to lack of suitable breeding habitats, this population is confined to these clearly defined habitat patches and the closest populations are 400 km away. Therefore, extensive studies of this colour-ringed population allow detailed monitoring of movement and, by recording annual resightings, reliable examination of survival (see Pakanen et al. 2016, 2017 for more details on field methods).

In 2013 and 2014, we deployed light-level geolocators (Intigeo-W65A9, Migrate Technology Ltd) with plastic (Salbex) leg-flags on the tibia of 53 breeding southern dunlins (Pakanen et al. 2015, 2018). The device including the flag weighed 0.8 g, which is about 1.5–2.0% (mean mass 46.4 g, SD 3.69) of their body mass. We mounted geolocators on 30 birds in 2013 (15 males, 15 females), and additionally 23 birds in 2014 (12 males, 11 females). We recaptured and removed the geolocator for 17 birds after one year, and for 9 birds after two years. Ten birds seen in 2014 and later were carrying a geolocator but never recaptured. These birds were thus equipped with a geolocator and resighted for a time period varying between 2 and 4 years. Birds that carried geolocators thus included 27 males and 26 females (sex ratio 0.96/1), and colour-ringed birds that never carried geolocators included 138 males and 147 females (sex ratio 0.94/1).

In this study, we used data on individually colour-marked breeding adults that were collected from 2002 to 2018 from 338 individuals. These included encounter histories from the 53 individuals that carried a geolocator and from 285 individuals that did not carry a geolocator. The individual encounter histories enable the estimation of recapture probabilities that are used in modelling of survival (Lebreton et al. 1992). Correcting for recapture probability is important when examining effects of tracking devices because birds with geolocators may have higher recapture probabilities because they are given more effort than non-geolocator birds, or they may have lower recapture rates if geolocators negatively affect breeding probability (van Wijk et al. 2015). We used these individual histories to analyse adult survival in program MARK by fitting multistate models (White and Burnham 1999, White et al. 2006), which included parameters for survival (Φ), recapture probabilities (p) and movement between states (ψ). We used three states; state 1: birds with no geolocator, state 2: birds carrying a geolocator, state 3: after geolocator was removed. We assessed goodness of fit using the software U-CARE 2.3.2 (Choquet et al. 2009). The overall test was not statistically significant in either sex (males: $\chi^2 = 29.367$, df = 35, p = 0.736; females: $\chi^2 = 21.095$, df = 38, p = 0.988).

Multistate models allowed us to model survival and recapture probabilities for these states, and to test for the effects of carrying a geolocator. To avoid a large number of models, we modelled the three parameters in sequence from movement probabilities between states to recapture probabilities, and finally survival probabilities. We used AIC model selection that was corrected for small sample size (AICc). We considered differences of 2 units to suggest differences in model support (Burnham and Anderson 2002). We quantified the relative support for explanatory variables with evidence ratios that were calculated by comparing Akaike weights (w) of models with effects included and models without the tracking device effect (w1/w2) (Burnham and Anderson 2002). We calculated survival estimates by averaging across the estimates derived for models within $2 \geq \Delta$AICc units using the Akaike weights (Burnham and Anderson 2002).

Our starting model structure for movement probabilities between states (ψ) included only movement probabilities from state 1 to state 2 and from state 2 to state 3, and thus required no further modelling. All other movements between states were not possible and we fixed them as zero. Our starting model structure for recapture probabilities (p) included status (three states; see above), sex and time (t; year) and the following interactions (×); state×sex and sex×time. We modelled recapture probabilities with a set of a priori selected structures, and found that recapture probabilities varied with sex (females 0.80 ± 0.026; males 0.89 ± 0.018) and time (year). The best model included also state (Supplementary information). Despite the low support for state (ΔAICc = 0.174 over the reduced model; Supplementary information), we used p(state + sex + t) as the

Table 1. Multistate models examining the effect of geolocators on adult survival of southern dunlin. Φ = survival, p = recapture rate, sex = sex of the individual; t = time (year); tsm = time since colour ringing; GEOC1 = no-geolocator vs geolocator, GEOC2 = linear effect of the years an individual had carried a geolocator; Q = quadratic effect; × = interaction, AICc = Akaike's information criterion; Δ = AICc(i) – AICc(min); w = Akaike weight; k = number of parameters. The structure for movement rates (ψ) included only state with movements from state 1 to state 2 and from state 2 to state 3. The structure for recapture rates was p(state + sex + t), where state includes state 1 (no-geolocator), state 2 (geolocator) and state 3 (geolocator removed).

