Journal of Animal Ecology

BRITISH ECOLOGICAL SOCIETY

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

Journal:	*Journal of Animal Ecology*
Manuscript ID	Draft
Manuscript Type:	Research Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Brlík, Vojtěch; Ustav Biologie Obratlovcu Akademie ved Ceske Republiky; Univerzita Karlova v Praze Prirodovedecka Fakulta, Department of Ecology Koleček, Jaroslav; Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, v.v.i., Burgess, Malcolm; Royal Society for the Protection of Birds Hahn, Steffen; Swiss Ornithological Institute, Bird Migration Humple, Diana; Point Blue Conservation Science Krist, Miloš; Palacky University, Zoology Ouwehand, Janne; Groningen Institute for Evolutionary Life Sciences, University of Groningen, Conservation Ecology Group Weiser, Emily; Kansas State University Division of Biology; US Geological Survey Upper Midwest Environmental Sciences Center Adamik, Peter; Palalacky University, Zoology; Museum of Natural History, Zoology Alves, Jose; Universidade de Aveiro, Dep. Biology & CESAM; University of Iceland, South Iceland Research Centre Arlt, Debora; Swedish University of Agricultural Sciences, Department of Ecology Barišić, Sanja; Hrvatska akademija znanosti i umjetnosti Becker, Detlef; Museum Heineanum Belda, Eduardo; Universidad Politecnica de Valencia, Beran, Václav; Palacky University, Zoology; Municipal Museum Ústí nad Labem; ALKA Wildlife o.p.s. Both, Christiaan; University of Groningen, Conservation Ecology Group Bravo , Susana; CIEMEP –CONICET , Ecodes Briedis, Martins; Schweizerische Vogelwarte, Chutný, Bohumír; Malinová 1650/27 Ćiković, Davor; Hrvatska akademija znanosti i umjetnosti Cooper, Nathan; Smithsonian Conservation Biology Institute Costa, Joana; Universidade de Aveiro, Dep. Biology & CESAM Cueto, Víctor; CIEMEP –CONICET , Ecodes Emmenegger, Tamara; Swiss Ornithological Institute, Bird Migration Fraser, Kevin; University of Manitoba Department of Biological Sciences Gilg, Olivier; Ecology Evolution, University of Burgundy; Group de recherche en Ecologie Arctique Guerrero, Marina; Servicio di Jardines Bosques y Huertas Hallworth, Michael; National Zoological Park, Migratory Bird Center Hewson, Chris; British Trust for Ornithology,

	Jiguet, Frederic; Centre d'Ecologie et des Sciences de la Conservation Johnson, James; US Fish and Wildlife Service Alaska Region Kelly, Tosha; Western University Department of Biology Kishkinev, Dmitry; Bangor University School of the Environment Natural Resources and Geography Leconte, Michel; Quartier du Caü Lislevand, Terje; Universitetsmuseet i Bergen Lisovski, Simeon; Schweizerische Vogelwarte, López, Cosme; Universidad de Sevilla Facultad de Biologia McFarland, Kent; Vermont Center for Ecostudies Marra, Peter; Smithsonian Migratory Bird Centre, National Zoological Park Matsuoka, Steven; US Fish and Wildlife Service Alaska Region; US Geological Survey Alaska Science Center Matyjasiak, Piotr; Cardinal Stefan Wyszynski University in Warsaw, Faculty of Biology and Environmental Sciences Meier, Christoph; Swiss Ornithological Institute, Bird Migration Metzger, Benjamin; Rua de Esperanca 43/3D Monros, Juan; University of Valencia, institute of Biodiversity and Evolutionary Biology Neumann, Roland; Kritzmower Weg 1 Newman, Amy; University of Guelph, Integrative Biology Norris, Ryan; University of Guelph , Integrative Biology Pärt, Tomas; Swedish University of Agricultural Sciences, Department of Ecology Pavel, Václav; Palacky University, Zoology; Jihoceska Univerzita v Ceskych Budejovicich Perlut, Noah; University of New England, Department of Environmental Studies

Key-words:	condition, migration, phenology, reproduction, return rate, survival, tracking device, tag effect

SCHOLARONE™
Manuscripts

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

Vojtěch Brlík[1,2], Jaroslav Koleček[1], Malcolm Burgess[3], Steffen Hahn[4], Diana Humple[5], Miloš Krist[6], Janne Ouwehand[7], Emily L. Weiser[8,9], Peter Adamík[6,10], José A. Alves[11,12], Debora Arlt[13], Sanja Barišić[14], Detlef Becker[15], Eduardo J. Belda[16], Václav Beran[6,17,18], Christiaan Both[7], Susana P. Bravo[19], Martins Briedis[4], Bohumír Chutný[20], Davor Ćiković[14], Nathan W. Cooper[21], Joana S. Costa[11], Víctor R. Cueto[19], Tamara Emmenegger[4], Kevin Fraser[22], Olivier Gilg[23,24], Marina Guerrero[25], Michael T. Hallworth[26], Chris Hewson[27], Frédéric Jiguet[28], James A. Johnson[29], Tosha Kelly[30], Dmitry Kishkinev[31], Michel Leconte[32], Terje Lislevand[33], Simeon Lisovski[4], Cosme López[34], Kent P. McFarland[35], Peter P. Marra[26], Steven M. Matsuoka[29,36], Piotr Matyjasiak[37], Christoph M. Meier[4], Benjamin Metzger[38], Juan S. Monrós[39], Roland Neumann[40], Amy Newman[41], Ryan Norris[41], Tomas Pärt[13], Václav Pavel[6,42], Noah Perlut[43], Markus Piha[44], Jeroen Reneerkens[7], Christopher C. Rimmer[35], Amélie Roberto-Charron[22], Chiara Scandolara[4], Natasha Sokolova[45,46], Makiko Takenaka[47], Dirk Tolkmitt[48], Herman van Oosten[49,50], Arndt H. J. Wellbrock[51], Hazel Wheeler[52], Jan van der Winden[53], Klaudia Witte[51], Brad Woodworth[54], Petr Procházka[1]

Author for correspondence: Vojtěch Brlík, The Czech Academy of Sciences, Institute of Vertebrate Biology, Květná 8, CZ-603 65 Brno, Czech Republic. E-mail: vojtech.brlik@gmail.com

Affiliations

[1] The Czech Academy of Sciences, Institute of Vertebrate Biology, Květná 8, 603 65 Brno, Czech Republic

