Weak effects of geolocators on small birds: a meta-analysis controlled for phylogeny and publication bias

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Abstract

1. Currently, the deployment of tracking devices is one of the most frequently used approaches to study movement ecology of birds. Recent miniaturisation of light-level geolocators enabled studying small bird species whose migratory patterns were widely unknown. However, geolocators may reduce vital rates in tagged birds and may bias obtained movement data.
2. There is a need for a complex assessment of the potential tag effects on small birds, as previous meta-analyses did not evaluate unpublished data and impact of multiple life-history traits, focused mainly on large species and the number of published studies tagging small birds has increased substantially.
3. We quantitatively reviewed 549 records extracted from 74 published and 48 unpublished studies on over 7,800 tagged and 17,800 control individuals to examine the effects of geolocator tagging on small bird species (body mass <100 g). We calculated the effect of tagging on apparent survival, condition, phenology and breeding performance and identified the most important predictors of the magnitude of effect sizes.
4. Even though the effects were not statistically significant in phylogenetically controlled models, we found a weak negative impact of geolocators on apparent survival. The negative effect on survival was stronger with increasing relative load of the device and with geolocators attached using elastic harnesses. Moreover, tagging effects were stronger in smaller species.
5. In conclusion, we found a weak effect on apparent survival of tagged birds and accomplished to pinpoint key aspects and drivers of tagging effects. We provide recommendations for establishing matched control group for proper effect size assessment in future studies and outline various aspects of tagging that need further investigation. Finally, our results encourage further use of geolocators on small bird species but the ethical aspects and scientific benefits should always be considered.

Keywords: condition, migration, phenology, reproduction, return rate, survival, tracking device, tag effect

Introduction

Tracking devices have brought undisputed insights into the ecology of birds. Use of these tags enabled researchers to gather valuable information about full annual cycles, year-round geographic distribution of populations and other ecological patterns in many species whose movement ecology was widely unknown (e.g. Patchett, Finch, & Cresswell, 2018; Stanley, MacPherson, Fraser, McKinnon, & Stutchbury, 2012; Weimerskirch et al., 2002). A significant proportion of recently published tracking studies uses light-level geolocators on small bird species (body mass up to 100 g; Bridge et al., 2013; McKinnon & Love, 2018); however, the increasing use of these tags on small birds raises questions about ethics of tagging and how representative the behaviour of tagged individuals is (Jewell, 2013; Wilson & McMahon, 2006).

Studies using tracking devices such as archival light-level geolocators (hereafter ‘geolocators‘) frequently report the effect of tagging. Nevertheless, there is a notable lack of comprehensive data reporting necessary for a proper assessment of this effect (Bodey et al., 2018). The published results on the effects of geolocator tagging are equivocal: some found reduced apparent survival, breeding success and parental care (Arlt, Low, & Pärt, 2013; Pakanen, Rönkä, Thomson, & Koivula, 2015; Scandolara et al., 2014; Weiser et al., 2016) while others report no obvious effects (Bell, Harouchi, Hewson, & Burgess, 2017; Fairhurst et al., 2015; Peterson et al., 2015; van Wijk, Souchay, Jenni-Eiermann, Bauer, & Schaub, 2015). Recent meta-analyses evaluating the effects of geolocators (Costantini & Møller, 2013) or tracking devices in general (Barron, Brawn, & Weatherhead, 2010; Bodey et al., 2018) showed slightly negative effects on apparent survival, breeding success and parental care. However, these studies involved mainly large bird species and there is thus a lack of complex evaluation of geolocator effects on small birds including species' life-history and ecological traits, geolocator design, and type of attachment. The relative load of the devices is the most frequently discussed aspect affecting the tagged birds. Previous meta-analyses showed stronger tagging effects with increasing tag mass (Costantini & Møller, 2013), or suggested multiple threshold values of relative load on birds (Barron et al., 2010; Bodey et al., 2018). However, these studies were based on relatively small samples of mainly larger species where the same additional relative load affects flight performance more than in smaller species (Caccamise & Hedin, 1985). Moreover, previous studies did not control for the effect of small-sample studies and phylogenetic non-independence as well as its uncertainty. There is thus a need for systematic assessment of tag load effects on small birds.