No.	Model for survival (Φ)	Recapture (p)	Movement (ψ)	AICc	Δ	w	k
1	sex + t + tsm + GEOC2	state + sex + t	S1–S2; S2–S3	2013.14	0.00	0.33	40
2	sex + t + tsm + GEOC1 + GEOC1×sex	state + sex + t	S1–S2; S2–S3	2013.28	0.14	0.31	41
3	sex + t + tsm + GEOC2 + GEOC2Q	state + sex + t	S1–S2; S2–S3	2014.48	1.34	0.17	41
4	sex + t + tsm + GEOC1	state + sex + t	S1–S2; S2–S3	2014.66	1.52	0.15	40
5	sex + t + tsm	state + sex + t	S1–S2; S2–S3	2017.31	4.17	0.04	39

structure for recapture probabilities when modelling survival because the model results suggested there may be some differences in recapture probabilities between the states during the years 2014–2018 (mean; no geolocators male 0.861 ± 0.055 and females 0.750 ± 0.083; geolocator males 0.971 ± 0.014 and females 0.937 ± 0.028; geolocator removed males 0.780 ± 0.077 and females 0.638 ± 0.097).

Our model structure for survival probabilities (Φ) always included sex and time (t; year) and time since marking (tsm; years since colour ringing). We kept time dependence in survival probabilities in all models to control for possible annual variation. In addition, we controlled for age effects by including a linear effect of time since colour marking (tsm; note not geolocator placement) because the age of these birds was not always known. We first examined whether survival differed between individuals that did not carry a geolocator and those from which a geolocator had been removed. There was no evidence of such differences as the reduced model received more support (Supplementary information). Because there was no evidence that survival was different between states 1 and 3, we did not include the state structure in survival, and examined the effect of geolocators on survival using three year-specific individual covariates. We first included the effect of the geolocator as I) a binary covariate (GEOC1, individual variables: 0 = no geolocator, 1 = geolocator). II) We used linear effects of the number of years that an individual had carried a geolocator. The variable included 3 classes (GEOC2, individual variables: 0 = no geolocator, 1 = carried for one year, 2 = pooled class for those that carried 2–5 years). The pooled class was used to take into account the decreasing amount of data with increasing years a geolocator was carried. III) We modelled quadratic effects (i.e. 0, 1, 4) of the years the birds carried geolocators to detect a possible non-linear relationship. In each of these covariates, individuals from whom the geolocators were removed received a covariate value of 0 for the following years after geolocator removal. Due to limited data, we examined interactions between sex and geolocator effects only with the binary variable of the geolocator effect.

Results

On the basis of evidence ratios, models that included the geolocator effects were 3.8–8.0 times more supported than the reduced model (Table 1). The best model included a negative linear effect of the time (i.e. years) a bird had carried a geolocator (on logit scale from model 1: $\beta_{GEOC2} = -0.525$, CI −0.928, −0.122; Table 1, Fig. 1; see all coefficients in Supplementary information). While the quadratic effect was not strong (Table 1), the decline in survival was evident only after the birds had carried the geolocator for at least two years. Model averaged estimates for the year between 2015 and 2016 (during which geolocator data were available) for males that were colour-ringed three years ago were highest for a bird that had not carried a geolocator (0.813) and declined to 0.748 after carrying a geolocator for one year and to 0.581 for birds that carried the geolocator at least 2 years (Fig. 1). Models with a binary effect of the geolocator (GEOC1) suggested that carrying a geolocator generally reduced survival (on logit scale from model 4: $\beta_{GEOC1} = -0.716$, CI −1.344, −0.090). An interaction between sex and geolocator (GEOC1) received some support, and the model-averaged