[2] Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, 128 44 Prague 2, Czech Republic

[3] Royal Society for the Protection of Birds – Centre for Conservation Science, The Lodge, Sandy, SG19 2DL Beds, UK

[4] Bird Migration Department, Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland

[5] Point Blue Conservation Science, 3820 Cypress Drive 11, Petaluma, California 94954, USA

[6] Department of Zoology, Faculty of Science, Palacký University, tř. 17. listopadu 50, 771 46 Olomouc, Czech Republic

[7] Conservation Ecology Group, Groningen Institute for Evolutionary Life Sciences, University of Groningen, Nijenborgh 7, 9747 AG Groningen, The Netherlands

[8] Kansas State University, Division of Biology, 116 Ackert Hall, Manhattan, Kansas 66506, USA

[9] U.S. Geological Survey, Upper Midwest Environmental Sciences Center, 2630 Fanta Reed Rd, La Crosse, Wisconsin 54603, USA

[10] Museum of Natural History, nám. Republiky 5, 771 73 Olomouc, Czech Republic

[11] Department of Biology & Centre for Environmental and Marine Studies, University of Aveiro, Campus Universitário de Santiago, 3810-193 Aveiro, Portugal

[12] University of Iceland, South Iceland Research Centre, Lindarbraut 4, IS-840 Laugarvatn, Iceland

[13] Department of Ecology, Swedish University of Agricultural Sciences, PO Box 7044, 75007 Uppsala, Sweden

[14] Institute of Ornithology, Croatian Academy of Sciences and Arts, Gundulićeva 24, 10000 Zagreb, Croatia

[15] Museum Heineanum, Domplatz 36, 38820 Halberstadt, Germany

[16] Universitat Politècnica de València, C/ Paranimfo, 1, 46730 Gandia, Valencia, Spain

[17] Municipal Museum of Ústí nad Labem, Masarykova 1000/3, 40001 Ústí nad Labem, Czech Republic

[18] ALKA Wildlife o.p.s., Lidéřovice 62, 38001 Dačice, Czech Republic

[19] Centro de Investigacion Esquel de Montaña y Estepa Patagonica, CONICET/UNPSJB, Roca 780, Esquel, CP 9200, Chubut, Argentina

[20] Malinová 1650/27, 10600 Prague 10, Czech Republic

[21] Migratory Bird Center, Smithsonian Conservation Biology Institute, National Zoological Park, PO Box 37012 MRC 5503, Washington, D.C. 20013, USA

[22] Avian Behaviour and Conservation Lab, Department of Biological Sciences, University of Manitoba, 50 Sifton Road, Winnipeg, Manitoba R3T 2N2, Canada

[23] UMR 6249 Chrono-environnement, Université de Bourgogne Franche-Comté, 16 route de Gray, 25000 Besançon, France

[24] Groupe de recherche en Ecologie Arctique, 16 rue de Vernot, 21440 Francheville, France

[25] Servicio de Jardines, Bosques y Huertas, Patronato de la Alhambra y el Generalife.C/ Real de la Alhambra, 18009 Granada, Spain

[26] Migratory Bird Center – Smithsonian Conservation Biology Institute, National Zoological Park, Washington DC 20013, USA

[27] British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK

[28] UMR7204 CESCO, MNHN-CNRS-Sorbonne Université, CP135, 43 Rue Buffon, 75005 Paris, France

[29] U.S. Fish and Wildlife Service, Migratory Bird Management, 1011 East Tudor Road, Anchorage, Alaska 99503, USA

[30] Advanced Facility for Avian Research, Western University, 32 Wellington Dr, N6G 4W4, London, Ontario, Canada

[31] School of Natural Sciences, Bangor University, Deiniol Road, Bangor, LL57 2UW, Gwynedd, UK

[32] Quartier du Caü, F-64260 Arudy, France

[33] University Museum of Bergen, Department of Natural History, University of Bergen, PO Box 7800, 5020 Bergen, Norway

[34] Department of Zoology, Faculty of Biology, Green Building, Avenue Reina Mercedes, 41012 Seville, Spain

[35] Vermont Center for Ecostudies, PO Box 420, Norwich, 05055 Vermont, USA

[36] USGS Alaska Science Center, 4210 University Drive, Anchorage, Alaska 99508, USA

[37] Department of Evolutionary Biology, Faculty of Biology and Environmental Sciences, Cardinal Stefan Wyszyński University in Warsaw, Wóycickiego 1/3, PL-01-938 Warsaw, Poland

[38] Rua da Esperanca 43/3D, 1200-655 Lisbon, Portugal

[39] Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, C/ Catedrático José Beltrán 2, E-46980 Paterna, València, Spain

[40] Kritzmower Weg 1, 18198 Stäbelow, Germany

[41] Department of Integrative Biology, University of Guelph, 50 Stone Rd E, Guelph, ON N1G 2W1, Canada

[42] Centre for Polar Ecology, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic

[43] University of New England, Department of Environmental Studies, 11 Hills Beach Rd, Biddeford, Maine, USA

[44] Finnish Museum of Natural History LUOMUS, University of Helsinki, PO Box 17, 00014 Helsinki, Finland

[45] Russian Academy of Sciences, Arctic Research Station of Institute of Plant and Animal Ecology, Ural Branch, Zelenaya Gorka Str. 21, 629400 Labytnangi, Russia

[46] Arctic Research Center of Yamal-Nenets Autonomous District, Respublika str. 73, 629008 Salekhard, Russia

[47] Tokai University Sapporo Campus, Minamisawa 5-1-1-1, Minami-ku, Sapporo, Hokkaido 005-8601, Japan

[48] Menckestraße 34, 04155 Leipzig, Germany

[49] Oenanthe Ecologie, Hollandseweg 42, 6706 KR Wageningen, The Netherlands

[50] Institute for Water and Wetland Research, Animal Ecology, Physiology & Experimental Plant Ecology, Radboud University, PO Box 9100, 6500 GL Nijmegen, The Netherlands

[51] Institute of Biology, Department of Chemistry – Biology, Faculty of Science and Technology, University of Siegen, Adolf-Reichwein-Str. 2, 57076 Siegen, Germany

[52] Wildlife Preservation Canada, 5420 Highway 6 North, Guelph, Ontario N1H 6J2, Canada

[53] Ecology Research & Consultancy, Dantelaan 115, 3533 VC Utrecht, The Netherlands

[54] School of Biological Sciences, The University of Queensland, Brisbane, Queensland, Australia