Almost all prior meta-analyses reporting effects of tagging relied only on published sources and could thus be affected by publication bias (Koricheva, Gurevitch, & Mengersen, 2013), as omitting unpublished sources in meta-analyses may obscure the result (see e.g. Sánchez-Tójar et al. 2018). The main source of publication bias in movement ecology could be a lower probability of publishing studies based on a small sample size, including studies where no or only few tagged birds were successfully recovered due to a strong tagging effect. Additionally, geolocator effects most frequently rely on comparisons between tagged and control birds and a biased choice of control individuals may directly lead to the misestimation of the tagging effect sizes. The bias in the control groups can be due to selection of smaller birds, birds being caught in different spatio-temporal conditions, including non-territorial individuals, or different effort into recapturing control and tagged individuals.

As the picture of the potential tag effects is incomplete and the number of studies tagging small birds is rapidly increasing each year, we aim at testing these effects on small bird species in a robust dataset of both published and unpublished studies to minimize the impact of publication bias. Moreover, we control for the species' ecological and life-history traits, type of control treatment as well as geolocator and attachment designs. We build on the most recent advances in meta-analytical statistical modelling to get unbiased estimates of the geolocator deployment effects controlled for phylogenetic non-independence and its uncertainty (Doncaster & Spake, 2017; Guillerme & Healy 2017; Hadfield, 2010; Viechtbauer, 2010).

Predictions

i) Geolocators will negatively affect apparent survival, condition, phenology and breeding performance of small birds.

ii) Negative effects will be stronger in unpublished studies than in published studies.

iii) Deleterious effects will be most prominent in studies establishing matched control groups compared to studies with potentially-biased control groups.

iv) Geolocators which constitute a higher relative load will imply stronger negative effects.

v) Geolocators with a light stalk/pipe will cause stronger negative effects because of increased drag in flight and thus energetic expenditure (Bowlin et al., 2010; Pennycuick, Fast, Ballerstädt, & Rattenborg, 2012). These effects will be stronger in aerial foragers than in other foraging guilds (Costantini & Møller, 2013).

vi) Non-elastic harnesses will cause stronger negative effects on tagged individuals than those tagged with elastic harnesses that may avoid flight ability restrictions during intra-annual body mass changes (Blackburn et al., 2016).

Material and Methods

Data search

We conducted an exhaustive search for both published and unpublished studies deploying geolocators on bird species with body mass up to 100 g. We searched the Web of Science Core Collection (search terms: TS = (geoloc* AND (bird* OR avian OR migra*) OR geologg*)) and Scopus databases (search terms: TITLE-ABS-KEY (geoloc* AND (bird* OR migra*) OR geologg*)), to find published studies listed to 18 February 2018. Moreover, we searched reference lists of studies using geolocators on small birds and included studies from previous comparative studies (Bridge et al., 2013; Costantini & Møller, 2013; Weiser et al., 2016). In order to get information from unpublished studies, we inquired geolocator producers and the Migrant Landbird Study Group to disseminate our request for unpublished study details among their customers and members, respectively. In addition, we asked the corresponding authors of the published studies to share any unpublished data. The major geolocator producers – Biotrack, Lotek, Migrate Technology and the Swiss Ornithological Institute – sent our request to their customers. To find whether the originally unpublished studies were published over the course of this study, we inspected their status on 30 November 2018. We found XX studies using data not presented in our analysis listed in the Web of Science Core Collection and in Scopus databases (search terms as above) on 30 November 2018. The tagging effects found in these studies did not affect the overall tagging effects presented in our analysis and we thus do not include them in our study. The entire process of search and selection of studies and records (described below) is presented in a flow-chart (Fig. S1).