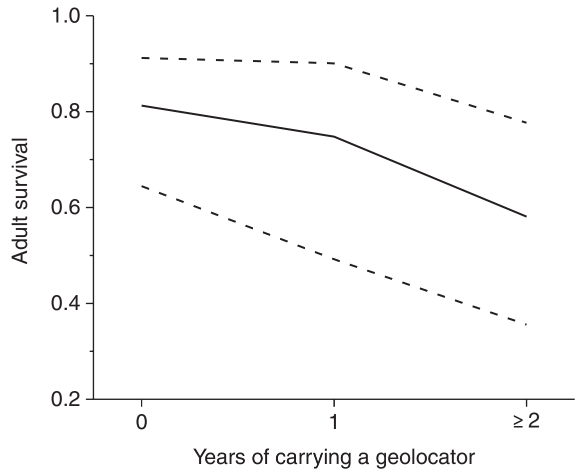

Figure 1. Adult survival of male southern dunlins (95% confidence intervals in dashed lines) in relation to the number of years they had carried a geolocator. Class 0 depicts survival for birds that did not carry a geolocator, 1 depicts survival of birds that carried a geolocator for one year and 2 depicts survival of birds that carried a geolocator for 2 years or more (pooled class). An age-specific change in survival was controlled using time since colour-ringing. These estimates were calculated for birds that were colour-ringed three years ago using model averaging models 1 and 3 (Table 1) for years 2015–2016.

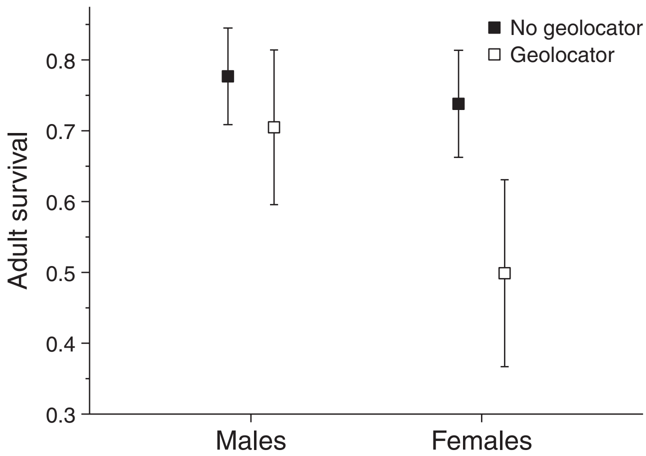

Figure 2. Adult survival (±SE) of male and female southern dunlin that carried a geolocator versus those that did not (binary variable). Estimates were calculated by model averaging models 2 and 4 (Table 1) for year 2015–2016 and for birds with time since colour-ringing of three years.

survival rates suggest that females were affected more than males (Fig. 2; model 2). Mean adult survival across all years for birds that did not carry a geolocator was 0.805 ± 0.019 for males and 0.759 ± 0.022 for females.

Discussion

Our long-term data analysed with capture–recapture methods that control for recapture probabilities show that carrying geolocators for multiple years reduces survival of the southern dunlin, a small migratory wader. This is congruent with studies investigating effects of other kinds of tracking devices (Saraux et al. 2011), but also a passerine study using geolocators (Taff et al. 2018). This is crucial information because our previous results from the southern dunlin (Pakanen et al. 2015), and the general view of impacts caused by leg flag mounted geolocators obtained from meta-analyses, suggest that carrying a geolocator for one year does not reduce survival (Weiser et al. 2016, Brlík et al. 2019). When examining one-year return rates, Weiser et al. (2016) showed negative effects in only two out of 23 (sub)species of shorebirds. Our results suggest, however, that short-term studies measuring return rates may not provide a full spectrum of possible effects caused by tracking devices.