ORCID

Vojtěch Brlík: https://orcid.org/0000-0002-7902-8123

Jaroslav Koleček: https://orcid.org/0000-0003-1069-6593

Malcolm Burgess: https://orcid.org/0000-0003-1288-1231

Steffen Hahn: https://orcid.org/ 0000-0002-4924-495X

Miloš Krist: https://orcid.org/0000-0002-6183-686X

Janne Ouwehand: https://orcid.org/0000-0003-2573-6287

Emily L. Weiser: https://orcid.org/0000-0003-1598-659X

Peter Adamík: https://orcid.org/0000-0003-1566-1234

Debora Arlt: https://orcid.org/0000-0003-0874-4250

Sanja Barišić: https://orcid.org/0000-0003-3472-3285

Eduardo J. Belda: https://orcid.org/0000-0003-1995-1271

Christiaan Both: https://orcid.org/0000-0001-7099-9831

Martins Briedis: https://orcid.org/0000-0002-9434-9056

Davor Ćiković: https://orcid.org/0000-0002-3234-0574

Joana S. Costa: https://orcid.org/0000-0002-1532-8936

Tamara Emmenegger: https://orcid.org/0000-0002-2839-6129

Olivier Gilg: https://orcid.org/0000-0002-9083-4492

Chris Hewson: https://orcid.org/0000-0002-8493-5203

Frédéric Jiguet: orcid.org/0000-0002-0606-7332

Terje Lislevand: https://orcid.org/0000-0003-1281-7061

Piotr Matyjasiak: https://orcid.org/0000-0003-0384-2935

Kent McFarland: https://orcid.org/0000-0001-7809-5503

Christoph M. Meier: https://orcid.org/0000-0001-9584-2339

Tomas Pärt: https://orcid.org/0000-0001-7388-6672

Markus Piha: https://orcid.org/0000-0002-8482-6162

Jeroen Reneerkens: https://orcid.org/0000-0003-0674-8143

Arndt H. J. Wellbrock: https://orcid.org/0000-0001-9929-7091

Klaudia Witte: https://orcid.org/0000-0002-2812-9936

Petr Procházka: https://orcid.org/0000-0001-9385-4547

Running head: Geolocator effects on small birds

Word count: 11099 words

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, 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 with bigger clutches and multiple broods.
5. In conclusion, we found 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 samples of mainly larger species where the same additional relative load affects flight performance more than in smaller species (Caccamise & Hedin, 1985). 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 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 phylogenetical 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 2017. 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 31 August 2018. 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. 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 effects 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. We then used the *mulTree* function from the mulTree package (Guillerme & Healy, 2017) to automatically fit a MCMCglmm model on each phylogenetical tree we sampled and summarized the results from all these models to obtain phylogenetically controlled overall effect size estimates. We used weakly informative inverse-gamma priors (V = 1, nu = 0.002) in all models. 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 phylogenetical 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 (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, an ecological model and models of publication bias. 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. 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 body and egg mass, clutch size and number of broods (Fig. S3). The PC2 explained 18.7% of variance and was characterised mainly by clutch sizes, number of broods and migration distances (Fig. S3). 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. 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. Because the phylogenetical relatedness of the species explained only a small amount of variation, we did not control for phylogeny in the multivariate models but incorporated the random effect of species and study site. 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. S4). 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 factor 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. S5) and the data contained information about 7,829 tagged and 17,834 control individuals of 69 species from 27 families and 7 orders (Table S6).

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. Although we found no statistically significant overall tagging effects in any trait category when controlling for phylogenetical relatedness, the estimates were similar to those not controlled for phylogeny (Fig. 1). The phylogenetical signal (H^2 = 59%) was statistically significant only for apparent survival, but the variance explained by phylogeny and species were very low for all models (Table S7).

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 effect of the control group type, sex, stalk length, foraging strategy or the interaction between stalk length and foraging strategy (Table 3). The ecological model suggested a relationship of apparent survival with the PC1, with negative effects being stronger with decreasing body and egg mass, increasing clutch size and in species having multiple broods (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. S4), 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

(Table S8). 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 with bigger clutches and multiple broods.

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 bigger clutches and multiple broods. 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 the 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 the size of every captured individual, they may be in the end more tightly fitted as some researches might tend to tag larger individuals or avoid too loose harnesses to prevent geolocator loss. 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 impact on tagging effect

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. All future studies should carefully set matched controls and transparently report on tagging effects. Finally, our results encourage further 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.

Acknowledgements

We thank James W. Fox (Migrate Technology), the Swiss Ornithological Institute, and Biotrack, Lotek employees for circulating the call for sharing the unpublished study results among their customers and Rien van Wijk for sharing our inquiry for unpublished data among the Migrant Landbird Study Group members. We are grateful to Carlos Camacho, Vladimir G. Grinkov, Helene M. Lampe, Ken Otter, Jaime Potti, Milica Požgayová, Scott M. Ramsay and Helmut Sternberg for providing unpublished data and to Marie Hánová for extracting part of the species-specific life-history data. We thank Adéla Stupková for the graphics and Martin Sládeček for valuable comments on the first version of the manuscript. The fieldwork in Greenland and Russia (Yamal Peninsula) was supported by the French Polar Institute (IPEV, program 1036 “Interactions”). The fieldwork of DK was supported by a Leverhulme Trust research grant to Richard Holland (RPG-2013288). The study was funded by the Czech Science Foundation (project no. 13-06451S) and by the Institutional Research Plan (RVO: 68081766). We are grateful to the funders, supporters and researchers of the many studies included herein.

Data accessibility

Dataset available in figshare https://doi.org/XXX (Brlík et al., XXXX).