Inclusion criteria; additional data requesting

We included studies that met the following criteria:

1. The study reported response variables (e.g. return rates, body masses) necessary for effect size calculation.

2. The study included a control group of birds alongside the geolocator-tagged individuals or reported a pairwise comparison of tagged birds during geolocator deployment and recovery.
3. As a control group, the study considered birds marked on the same site and year, of the same sex and age class without any indication of a difference in recapture effort between tagged and control groups.
4. For pairwise comparisons, the study presented correlation coefficients or raw data.
5. The variable of interest was presented outside the interaction with another variable.

We asked the corresponding authors for missing data or clarification when the criteria were not met or when it was not clear whether the study complied with the criteria (70% response rate [n = 115]). In addition, we excluded birds that had lost geolocators before subsequent recapture as we did not know when the bird lost the geolocator, and excluded all individuals tagged repeatedly over years because of possible inter-annual carry-over effects of the devices. VB assessed all studies for eligibility and extracted data, the final dataset was cross-checked by JK and PP. A list of all published studies included in the meta-analysis is provided in the Published Data Sources section.

Trait categories; effect size calculation; explanatory variables

We divided all collected data into four trait categories: apparent survival, condition, phenology and breeding performance based on the response variables reported (e.g. inter-annual recapture rates, body mass changes, arrival dates, or clutch sizes; Table S2). These categories represent the main traits possibly affected in the geolocator-tagged individuals. Subsequently, analyses were run separately for each trait category. We calculated the effect sizes for groups of tagged birds from the same study site and year of attachment, of the same sex (if applicable) and specific geolocator and attachment type accompanied with the corresponding control groups. For simplicity, we call these units *records* throughout the text. For each record, we extracted a contingency table with the treatment arm continuity correction (Schwarzer, Carpenter, & Rücker, 2014) or mean, variance, and sample size, to calculate the unbiased standardised mean difference – Hedges' *g* (Borenstein, Hedges, Higgins, & Rothstein, 2009) – and its variance with correction for the effect of small sample sizes (Doncaster & Spake, 2018). We used the equation from Sweeting et al. (2004) to calculate variance in pairwise comparisons. When raw data were not provided, we used the reported test statistics (F, t or χ^2) and sample sizes to calculate the effect size using the R package compute.es (Del Re 2013). Besides the effect size measures, we extracted additional variables of potential interest – ecological and life-history traits per species, methodological aspects of the study, geolocator design and harness material elasticity (Table 1).

Accounting for dependency

We accounted for data non-independence on several levels. When multiple records shared one control group (e.g. several geolocator types and attachment designs used in one year), we split the sample size in the shared control group by the number of records to avoid a false increase in record precisions. When multiple measures were available for the same individuals, we randomly chose one effect size measure in each trait category (n = 8). If the study provided both recapture and re-encounter rates, we chose the re-encounter rate as a more objective measure of apparent survival. Re-encounters included captures and observations of tagged birds and thus the bias towards the tagged birds caused by the potentially higher recapture effort to retrieve the geolocators should be lower. Finally, we accounted for phylogenetic non-independence between the species and the uncertainty of these relationships using 100 phylogenetic trees (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) downloaded from the BirdTree.org (www.birdtree.org) using the backbone of Hackett et al. (2008). Moreover, we used the random intercepts of species and study sites in all models, the latter to account for possible site-specific differences (such as different netting effort or other field methods used by particular research teams).