Our most important finding was that survival decreased with the time a bird had carried the geolocator. This pattern may explain why studies examining return rates over only one year rarely find survival costs of carrying geolocators. The ability to withstand the negative impacts of tracking devices may decrease with time (Wilson and McMahon 2006). Tracking devices may increase stress, reduce energy reserves, increase energy expenditure of flight and alter foraging behaviour (Gales et al. 1990, Weimerskirch et al. 2000, Hawkins 2004, Navarro et al. 2008, Barron et al. 2010, Elliott et al. 2012, Vandenabeele et al. 2012, Bodey et al. 2018). These effects may accumulate and reduce long-term viability by reducing the ability to escape predators (Burns and Ydenberg 2002) or by impairing resistance to diseases (Siegel 1980, Klasing 1998). Alternatively, carrying the devices can make survival through periods of tougher environmental conditions less likely, which individuals will eventually encounter (Bro et al. 1999). Furthermore, the physical damage and abrasion caused by the device may increase with time. After removing the geolocators, we observed somewhat thinner and softer skin on their tibia (Pakanen et al. 2015). Therefore, it is possible that the plastic flag system to which the geolocator was attached can alter the skin and make it more susceptible to injury or infection. However, there was no evidence that this was more severe in birds that had carried the geolocator for two years compared to only one year.

The mechanisms through which geolocators reduced survival had a stronger effect on the survival of females. A similar pattern in barn swallows *Hirundo rustica* was likely caused by morphological differences (wing length; Scandolara et al. 2014). In our case, the stronger effect on females is surprising given their larger size (females: 46.2 g; males: 43.9 g; Pakanen et al. 2015) which suggests that they should be better able to cope with a geolocator (Pakanen et al. 2015, Weiser et al. 2016). It seems, therefore, that some parts of the life history may differ between males and females. Females may be physiologically more strained than males during and after the breeding season as they lay eggs that comprise a large portion of their mass (one brood weighs ca 80% of female mass). In our study area, southern dunlins lay replacement clutches (i.e. renest) readily after losing their nest to flooding (Pakanen et al. 2014). In 2015, females were forced to renest multiple times as the rising sea water destroyed their nests several times during the laying season. Multiple renesting may cause a substantial increase in energy expenditure via egg laying (Monaghan and Nager 1997), and females may therefore be in a poor condition at the start of migration. Interestingly, females also depart on migration earlier than males, leaving less time for preparation (Pakanen et al. 2018). Therefore, the additional energy expenditure and stress caused by a tracking device during migration may be fatal. It should be noted that birds from 2015 included a large portion of the individuals that carried geolocators for longer than one year, because they were not caught in that year due to the repeated floods. This could be the kind of difficult environmental conditions in which birds carrying geolocators incur more costs. Permanent emigration outside our study area is an unlikely explanation because there is little breeding habitat elsewhere within the Bothnian Bay area (Pakanen et al. 2017), which is one of the advantages of studying survival in this population.

We showed that tracking devices can have cumulative effects on survival of a small shorebird (45 g) even though the device weighed only 1.5–2.0% of their mass. With similar relative loads, van Wijk et al. (2015) found no detectable effects of geolocators on survival of hoopoes *Upupa epops* when analysing long-term data with capture–recapture methods. The difference may be due to different migratory behaviour as hoopoes use multiple stopovers (Bächler et al. 2010, van Wijk et al. 2015), whereas southern dunlins may fly up to 4500 km nonstop during autumn migration (Pakanen et al. 2018). Our results suggest that such a relatively small load may not be sustainable in the long term, especially when facing adverse conditions. Mortality effects of tracking devices are smaller with lighter devices (Scandolara et al. 2014, Rodríguez-Ruiz et al. 2016), hence tracking devices may need to weigh less than 1% of the bird mass to not have any negative effects (Bodey et al. 2018). As most mortality costs are subject only to individuals that are not caught after the first year, we recommend that the detrimental effects of tagging are avoided by developing attachment methods that are automatically released after one year, e.g. biodegradable materials. Our results raise concerns about the long-term consequences of tracking devices in the study of bird migration (Bridge et al. 2013, Costantini and Møller 2013, Scandolara et al. 2014), and warrant more research extending over one year, including sex-specific differences, to verify impact of long-term tracking research on these animals (McMahon Clive et al. 2012). Studies examining long-term effects of harness-mounted tracking devices on species with different migration strategies can provide valuable information about alternative attachment methods for long-term studies.