References

Adams, J., Scott, D., McKechnie, S., Blackwell, G., Shaffer, S. A., & Moller, H. (2009). Effects of geolocation archival tags on reproduction and adult body mass of sooty shearwaters (*Puffinus griseus*). *New Zealand Journal of Zoology*, *36*, 355–366. https://doi.org/10.1080/03014220909510160

Arlt, D., Low, M., & Pärt, T. (2013). Effect of geolocators on migration and subsequent breeding performance of a long-distance passerine migrant. *PLoS ONE*, *8*, e82316. https://doi.org/10.1371/journal.pone.0082316

Bairlein, F., Norris, D. R., Nagel, R., Bulte, M., Voigt, C. C., Fox, J., … Schmalljohann, H. (2012). Cross-hemisphere migration of a 25 g songbird. *Biology Letters*, *8*, 505–507. https://doi.org/10.1098/rsbl.2011.1223

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. https://doi.org/10.1111/j.2041-210X.2010.00013.x

Bell, S. C., Harouchi, M. E. L., Hewson, C. M., & Burgess, M. D. (2017). No short- or long-term effects of geolocator attachment detected in Pied Flycatchers *Ficedula hypoleuca*. *Ibis*, *159*, 734–743. https://doi.org/10.1111/ibi.12493

Blackburn, E., Burgess, M., Freeman, B., Risely, A., Izang, A., Ivande, S., … Cresswell, W. (2016). An experimental evaluation of the effects of geolocator design and attachment method on between-year survival on Whinchats *Saxicola rubetra*. *Journal of Avian Biology*, *47*, 530–539. https://doi.org/10.1111/jav.00871

Bodey, T. W., Cleasby, I. R., Bell, F., Parr, N., Schultz, A., Votier, S. C., & 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 in Ecology and Evolution*, *9*, 946–955. https://doi.org/10.1111/2041-210X.12934

Bodey, T. W., Cleasby, I. R., Bell, F., Parr, N., Schultz, A., Votier, S. C., & 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. *Dryad Digital Depository*, https://doi.org/10.5061/dryad.0rp52

Borenstein, M., Hedges, L. V., Higgins, J. P. T., & Rothstein, H. R. (2009). *Introduction to meta-analysis*. *John Wiley & Sons*. John Wiley & Sons. https://doi.org/10.1002/9780470743386

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*, *1*, 398–402. https://doi.org/10.1111/j.2041-210X.2010.00043.x

Bridge, E. S., Kelly, J. F., Contina, A., Gabrielson, R. M., MacCurdy, R. B., & Winkler, D. W. (2013). Advances in tracking small migratory birds: A technical review of light-level geolocation. *Journal of Field Ornithology*, *84*, 121–137. https://doi.org/10.1111/jofo.12011

Brlík, V., Koleček, J., Burgess, M. D., Hahn, S., Humple, D., Krist, M., … Procházka, P. (XXXX). Data from: Weak effect of geolocators on small birds: a meta-analysis controlled for phylogeny and potential publication bias. *figshare*, https://doi.org/XXX

Caccamise, D. F., & Hedin, R. S. (1985). An aerodynamic basis for selecting transmitter loads in birds. *The Wilson Bulletin*, *97*, 306–318.

Costantini, D., & Møller, A. P. (2013). A meta-analysis of the effects of geolocator application on birds. *Current Zoology*, *59*, 697–706. https://doi.org/10.1093/czoolo/59.6.697

Cramp, S., Perrins, C. M., (1977–1994). The birds of the Western Palearctic. Volumes 1–9. Oxford, UK: Oxford University Press.

Del Re, A. C. (2013). compute.es: Compute effect sizes. R package version 0.2-2. URL: https://cran.r-project.org/web/packages/compute.es/index.html

Doncaster, C. P., & Spake, R. (2018). Correction for bias in meta-analysis of little-replicated studies. *Methods in Ecology and Evolution*, *9*, 634–644. https://doi.org/10.1111/2041-210X.12927

Elliott, K. H., McFarlane, L., Burke, C. M., Hedd, A., Montevecchi, W. A., & Anderson, W. G. (2012). Year-long deployments of small geolocators increase corticosterone levels in murres. *Marine Ecology Progress Series, 466*, 1–7. https://doi.org/10.3354/meps09975

Fairhurst, G. D., Berzins, L. L., David, W., Laughlin, A. J., Romano, A., Romano, M., … Clark, R. G. (2015). Assessing costs of carrying geolocators using feather corticosterone in two species of aerial insectivore. *Royal Society Open Science*, *2*, 150004. https://doi.org/10.1098/rsos.150004

Guillerme, T., & Healy, K. (2017). mulTree: Performs MCMCglmm on multiple phylogenetic trees. R package version 1.3.1. https://github.com/TGuillerme/mulTree

Hackett, S., Kimball, R., Reddy, S., Bowie, R., Braun, E., Braun, M., … Yuri, T. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science*, *320*, 1763–1768. https://doi.org/10.1126/science.1157704

Hadfield, J. D. (2010). MCMC methods for multi-response generalized linear mixed models: The MCMCglmm R package. *Journal of Statistical Software*, *33*, 1–22.

Hadfield, J. D., & Nakagawa, S. (2010). General quantitative genetic methods for comparative biology: Phylogenies, taxonomies and multi-trait models for continuous and categorical characters. *Journal of Evolutionary Biology*, *23*, 494–508. https://doi.org/10.1111/j.1420-9101.2009.01915.x

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, *491*, 444–448. https://doi.org/10.1038/nature11631

Jewell, Z. (2013). Effect of monitoring technique on quality of conservation science. *Conservation Biology*, *27*(3), 501–508. https://doi.org/10.1111/cobi.12066

Koricheva, J., Gurevitch, J., & Mengersen, K. (2013). *Handbook of meta-analysis in ecology and evolution*. Princeton University Press.

Lislevand, T., Chutný, B., Byrkjedal, I., Pavel, V., Briedis, M., Adamík, P., & Hahn, S. (2015). Red-spotted Bluethroats *Luscinia s. svecica* migrate along the Indo-European flyway: a geolocator study. *Bird Study*, *62*, 508–515. https://doi.org/10.1080/00063657.2015.1077781

López-López, J. A., Marín-Martínez, F., Sánchez-Meca, J., Van den Noortgate, W., & Viechtbauer, W. (2014). Estimation of the predictive power of the model in mixed-effects meta-regression: A simulation study. *British Journal of Mathematical and Statistical Psychology*, *67*, 30–48. https://doi.org/10.1111/bmsp.12002

McKinnon, E. A., & Love, O. P. (2018). Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging. *The Auk*, *135*, 834–856. https://doi.org/10.1642/AUK-17-202.1

Morganti, M., Rubolini, D., Åkesson, S., Bermejo, A., de la Puente, J., Lardelli, R., … Ambrosini, R. (2018). Effect of light-level geolocators on apparent survival of two highly aerial swift species. *Journal of Avian Biology*, *49*, jav-01521. https://doi.org/10.1111/jav.01521

Naef-Daenzer, B. (2007). An allometric function to fit leg-loop harnesses to terrestrial birds. *Journal of Avian Biology*, *38*, 404–407. https://doi.org/10.1111/j.2007.0908-8857.03863.x

Nakagawa, S., & Santos, E. S. A. (2012). Methodological issues and advances in biological meta-analysis.