Overall effect sizes and heterogeneity

We calculated the overall effect size for each trait category from all available records using meta-analytical null models. We employed the *MCMCglmm* function from the MCMCglmm package (Hadfield, 2010) to estimate overall effect sizes not controlled for phylogeny (model 1, Table S3). We then used the *mulTree* function from the mulTree package (Guillerme & Healy, 2017) to automatically fit a MCMCglmm model on each phylogenetic tree we sampled and summarized the results from all these models to obtain phylogenetically controlled overall effect size estimates (model 2, Table S3). We used weakly informative inverse-Gamma priors (V = 1, nu = 0.002) in all models. All fitted MCMCglmm models converged and Gelman-Rubin statistic was always <1.1 for all parameters. As our data contained many effect sizes based on small sample sizes, which could lead to a biased estimate of the overall effect size variance, all effect sizes were weighted by their mean-adjusted sampling variance (Doncaster & Spake, 2018). We considered effect sizes of 0.2, 0.5 and 0.8 Hedge's *g* a weak, moderate and large effects, respectively. Moreover, we calculated the amount of between-study heterogeneity in all null models using the equation described in Nakagawa and Santos (2012). Phylogenetic heritability (H^2) expressing the phylogenetic signal was estimated as the ratio of phylogenetic variance ($\sigma^2_{phylogeny}$) against the sum of phylogenetic and species variance ($\sigma^2_{species}$) from the models (Table S3; Hadfield & Nakagawa, 2010):

$$H^2 = \sigma^2_{phylogeny} / (\sigma^2_{phylogeny} + \sigma^2_{species})$$

Multivariate meta-analysis

To unveil the most important dependencies of the geolocator effects, we calculated three types of multivariate models: a full trait model (model 3), an ecological model (model 4) and models of publication bias (models 5, Table S3). In the full trait model, we used all methodological, species, geolocator specification and attachment variables (Table 1) to estimate their impact on trait category with overall effect (model 3). Prior to fitting the ecological model, we employed a principal component analysis of the inter-correlated log continuous life-history traits and extracted the two most important ordination axes – PC1 and PC2 (Table 1). The PC1 explained 54.4% of the variability and expressed a gradient of species characterised mainly by increasing body mass, egg mass and clutch mass (Fig. S4). The PC2 explained 18.7% of variance and was characterised mainly by increasing clutch sizes, number of broods and decreasing migration distances (model 4, Fig. S4). These axes together with the categorical ecological traits (Table 1) then entered the ecological model to estimate their effect on trait category with overall effect. Finally, we tested for differences in effect sizes between published and unpublished results in each trait category using all available records (model 5). In all models, we employed the *rma.mv* function from the R package metafor (Viechtbauer, 2010) weighted by the mean-adjusted sampling error (Doncaster & Spake, 2018). Continuous predictors were scaled and centred. None of the model residuals violated the assumption of normal distribution. Because the phylogenetic relatedness of the species explained only a small amount of variation and the phylogenetic relatedness correlates with the life-history and ecological traits, we did not control for phylogeny in the multivariate models but incorporated the random intercepts of species and study site. We also considered the biological relevance of all variables as a random slope in the full trait model. We found relative load to be a relevant random slope variable as it could control for the potential variation in slopes of tagging effects between species. However, this model did not achieve convergence likely due to a small variation of values within species and we thus present the full trait model with random intercepts of species and study site only. We calculated R^2 for the full trait and ecological models using the residual between-study variability ($\tau^2_{residual}$) and the total between-study variability (τ^2_{total}) according to the equation (López-López, Marín-Martínez, Sánchez-Meca, Van den Noortgate, & Viechtbauer, 2014):

$$R^2 = (1 - \tau^2_{residual} / \tau^2_{total}) \times 100$$

Publication bias; body mass manipulation

We used funnel plots to visually check for potential asymmetry caused by publication bias in each trait category (Fig. S5). To quantify the level of asymmetry in each trait category, we applied the Egger's regression tests of the meta-analytical residuals from all null models of the trait categories (calculated using the *rma.mv* function) against effect size precision (1 / mean-adjusted standard error; Nakagawa & Santos, 2012). An intercept significantly differing from zero suggested the presence of publication bias. In order to find differences in log body mass between the tagged and control individuals during the tagging and marking, we applied a linear mixed-effect model with species and study site as a random intercept weighted by the sample sizes. We considered all effect sizes significant when the 95% credible interval (CrI) or confidence interval (CI) did not overlap zero. All analyses were conducted in R version 3.3.1 (R Core Team, 2016).