Acknowledgements – This study was funded by the Academy of Finland (278759), the Faculty of Natural Sciences of the Univ. of Oulu, the Emil Aaltonen foundation and the Univ. of Oulu Scholarship Foundation and Stiftelsen Olle Engkvist Byggmästare. We thank Vojtech Brlík, Will Creswell and two anonymous referees for helpful comments on the manuscript. This study complied with national law and was conducted under permission from the regional Centre for Economic Development, Transport and the Environment (license numbers POPELY/213/07.01/2013; POPELY/15/07.01/2013). The authors declare no conflict of interests.

Transparent Peer Review

The peer review history for this article is available at https://publons.com/publon/10.1111/jav.02555

Data deposition

Data will be available from the Dryad Digital Repository: <https://dx.doi.org/.6m905qfxp> (Pakanen et al. 2020).

References

Barron, D. G., Brawn, J. D. and Weatherhead, P. J. 2010. Meta-analysis of transmitter effects on avian behaviour and ecology. – Methods Ecol. Evol. 1: 180–187.

Bodey, T. W., Cleasby, I. R., Bell, F., Parr, N., Schultz, A., Votier, S. C. and Bearhop, S. 2018. A phylogenetically controlled meta-analysis of biologging device effects on birds: deleterious effects and a call for more standardized reporting of study data. – Methods Ecol. Evol. 9: 46–553.

Bridge, E. S., Kelly, J. F., Contina, A., Gabrielson, R. M., MacCurdy, R. B. and Winkler, D. W. 2013. Advances in tracking small migratory birds: a technical review of light-level geolocation. – J. Field Ornithol. 84: 121–137.

Briedis, M., Kurlavičius, P., Mackevičienė, R. et al 2018. Loop migration, induced by seasonally different flyway use, in northern European barn swallows. – J. Ornithol. 159: 885–891.

Brlík, V., Kolecek, J., Burgess, M., Hahn, S., Humple, D., Krist, M., Ouwehand, J., Weiser, E. L., Adamik, P., Alves, J. A., Arit, D., Barisic, S., Becker, D., Belda, E. J., Both, C., Bravo, S. P., Briedis, M., Chutny, B., Cikovic, D., Cooper, N. W., Costa, J. S., Cueto, V. R., Emmenegger, T., Fraser, K., Gilg, O., Guerrero, M., Hallworth, M. T., Hewson, C., Jiguet, F., Johnson, J. A., Kelly, T., Kishkinev, D., Leconte, M., Lislevand, T., Lisovski, S., Lopez, C., McFarland, K. P., Marra, P. P., Matsuoka, S. M., Matyjasiak, P., Meier, C. M., Metzger, B., Monros, J. S., Neumann, R., Newman, A. E. M., Norris, D. R., Part, T., Pavel, V., Perlut, N., Piha, M., Reneerkens, J., Takenaka, M., Tolkmitt, D., van Oosten, H., Wellbrock, A. H. J., Wheeler, H., van der Winden, J., Witte, K., Woodworth, B. K. and Prochazka, P. 2019. Weak effects of geolocators on small birds: a meta-analysis controlled for phylogeny and publication bias. – J. Anim. Ecol. 89: 207–220.

Bro, E., Clobert, J. and Reitz, F. 1999. Effects of radio transmitters on survival and reproductive success of gray partridge. – J. Wildl. Manage. 63: 1044–1051.

Burnham, K. P. and Anderson, D. R. 2002: Model selection and multimodel inference: a practical information–theoretic approach. – Springer-Verlag.

Burns, J. G. and Ydenberg, R. C. 2002. The effects of wingloading and gender on the escapeflights of least sandpipers *(Calidris minutilla)* and western sandpipers *(Calidris mauri)*. – Beh. Ecol. Sociobiol. 52: 128–136.