Evolutionary Ecology, *26*, 1253–1274. https://doi.org/10.1007/s10682-012-9555-5

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

Patchett, R., Finch, T., & Cresswell, W. (2018). Population consequences of migratory variability differ between flyways. *Current Biology*, *28*, R340–R341. https://doi.org/10.1016/j.cub.2018.03.018

Pennycuick, C. J., Fast, P. L. F., Ballerstädt, N., & Rattenborg, N. (2012). The effect of an external transmitter on the drag coefficient of a bird’s body, and hence on migration range, and energy reserves after migration. *Journal of Ornithology*, *153*, 633–644. https://doi.org/10.1007/sl0336-011-0781-3

Peterson, S. M., Streby, H. M., Kramer, G. R., Lehman, J. a., Buehler, D. a., & Andersen, D. E. (2015). Geolocators on Golden-winged Warblers do not affect migratory ecology. *The Condor*, *117*, 256–261. https://doi.org/10.1650/CONDOR-14-200.1

Portugal, S. J., & White, C. R. (2018). Miniaturisation of biologgers is not alleviating the 5% rule. *Methods in Ecology and Evolution*, *9*, 1662–1666. https://doi.org/10.1111/2041-210X.13013

R Core Team 2018. R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. URL: https://www.R-project.org/

Rodewald, P. (2015). The birds of North America. Cornell Laboratory of Ornithology, Ithaca, NY. URL: https://birdsna.org

Sánchez-Tójar, A., Nakagawa, S., Sánchez-Fortún, M., Martin, D. A., Ramani, S., Girndt, A., … Schroeder, J. (2018). Meta-analysis challenges a textbook example of status signalling: evidence for publication bias. *BioRχiv*, 1–41. https://doi.org/10.1101/283150

Saraux, C., Le Bohec, C., Durant, J. M., Viblanc, V. A., Gauthier-Clerc, M., Beaune, D., … Le Maho, Y. (2011). Reliability of flipper-banded penguins as indicators of climate change. *Nature*, *469*, 203–206. https://doi.org/10.1038/nature09630

Scandolara, C., Rubolini, D., Ambrosini, R., Caprioli, M., Hahn, S., Liechti, F., … Saino, N. (2014). Impact of miniaturized geolocators on barn swallow *Hirundo rustica* fitness traits. *Journal of Avian Biology*, *45*, 417–423. https://doi.org/10.1111/jav.00412

Schacter, C. R., & Jones, I. L. (2017). Effects of geolocation tracking devices on behavior, reproductive success, and return rate of *Aethia* auklets: An evaluation of tag mass guidelines. *The Wilson Journal of Ornithology*, *129*, 459–468. https://doi.org/10.1676/16-084.1

Schmaljohann, H., Buchmann, M., Fox, J. W., & Bairlein, F. (2012). Tracking migration routes and the annual cycle of a trans-Sahara songbird migrant. *Behavioral Ecology and Sociobiology*, *66*, 915–922. https://doi.org/10.1007/s00265-012-1340-5

Schönwetter, M. (1960–1992). Handbuch der Oologie. Akademie Verlag, Berlin.

Schwarzer, G., Carpenter, J. R., & Rücker, G. (2014). *Meta-analysis with R*. Springer. https://doi.org/10.1007/978-3-319-21416-0

Snijders, L., Nieuwe Weme, L. E., De Goede, P., Savage, J. L., Van Oers, K., & Naguib, M. (2017). Context-dependent effects of radio transmitter attachment on a small passerine. *Journal of Avian Biology*, *48*, 650–659. https://doi.org/10.1111/jav.01148

Stach, R., Kullberg, C., Jakobsson, S., Ström, K., & Fransson, T. (2016). Migration routes and timing in a bird wintering in South Asia, the Common Rosefinch *Carpodacus erythrinus*. *Journal of Ornithology*, *157*, 756–767. https://doi.org/10.1007/s10336-016-1329-3

Stanley, C. Q., MacPherson, M., Fraser, K. C., McKinnon, E. A., & Stutchbury, B. J. M. (2012). Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. *PLoS ONE*, *7*, e40688. https://doi.org/10.1371/journal.pone.0040688

Streby, H. M., McAllister, T. L., Peterson, S. M., Kramer, G. R., Lehman, J. a., & Andersen, D. E. (2015). Minimizing marker mass and handling time when attaching radio-transmitters and geolocators to small songbirds. *The Condor*, *117*, 249–255. https://doi.org/10.1650/CONDOR-14-182.1

Sweeting, M. J., Sutton, A. J., & Lambert, P. C. (2004). What to add to nothing? Use and avoidance of continuity corrections in meta-analysis of sparse data. *Statistics in Medicine*, *23*, 1351–1375. https://doi.org/10.1002/sim.1761

Trefry, S. A., Diamond, A. W., & Jesson, L. K. (2012). Wing marker woes: a case study and meta-analysis of the impacts of wing and patagial tags. *Journal of Ornithology*, *154*, 1–11. https://doi.org/10.1007/s10336-012-0862-y

van Wijk, R. E., Souchay, G., Jenni-Eiermann, S., Bauer, S., & Schaub, M. (2015). No detectable effects of lightweight geolocators on a Palaearctic-African long-distance migrant. *Journal of Ornithology*, *157*, 255–264. https://doi.org/10.1007/s10336-015-1274-6

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal Of Statistical Software*, *36*, 1–48.

Weimerskirch, H., Bonadonna, F., Bailleul, F., Mabille, G., Dell'Omo, G., & Lipp, H.-P. (2002). GPS tracking of foraging albatrosses. *Science*, *295*, 1259. https://doi.org/10.1126/science.1068034

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. *Movement Ecology*, *4*, 12. https://doi.org/10.1186/s40462-016-0077-6

Wilson, R. P., & McMahon, C. R. (2006). Measuring devices on wild animals: what constitutes acceptable practice? *Frontiers in Ecology and the Environment*, *4*, 147–154. https://doi.org/10.1890/1540-9295(2006)004[0147:MDOWAW]2.0.CO;2

Wilson, R. P., Sala, J. E., Gómez-Laich, A., Ciancio, J., & Quintana, F. (2015). Pushed to the limit: Food abundance determines tag-induced harm in penguins. *Animal Welfare*, *24*, 37–44. https://doi.org/10.7120/09627286.24.1.037

Published Data Sources

Alonso, D., Arizaga, J., Meier, C. M., & Liechti, F. (2017). Light-level geolocators confirm resident status of a Southern European Common Crossbill population. *Journal of Ornithology*, *158*, 75–81. https://doi.org/10.1007/s10336-016-1388-5

Arbeiter, S., Schulze, M., Todte, I., & Hahn, S. (2012). Das Zugverhalten und die Ausbreitung von in Sachsen-Anhalt brütenden Bienenfressern (Merops apiaster). *Berichte Der Vogelwarte Hiddensee*, *21*, 33–41.