Results

We assessed 854 records for eligibility of effect size calculation. Consequently, we excluded 36% of these records mainly due to a missing control group (59%) or missing essential values for effect size calculation (21%; Fig. S1). Finally, a total of 122 studies containing 549 effect sizes were included in our meta-analysis wherein 35% effect sizes originated from unpublished sources (Table 2). The vast majority of the analysed effect sizes originated from Europe or North America (94%; Fig. S6) and the data contained information about 7,829 tagged and 17,834 control individuals of 69 species from 27 families and 7 orders (Table S7).

We found a weak overall negative effect (Hedges' *g*: –0.2; 95% CrI –0.29, –0.11; P <0.001) only on apparent survival in the model not controlled for phylogeny (model 1). Although we found no statistically significant overall tagging effects in any trait category when controlling for phylogenetic relatedness, the estimates were similar to those not controlled for phylogeny (model 2, Fig. 1). The phylogenetic signal (H^2 = 59%) was statistically significant only for apparent survival, suggesting that closely related species have more similar response to tagging than less related species, but the variance explained by phylogeny and species were very low for all models (Table S8).

The full trait model of apparent survival revealed that tagging effects were stronger with increasing load on tagged individuals and geolocators with elastic harnesses affected birds more than geolocators with non-elastic harnesses (Table 3, Fig. 2). However, we found no statistically significant effect of the control group type, sex, stalk length, foraging strategy or the interaction between stalk length and foraging strategy (model 3, Table 3). The ecological model suggested a relationship of apparent survival with the PC1, with negative effects being stronger with decreasing body, egg and clutch mass (model 4, Table 3). The full trait model explained 21.1% and the ecological model 11.8% of the between-study variance.

We did not find any evidence for publication bias, either visually in the funnel plots (Fig. S5), or using Egger's regression tests (Table 2) in any of the trait categories. Moreover, none of the publication bias models found statistically significant differences between published and unpublished effect sizes (model 5, Table S9). The geolocator-tagged birds were on average 3.8% heavier than control individuals prior to the geolocator deployment and marking (LMM: estimate 0.008 ± 0.003, t = 2.47, P = 0.014).

Discussion

Geolocator deployment has a potential to reduce a birds' apparent survival, condition, breeding performance, or may delay events of an annual cycle leading to biases in movement data. By conducting a quantitative review of published studies deploying geolocators on small bird species and incorporating unpublished data, we revealed only a weak overall effect of geolocators on apparent survival of tagged birds while we found no clear overall effect on condition, phenology and breeding performance.

Moreover, we found no statistically significant effects of tagging in any of trait categories when accounting for phylogenetic relationships. Tagging effects on apparent survival were stronger in individuals with a higher relative load, when the geolocators were attached with elastic harnesses and in small-bodied species.

Overall tag effects

A negative overall effect of geolocator tagging on apparent survival found in this study seems to be consistent across previous comparative studies of tagging effects (Barron et al., 2010; Bodey et al., 2018; Costantini & Møller, 2013; Trefry, Diamond, & Jesson, 2012; Weiser et al., 2016). However, unlike in previous comparative (Barron et al., 2010; Bodey et al., 2018) and primary studies (e.g. Adams et al., 2009; Arlt et al., 2013; Snijders et al., 2017), we found no overall negative effects on variables associated with breeding performance in our analysis. No evidence for overall effect on condition and phenology found in this study is in agreement with equivocal results of the previous studies: some found reduced condition (Adams et al. 2009, Elliott et al., 2012) or timing of annual cycle events (Arlt et al., 2013, Scandolara et al., 2014) while others found no evidence for tagging effects on these traits (Bell et al., 2017; Fairhurst et al., 2015; Peterson et al., 2015; van Wijk et al., 2015).