Bächler, E., Hahn, S., Schaub, M., Arlettaz, R., Jenni, L., Fox, J. W., Afanasyev, V. and Liechti, F. 2010. Year-round tracking of small trans-Saharan migrants using light-level geolocators. – PLoS One 5: e9566.

Choquet, R., Lebreton, J. D., Gimenez, O., Reboulet, A. M. and Pradel, R. 2009. U-CARE: utilities for performing goodness of fit tests and manipulating Capture–REcapture data. — Ecography 32: 1071–1074.

Costantini, D. and Møller, A. P. 2013. A meta-analysis of the effects of geolocator application on birds. – Curr. Zool. 59: 697–706.

Elliott, K. H., McFarlane-Tranquilla, L., Burke, C. M., Hedd, A., Montevecchi, W. A. and Anderson, V. G. 2012. Year-long deployments of small geolocators increase corticosterone levels in murres. – Mar. Ecol. Progr. Ser. 466: 1–7.

Gales, R., Williams, C. and Ritz, D. 1990. Foraging behavior of the little penguin, eudyptula-minor – initial results and assessment of instrument effect. – J. Zool. 220: 61–85

Geen, G. R., Robinson, R. A. and Baillie, S. R. 2019. Effects of tracking devices on individual birds – a review of the evidence. – J. Avian Biol. 50. doi.org/10.1111/jav.01823.

Hawkins, P. 2004. Bio-logging and animal welfare: practical refinements. – Memoirs of the National Institute of Polar Research, Special Issue 58: 58e68.

Lebreton, J.-D., Burnham, K. P., Clobert, J. and Anderson, D. R. 1992. Modelling survival and testing biological hypothesis using marked animals: a unified approach with case studies. – Ecol. Monogr. 62: 67–118.

Klasing, K. C. 1998. Nutritional modulation of resistance to infectious diseases. – Poultry Sci. 77: 1119–1125.

McKinnon, E. A. and Love, O. P. 2018. Ten years tracking the migrations of small landbirds: lessons learned in the golden age of bio-logging. – Auk 135: 834–856.

McMahon Clive, R., Hindell Mark, A. and Harcourt Robert, G. 2012. Publish or perish: why it's important to publicise how, and if, research activities affect animals. – Wildl. Res. 39: 375–377.

Monaghan, P. and Nager, R. G. 1997. Why don't birds laymore eggs? – Trends Ecol. Evol. 12: 270–274.

Morganti, M., Rubolini, D., Åkesson, S., Bermejo, A., de la Puente, J., Lardelli, R., Liechti, F., Boano, G., Tomassetto, E., Ferri, M., Caffi, M., Saino, N. and Ambrosini, R. 2018. Effect of light-level geolocators on apparent survival of two highly aerial swift species. – J. Avian Biol. 49. doi.org/10.1111/jav.01521.

Navarro, J., González-Solís, J., Viscor, G. and Chastel, O. 2008. Ecophysiological response to an experimental increase of wing loading in a pelagic seabird. – J. Exp. Mar. Biol. Ecol. 358: 14–19.

Pakanen, V.-M., Luukkonen, A. and Koivula, K. 2011. Nest predation and trampling as management risks in grazed coastal meadows. – Biodivers. Conserv. 20: 2057–2073.

Pakanen, V. M., Rönkä, N., Thomson, R. L. and Koivula, K. 2014. Informed renesting decisions: the effect of nest predation risk. – Oecologia 174: 1159–1167.

Pakanen, V. M., Rönkä, N., Thomson, R. L. and Koivula, K. 2015. No strong effects of leg-flagged geolocators on return rates or reproduction of a small long-distance migratory shorebird. – Ornis Fenn. 92: 101–111.

Pakanen V.-M., Aikio S., Luukkonen A. and Koivula K. 2016. Grazed wet meadows are sink habitats for the southern dunlin *Calidris alpina schinzii* due to nest trampling by cattle. – Ecol. Evol. 6: 7176–7187.