Arlt, D., Low, M., & Pärt, T. (2013). Effect of geolocators on migration and subsequent breeding performance of a long-distance passerine migrant. *PLoS ONE*, *8*, e82316. https://doi.org/10.1371/journal.pone.0082316

Arlt, D., Olsson, P., Fox, J. W., Low, M., & Pärt, T. (2015). Prolonged stopover duration characterises migration strategy and constraints of a long-distance migrant songbird. *Animal Migration*, *2*, 47–62. https://doi.org/10.1515/ami-2015-0002

Bächler, E., Hahn, S., Schaub, M., Arlettaz, R., Jenni, L., Fox, J. W., … Liechti, F. (2010). Year-round tracking of small trans-Saharan migrants using light-level geolocators. *PLoS ONE*, *5*, e9566. https://doi.org/10.1371/journal.pone.0009566

Bairlein, F., Norris, D. R., Nagel, R., Bulte, M., Voigt, C. C., Fox, J., … Schmalljohann, H. (2012). Cross-hemisphere migration of a 25 g songbird. *Biology Letters*, *8*, 505–507. https://doi.org/10.1098/rsbl.2011.1223

Bell, S. C., Harouchi, M. E. L., Hewson, C. M., & Burgess, M. D. (2017). No short- or long-term effects of geolocator attachment detected in Pied Flycatchers *Ficedula hypoleuca*. *Ibis*, *159*, 734–743. https://doi.org/10.1111/ibi.12493

Blackburn, E., Burgess, M., Freeman, B., Risely, A., Izang, A., Ivande, S., … Cresswell, W. (2016). An experimental evaluation of the effects of geolocator design and attachment method on between-year survival on Whinchats *Saxicola rubetra*. *Journal of Avian Biology*, *47*, 530–539. https://doi.org/10.1111/jav.00871

Bravo, S. P., Cueto, V. R., & Andre, C. (2017). Migratory timing, rate, routes and wintering areas of White-crested Elaenia (*Elaenia albiceps chilensis*), a key seed disperser for Patagonian forest regeneration. *PLoS ONE*, *12*, e0170188. https://doi.org/10.1371/journal.pone.0170188

Briedis, M., Beran, V., Hahn, S., & Adamík, P. (2016). Annual cycle and migration strategies of a habitat specialist, the Tawny Pipit *Anthus campestris*, revealed by geolocators. *Journal of Ornithology*, *157*, 619–626. https://doi.org/10.1007/s10336-015-1313-3

Briedis, M., Hahn, S., Gustafsson, L., Henshaw, I., Träff, J., Král, M., & Adamík, P. (2016). Breeding latitude leads to different temporal but not spatial organization of the annual cycle in a long-distance migrant. *Journal of Avian Biology*, *47*, 743–748. https://doi.org/10.1111/jav.01002

Briedis, M., Träff, J., Hahn, S., Ilieva, M., Král, M., Peev, S., & Adamík, P. (2016). Year-round spatiotemporal distribution of the enigmatic Semi-collared Flycatcher *Ficedula semitorquata*. *Journal of Ornithology*, *157*, 895–900. https://doi.org/10.1007/s10336-016-1334-6

Brlík, V., Ilieva, M., Lisovski, S., Voigt, C. C., & Procházka, P. (2018). First insights into the migration route and migratory connectivity of the Paddyfield Warbler using geolocator tagging and stable isotope analysis. *Journal of Ornithology*, *159*, 879–882. https://doi.org/10.1007/s10336-018-1557-9

Callo, P. A., Morton, E. S., & Stutchbury, B. J. M. (2013). Prolonged spring migration in the Red-eyed Vireo (*Vireo olivaceus*). *The Auk*, *130*, 240–246. https://doi.org/10.1525/auk.2013.12213

Cooper, N. W., Hallworth, M. T., & Marra, P. P. (2017). Light-level geolocation reveals wintering distribution, migration routes, and primary stopover locations of an endangered long-distance migratory songbird. *Journal of Avian Biology*, *48*, 209–2019. https://doi.org/10.1111/jav.01096

Cormier, R. L., Humple, D. L., Gardali, T., & Seavy, N. E. (2013). Light-level geolocators reveal strong migratory connectivity and within-winter movements for a coastal California Swainson’s thrush (*Catharus ustulatus*) population. *The Auk*, *130*, 283–290. https://doi.org/10.1525/auk.2013.12228

Cormier, R. L., Humple, D. L., Gardali, T., & Seavy, N. E. (2016). Migratory connectivity of Golden-crowned Sparrows from two wintering regions in California. *Animal Migration*, *3*, 48–56. https://doi.org/10.1515/ami-2016-0005

Cresswell, B., & Edwards, D. (2013). Geolocators reveal wintering areas of European Nightjar (*Caprimulgus europaeus*). *Bird Study*, *60*, 77–86. https://doi.org/10.1080/00063657.2012.748714

DeLuca, W. V., Woodworth, B. K., Rimmer, C. C., Marra, P. P., Taylor, P. D., McFarland, K. P., … Norris, D. R. (2015). Transoceanic migration by a 12 g songbird. *Biology Letters*, *11*, 20141045. https://doi.org/10.1098/rsbl.2014.1045

Evens, R., Convay, G. J., Henderson, I. G., Creswell, W., Jiguet, F., Moussy, C., … Artois, T. (2017). Migratory pathways, stopover zones and wintering destinations of Western European Nightjars *Caprimulgus europaeus*. *Ibis*, *159*, 680–686. https://doi.org/10.1111/ijlh.12426

Fairhurst, G. D., Berzins, L. L., Bradley, D. W., Laughlin, A. J., Romano, A., Romano, M., … Clark, R. G. (2015). Assessing costs of carrying geolocators using feather corticosterone in two species of aerial insectivore. *Royal Society Open Science*, *2*, 150004. https://doi.org/10.1098/rsos.150004