Tagging effects derive from individuals that returned to the study site and are potentially in better condition than individuals that did not return causing the weak effects on condition, phenology and breeding performance. However, the lack of effect we found on phenology and breeding performance could also be an artefact of the small sample size, as collecting these data is probably more challenging in small avian species than in relatively heavier species included in the previous studies. Similarly, effects of tagging on condition could be underestimated due to initial differences we found between the body mass of tagged and control birds. Additionally, the intra-annual body mass changes could cause a significant bias in studies where timing of geolocator deployment and geolocator recovery differs.

Overall, the weak effects of tagging we found support several species-specific studies (e.g. Bell et al., 2017; Fairhurst et al., 2015; Peterson et al., 2015; van Wijk et al., 2015) and might be encouraging from the perspective of deleterious impacts as well as credibility of obtained behaviour of birds. On the other hand, care should be taken as the tagging effect may be specific for populations, or species. For example, Weiser et al. (2016) found a negligible overall effect but significant reduction of return rates in the smallest species in their meta-analysis. The negative effect of geolocators can also vary between years (Bell et al., 2017, Scandolara et al., 2014), or be induced by occasional bad weather conditions (Snijders et al., 2017), or food shortages (Saraux et al., 2011; Wilson et al., 2015).

Inferring unbiased overall effect sizes

We minimised the publication bias in our estimates of overall effects by including substantial amount of unpublished results (192 records of 38 species) and contacting authors of published studies for additional results. Still, some of these data might get published in the future despite the delay between our data collation and the final analysis. We did not find any evidence that tagging effects differed between published and unpublished studies, suggesting that it may not be a critical consideration for publishing a study.

Moreover, we found no support for tag effects in studies with matched control individuals to be stronger compared to studies with less strict control treatments. Nevertheless, the difference we found in body mass between tagged and control birds could have led to deployment of geolocators on individuals in better condition with lower load resulting in underestimation of the overall effect size. We suggest establishing carefully matched control groups in all future studies to enable a more reliable estimation of tagging effects. Such a control group should include: i) randomly selected individuals of the same species, sex and age class; ii) individuals caught at the same time of the season and year; iii) at the same time of the day; iv) of similar size and condition as tagged individuals, and v) exclude non-territorial breeders or individuals passing through the site.

Influence of relative load and species' life-histories

Our results support the current evidence (Bodey et al., 2018; Weiser et al., 2016) for reduced apparent survival in studies with a relatively higher tag load on treated individuals. Moreover, we found an increasing negative effect in studies tagging smaller species with smaller eggs and clutch masses. The lower body mass in these species is likely accompanied with a higher relative tag load due to lower limits in tag weights due to technical constraints. Although recent miniaturisation has led to the development of smaller tags, these tags have been predominantly applied to smaller species instead of reducing tag load in larger species (Portugal & White, 2018). The various relative loads used without observed tagging effects (e.g. Bell et al., 2017, Peterson et al., 2015; van Wijk et al., 2015) indicate the absence of a generally applicable rule for all small bird species (Schacter & Jones, 2017) and we thus recommend the use of reasonably small tags despite potential disadvantages (e.g. reduced battery lifespan or light sensor quality).

Harness material

Contrary to our prediction, we found higher apparent survival in birds tagged with harnesses made of non-elastic materials. Non-elastic harnesses are usually individually adjusted on each individual, whereas elastic harnesses are often prepared before attachment to fit the expected body size of the tagged individuals according to allometric equations (e.g. Naef-Daenzer, 2007). As pre-prepared elastic harnesses cannot match perfectly the size of every captured individual, they may be in the end more frequently tightly fitted as some researches might tend to tag larger individuals or avoid too loose harnesses to prevent geolocator loss. Non-elastic harnesses may also be more frequently looser than elastic harnesses as researchers try to reduce the possibility of non-elastic harness getting tight when birds accumulate fat. Harness tightness was found to significantly reduce the return rates (Blackburn et al. 2016), moreover, the movement ability restrictions may be difficult to register during deployment of tag with elastic harnesses. In contrast, non-elastic harnesses can be tailored according to the actual size and made sufficiently loose to account for body mass changes of each individual. Prepared elastic harnesses are usually used to reduce the handling time during the geolocator deployment (Streby et al. 2015) but this advantage may be outweighed by the reduced apparent survival of geolocators with tied elastic harnesses. We thus suggest to consider stress during geolocator deployment together with the potentially reduced apparent survival and the risk of tag loss when choosing harness material.