Pakanen, V. M., Koivula, K., Flodin, L.-Å., Grissot, A., Hagstedt, R., Larsson, M., Pauliny, A., Rönkä, N. and Blomqvist, D. 2017. Between-patch natal dispersal declines with increasing natal patch size and distance to other patches in the endangered southern dunlin *Calidris alpina schinzii*. – Ibis 159: 611–622.

Pakanen, V.-M., Jaakkonen, T., Saarinen, J., Rönkä, N., Thomson, R. L. and Koivula, K. 2018. Migration strategies of the Baltic dunlin: rapid jump migration in the autumn but slower skipping type spring migration. – J. Avian Biol. 49. doi.org/10.1111/jav.01513.

Pakanen, V.-M., Rönkä, N., Thomson, R. L., Blomqvist, D. and Koivula, K. 2020. Data from: Survival probability in a small shorebird decreases with the time an individual carries a tracking device. – Dryad Digital Repository. <https://dx.doi.org/.6m905qfxp>

Supplementary information (available online as Appendix jav-02555 at <www.avianbiology.org/appendix/jav-02555>). Appendix 1.

Procházka, P., Brlík, V., Yohannes, E., Meister, B., Auerswald, J., Ilieva, M. and Hahn, S. 2018. Across a migratory divide: divergent migration directions and non-breeding grounds of Eurasian reed warblers revealed by geolocators and stable isotopes. – J. Avian Biol. 49. doi.org/10.1111/jav.01513.

Rodríguez-Ruiz, J., Parejo, D., Puente, J., Valera, F., Calero-Torralbo, M. A., Bermejo, A., Catry, I. and Avilés, J. M. 2016. Short- and long-term effects of tracking devices on the European roller *Coracias garrulus*. – Ibis 158: 179–183.

Saraux, C., Le Bohec, C., Durant, J. M., Viblanc, V. A., Gauthier-Clerc, M., Beaune, D., Park, Y. H., Yoccoz, N. G., Stenseth, N. C. and Le Maho, Y. 2011. Reliability of flipper-banded penguins as indicators of climate change. – Nature 469: 203–206.

Scandolara, C., Rubolini, D., Ambrosini, R., Caprioli, M., Hahn, S., Liechti, F., Romano, A., Romano, M., Sicurella, B. and Saino, N. 2014. Impact of miniaturized geolocators on barn swallow *Hirundo rustica* fitness traits. – J. Avian Biol. 45: 417–423.

Siegel, H. S. 1980. Physiological stress in birds. – BioScience 30: 529–534.

Taff, C. C., Freeman-Gallant, C. R., Streby, H. M. and Kramer, G. R. 2018. Geolocator deployment reduces return rate, alters selection and impacts demography in a small songbird. – PLoS One 13: e0207783.

Vandenabeele, S. P., Shepard, E. L., Grogan, A. and Wilson, R. P. 2012. When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. – Mar. Biol. 159: 1–14.

Weimerskirch, H., Guionnet, T., Martin, J., ShaVer, S. and Costa, D. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. – Proc. R. Soc. B 267: 1869–1874.

Weiser, E. L., Lanctot, R. B., Brown, S. C., Alves, J. A., Battley, P. F., Bentzen, R., … Sandercock, B. K. 2016. Effects of geolocators on hatching success, return rates, breeding movements and change in body mass in 16 species of Arctic-breeding shorebirds. – Movem. Ecol. 4: 12.

van Wijk, R. E., Souchay, G., Jenni-Eiermann, S., Bauer, S. and Schaub, M. 2015. No detectable effects of lightweight geolocators on a Palaearctic-African long-distance migrant. – J. Ornithol. 157: 255–264.

Wilson, R. P. and McMahon, C. R. 2006. Measuring devices on wild animals: what constitutes acceptable practice? – Front. Ecol. Environ. 4: 147–154.

White, G. C. and Burnham, K. P. 1999. Program MARK: survival estimation from populations of marked animals. – Bird Study 46: 120–138.

White, G. C., Kendall, W. L. and Barker, R. J. 2006. Multistate survival models and their extensions in program MARK. – J. Wildl. Manage. 70: 1521–1529.