Fairhurst, G. D., Berzins, L. L., Bradley, D. W., Laughlin, A. J., Romano, A., Romano, M., … Clark, R. G. (2015). Data from: Assessing costs of carrying geolocators using feather corticosterone in two species of aerial insectivore. *Dryad Digital Repository,* https://doi.org/10.5061/dryad.sq184

Fraser, K. C., Cousens, B., Simmons, M., Nightingale, A., Cormier, L., Humple, D. L., & Shave, A. C. (2018). Classic pattern of leapfrog migration in Sooty Fox Sparrow (*Passerella iliaca unalaschcensis*) is not supported by direct migration tracking of individual birds. *Auk*, *135*, 572–582. https://doi.org/10.1642/AUK-17-224.1

Fraser, K. C., Stutchbury, B. J. M., Silverio, C., Kramer, P. M., Barrow, J., Newstead, D., … Tautin, J. (2012). Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. *Proceedings of the Royal Society B-Biological Sciences*, *279*, 4901–4906. https://doi.org/10.1098/rspb.2012.2207

Gersten, A., & Hahn, S. (2016). Timing of migration in Common Redstarts (*Phoenicurus phoenicurus*) in relation to the vegetation phenology at residence sites. *Journal of Ornithology*, *157*, 1029–1036. https://doi.org/10.1007/s10336-016-1359-x

Gómez, J., Michelson, C. I., Bradley, D. W., Ryan Norris, D., Berzins, L. L., Dawson, R. D., & Clark, R. G. (2014). Effects of geolocators on reproductive performance and annual return rates of a migratory songbird. *Journal of Ornithology*, *155*, 37–44. https://doi.org/10.1007/s10336-013-0984-x

Hallworth, M. T., Sillett, T. S., Van Wilgenburg, S. L., Hobson, K. A., & Marra, P. P. (2015). Migratory connectivity of a neotropical migratory songbird revealed by archival light-level geolocators. *Ecological Applications*, *25*, 336–347. https://doi.org/10.1890/14-0195.1

Heckscher, C. M., Taylor, S. M., Fox, J. W., & Afanasyev, V. (2011). Veery (*Catharus fuscescens*) wintering locations, migratory connectivity, and a revision of its winter range using geolocator technology. *The Auk*, *128*, 531–542. https://doi.org/10.1525/auk.2011.10280

Horns, J., Buechley, E., Chynoweth, M., Aktay, L., Çoban, E., Kırpık, M., … Şekercioğlu, Ç. H. (2016). Geolocator tracking of great reed warbler (*Acrocephalus arundinaceus*) identifies key regions of importance to migratory wetland specialist throughout the Middle East and Sub-Saharan Africa. *The Condor*, *118*, 835–849. https://doi.org/10.1650/CONDOR-16-63.1

Jimenéz, J. E., Jahn, A. E., Rozzi, R., & Seavy, N. E. (2016). First documented migration of individual White-Crested Elaenias (*Elaenia albiceps chilensis*) in South America. *The Wilson Journal of Ornithology*, *128*, 419–425. https://doi.org/10.1163/187529271X00756

Johnson, J. A., Matsuoka, S. M., Tessler, D. F., Greenberg, R., & Fox, J. W. (2012). Identifying migratory pathways used by Rusty Blackbirds breeding in southcentral Alaska. *The Wilson Journal of Ornithology*, *124*, 698–703. https://doi.org/10.1676/1559-4491-124.4.698

Koleček, J., Procházka, P., El-Arabany, N., Tarka, M., Ilieva, M., Hahn, S., … Hansson, B. (2016). Cross-continental migratory connectivity and spatiotemporal migratory patterns in the great reed warbler. *Journal of Avian Biology*, *47*, 756–767. https://doi.org/10.1111/jav.00929

Laughlin, A. J., Taylor, C. M., Bradley, D. W., LeClair, D., Clark, R. G., Dawson, R. D., … Norris, D. R. (2013). Integrating information from geolocators, weather radar, and citizen science to uncover a key stopover area of an aerial insectivore. *The Auk*, *130*, 230–239. https://doi.org/10.1525/auk.2013.12229

Lemke, H. W., Tarka, M., Klaassen, R. H. G., Åkesson, M., Bensch, S., Hasselquist, D., & Hansson, B. (2013). Annual cycle and migration strategies of a trans-Saharan migratory songbird: A geolocator study in the great reed warbler. *PLoS ONE*, *8*, e79209. https://doi.org/10.1371/journal.pone.0079209

Liechti, F., Scandolara, C., Rubolini, D., Ambrosini, R., Korner-Nievergelt, F., Hahn, S., … Saino, N. (2015). Timing of migration and residence areas during the non-breeding period of barn swallows *Hirundo rustica* in relation to sex and population. *Journal of Avian Biology*, *46*, 254–265. https://doi.org/10.1111/jav.00485

Liechti, F., Witvliet, W., Weber, R., & Bächler, E. (2013). First evidence of a 200-day non-stop flight in a bird. *Nature Communications*, *4*, 2554. https://doi.org/10.1038/ncomms3554

Lislevand, T., Briedis, M., Heggøy, O., & Hahn, S. (2016). Seasonal migration strategies of Common Ringed Plovers *Charadrius hiaticula*. *Ibis*, *159*, 225–229. https://doi.org/10.1111/ibi.12424

Lislevand, T., Chutný, B., Byrkjedal, I., Pavel, V., Briedis, M., Adamík, P., & Hahn, S. (2015). Red-spotted Bluethroats *Luscinia s. svecica* migrate along the Indo-European flyway: a geolocator study. *Bird Study*, *62*, 508–515. https://doi.org/10.1080/00063657.2015.1077781

Lislevand, T., & Hahn, S. (2013). Effects of geolocator deployment by using flexible leg-loop harnesses in a small wader. *Wader Study Group Bulletin*, *120*, 108–113.

Macdonald, C. A., Mckinnon, E. A., Gilchrist, H. G., & Love, O. P. (2016). Cold tolerance, and not earlier arrival on breeding grounds, explains why males winter further north in an Arctic-breeding songbird. *Journal of Avian Biology*, *47*, 7–15. https://doi.org/10.1111/jav.00689

Matyjasiak, P., Rubolini, D., Romano, M., & Saino, N. (2016). No short-term effects of geolocators on flight performance of an aerial insectivorous bird, the Barn Swallow (*Hirundo rustica*). *Journal of Ornithology*, *157*, 653–661. https://doi.org/10.1007/s10336-015-1314-2

McNeil, S. E. M., Tracy, D., & Cappello, C. D. (2015). Loop migration by a Western Yellow-billed Cuckoo wintering in the gran chaco. *Western Birds*, *46*, 244–255.