Variables without statistically significant impact of tagging

Migratory distance did not affect the magnitude of the effect sizes, contrasting with some previous findings (Bodey et al., 2018; Costantini & Møller, 2013). However, none of these studies used population-specific distances travelled, instead using latitudinal spans between ranges of occurrence (Costantini & Møller, 2013) or travelled distance categorised into three distances groups (Bodey et al., 2018). These types of distance measurements could greatly affect the results especially in species that migrate mainly in an east-west direction (Lislevand et al., 2015; Stach, Kullberg, Jakobsson, Ström, & Fransson, 2016) or in species whose populations largely differ in their travel distances (Bairlein et al., 2012; Schmaljohann, Buchmann, Fox, & Bairlein, 2012). Additionally, we found no overall effect of species' foraging strategy, contrary to the strong overall effect found in Costantini and Møller (2013). Despite tag shape altering the drag and thus energy expenditure during flight (Bowlin et al., 2010; Pennycuick et al., 2012), apparent survival tended to be better in individuals fitted with stalked geolocators and we found no interaction between stalk length and foraging strategy on the tagging effect size. Geolocators with longer stalks have been more frequently used in heavier birds with low relative load where the expected tag effect is weak. Moreover, previous results of strong negative effects in aerial foragers led to a preferential use of stalkless geolocators in these species and probably minimised the tagging effect in this foraging guild (Morganti et al., 2018; Scandolara et al., 2015). However, the evidence for the negative effects in non-aerial foragers is low as there is only one field study focusing on stalk length effects on the return rates (Blackburn et al., 2016).

Future considerations

Further studies should focus on inter-annual differences in tagging effects, effects of varying relative loads, different stalk lengths or different attachment methods to minimise the negative effects of tagging. We also suggest to focus on the impact of various movement strategies on the tagging effect such as fattening or moulting schedules. All future studies should carefully set matched controls and transparently report on tagging effects. Finally, our results encourage use of geolocators on small bird species but the ethical and scientific benefits should always be considered.

Authors' contributions

VB, JK and PP conceived the idea and designed the methodology. VB reviewed the literature and collected data, JK and PP checked the data extracted for analysis. VB and PP analysed the data. VB led the writing of the manuscript with significant contributions from JK and PP. MB, SH, DH, MK, JO and EW contributed with unpublished data and their comments and suggestions significantly improved the manuscript. PA, JA, DA, SB, DB, EB, VBe, CB, SB, MBr, BC, DC, NC, JC, VC, TE, KF, OG, MG, MH, CH, FJ, JJ, TK, DK, ML, TL, SL, CL, KM, PMar, SM, PMat, CM, BM, JM, RNe, AN, RNo, TP, VP, NP, MP, JR, CR, AR, CS, NS, MT, DT, HO, AW, HW, JW, KW and BW contributed unpublished data and critically revised the manuscript. All authors gave final approval for publication.

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Data accessibility

Data described in this article are available at https://doi.org/XXX (Brlík et al., 2018).

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Table 1. Explanatory variables used in the multivariate meta-analysis of apparent survival extracted from published and unpublished geolocator studies or from the literature. *N* presents the number of records specified as the groups of tagged birds from the same study site, year of attachment, of the same sex, and the specific geolocator and the attachment type accompanied with the corresponding control groups.

Methodological aspect	*Description*	*N*
Published data	Published – data from published studies (for details see Methods), data from unpublished sources from years following an already published study, or data initially collected as unpublished but published by 31 August 2018	303
	Unpublished – data from unpublished studies	123
Control group	Matched – birds handled in the exactly same way as geolocator-tagged birds except for geolocator deployment	102
	Marked only – birds of the same sex, age, from the same year and study site or birds from the same site, from different years	324
Species trait		
Foraging strategy[1,2]	Aerial forager	122
	Non-aerial forager	304
Sex	Males	195
	Females	120
Geolocator specification		
Relative load	% of geolocator mass (including the harness) of the body mass of the tagged birds	418

Stalk/pipe length*	Length (mm) of the stalk/pipe holding the light sensor or guiding the light towards the sensor (0 mm for stalkless models)	371
Attachment specification		
Attachment type	Leg-loop harness	304
	Full-body harness	80
	Leg-flag attachment	42
Material elasticity*	Elastic – elastan, ethylpropylen, neoprene, rubber, silicone, silastic, or Stretch Magic	235
	Non-elastic – cord, kevlar, nylon, plastic, polyester, or teflon	146
Ecological trait		
Life-histories	Great circle distance between geolocator deployment site and population-specific centroid of the non-breeding (or breeding) range	426
	Male body mass (g)	426
	Female body mass (g)	426
	Nest type – open/close	426
	Clutch size (number of eggs)	426
	Number of broods per year	426
	Dense habitat preference (species occurs especially in dense habitats e.g. reeds or scrub) – yes/no	426
	Egg mass (g) – mean fresh mass[3]	426
	Clutch mass (g) – egg mass × clutch size	426

* only used for harness attachments

[1] Cramp & Perrins, 1977–1994

[2] Rodewald, 2015

[3] Schönwetter, 1960–1992

Table 2. Number of unpublished effect sizes included in the analysis and Egger's regression tests of the null model residuals against their precision to assess the presence of publication bias.

Trait category	*Unpublished (%)*		*Egger's regression*			
	Effect sizes	*N*	*Intercept*	*t*	*SE*	*P*
Apparent survival	28.9	426	0.12	1.53	0.08	0.121
Condition	63.3	79	–0.36	–1.70	0.21	0.088
Phenology	59.1	22	–0.26	–1.28	0.21	0.217
Breeding performance	27.3	22	–0.01	–0.01	0.61	0.993

Table 3. Summary of the full trait model (n = 281) and the ecological model (n = 426) of the geolocator effects on apparent survival. Levels contrasted against the reference level are given in parentheses.

Full trait model

Trait	*Estimate*	*SE*	*Z*	*95% CI*	*P*
Intercept	–0.25	0.10	–2.59	(–0.44; –0.06)	0.010
Published (published)	0.14	0.10	1.39	(–0.06; 0.34)	0.164
Control type (matched)	–0.05	0.09	–0.61	(–0.23; 0.12)	0.542
Foraging strategy (aerial)	–0.09	0.14	–0.61	(–0.36; 0.19)	0.540
Sex (males)	–0.07	0.05	–1.30	(–0.17; 0.03)	0.192
Relative load	–0.12	0.05	–2.36	(–0.23; –0.02)	0.018
Stalk/pipe length	0.07	0.04	1.77	(–0.01; 0.15)	0.077
Material elasticity (non-elastic)	0.19	0.08	2.21	(0.03; 0.35)	0.026
Foraging strategy (aerial) × stalk length	–0.10	0.07	–1.40	(–0.25; 0.04)	0.161

Ecological model

Trait	*Estimate*	*SE*	*Z*	*95% CI*	*P*
Intercept	–0.26	0.08	–3.20	(–0.42; –0.10)	0.001
PC1	0.06	0.03	2.32	(0.01; 0.11)	0.026
PC2	0.02	0.03	0.47	(–0.05; 0.08)	0.638
Dense habitat (yes)	0.03	0.13	0.21	(–0.22; 0.27)	0.834
Nest type (open)	0.14	0.11	1.27	(–0.08; 0.36)	0.205