Meier, C. M., Karaard, H., Aymí, R., Peev, S. G., Bächler, E., Weber, R., … Liechti, F. (2018). What makes Alpine swift ascend at twilight? Novel geolocators reveal year-round flight behaviour. *Behavioral Ecology and Sociobiology*, *72*, 45. https://doi.org/10.1007/s00265-017-2438-6

Minton, C., Gosbell, K., Johns, P., Christie, M., Klaassen, M., Hassell, C., … Fox, J. (2013). New insights from geolocators deployed on waders in Australia. *Wader Study Group Bulletin*, *120*, 37–46.

Minton, C., Gosbell, K., Johns, P., Christie, M., Klaassen, M., Hassell, C., … Fox, J. W. (2011). Geolocator studies on Ruddy Turnstones *Arenaria interpres* and Greater Sandplovers *Charadrius leschenaultii* in the East Asian- Australasia Flyway reveal widely different migration strategies. W*ader Study Group Bulletin*, *118*, 87–96.

Nelson, A. R., Cormier, R. L., Humple, D. L., Scullen, J. C., Sehgal, R., & Seavy, N. E. (2016). Migration patterns of San Francisco Bay Area Hermit Thrushes differ across a fine spatial scale. *Animal Migration*, *3*, 1–13. https://doi.org/10.1515/ami-2016-0001

Norevik, G., Åkesson, S., & Hedenström, A. (2017). Migration strategies and annual space-use in an Afro-Palaearctic aerial insectivore – the European nightjar. *Journal of Avian Biology*, *48*, 738–747. https://doi.org/10.1111/jav.01071

Ouwehand, J., Ahola, M. P., Ausems, A. N. M. A., Bridge, E. S., Burgess, M., Hahn, S., … Both, C. (2016). Light-level geolocators reveal migratory connectivity in European populations of pied flycatchers *Ficedula hypoleuca*. *Journal of Avian Biology*, *47*, 69–83. https://doi.org/10.1111/jav.00721

Ouwehand, J., & Both, C. (2017). African departure rather than migration speed determines variation in spring arrival in pied flycatchers. *Journal of Animal Ecology*, *86*, 88–97. https://doi.org/10.1111/1365-2656.12599

Ouwehand, J., & Both, C. (2017). Data from: African departure rather than migration speed determines variation in spring arrival in pied flycatchers. *Dryad Digital Depository*, https://doi.org/10.5061/dryad.k6q68

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

Perlut, N. G. (2018). Prevalent transoceanic fall migration by a 30-gram songbird, the Bobolink. *The Auk*, *135*, 992–997. https://doi.org/10.1642/AUK-18-56.1

Peterson, S. M., Streby, H. M., Kramer, G. R., Lehman, J. a., Buehler, D. a., & Andersen, D. E. (2015). Geolocators on Golden-winged Warblers do not affect migratory ecology. *The Condor*, *117*, 256–261. https://doi.org/10.1650/CONDOR-14-200.1

Pillar, A. G., Marra, P. P., Flood, N. J., & Reudink, M. W. (2016). Moult migration in Bullock's orioles (*Icterus bullockii*) confirmed by geolocators and stable isotope analysis. *Journal of Ornithology*, *157*, 265–275. https://doi.org/10.1007/s10336-015-1275-5

Procházka, P., Brlík, V., Yohannes, E., Meister, B., Auerswald, J., Ilieva, M., & Hahn, S. (2018). Across a migratory divide: divergent migration directions and non-breeding grounds of Eurasian reed warblers revealed by geolocators and stable isotopes. *Journal of Avian Biology*, *49*, jav-012516. https://doi.org/10.1111/jav.01769

Renfrew, R. B., Kim, D., Perlut, N., Smith, J., Fox, J., & Marra, P. P. (2013). Phenological matching across hemispheres in a long-distance migratory bird. *Diversity and Distributions*, *19*, 1008–1019. https://doi.org/10.1111/ddi.12080

Ross, J. D., Bridge, E. S., Rozmarynowycz, M. J., & Bingman, V. P. (2014). Individual variation in migratory path and behaviour among Eastern Lark Sparrows. *Animal Migration*, *2*, 29–33. https://doi.org/10.2478/ami-2014-0003

Ryder, T. B., Fox, J. W., & Marra, P. P. (2011). Estimating migratory connectivity of Gray Catbirds (*Dumetella carolinensis*) using geolocator and mark—recapture data. *The Auk*, *128*, 448–453. https://doi.org/10.1525/auk.2011.11091

Salewski, V., Flade, M., Poluda, A., Kiljan, G., Liechti, F., Lisovski, S., & Hahn, S. (2013). An unknown migration route of the "globally threatened" Aquatic Warbler revealed by geolocators. *Journal of Ornithology*, *154*, 549–552. https://doi.org/10.1007/s10336-012-0912-5

Scandolara, C., Rubolini, D., Ambrosini, R., Caprioli, M., Hahn, S., Liechti, F., … Saino, N. (2014). Impact of miniaturized geolocators on barn swallow *Hirundo rustica* fitness traits. *Journal of Avian Biology*, *45*, 417–423. https://doi.org/10.1111/jav.00412

Schmaljohann, H., Buchmann, M., Fox, J. W., & Bairlein, F. (2012). Tracking migration routes and the annual cycle of a trans-Sahara songbird migrant. *Behavioral Ecology and Sociobiology*, *66*, 915–922. https://doi.org/10.1007/s00265-012-1340-5

Schmaljohann, H., Meier, C., Arlt, D., Bairlein, F., van Oosten, H., Morbey, Y. E., … Eikenaar, C. (2016). Proximate causes of avian protandry differ between subspecies with contrasting migration challenges. *Behavioral Ecology*, *27*, 321–331. https://doi.org/10.1093/beheco/arv160

Seavy, N. E., Humple, D. L., Cormier, R. L., & Gardali, T. (2012). Establishing the breeding provenance of a temperate-wintering north american passerine, the golden-crowned sparrow, using light-level geolocation. *PLoS ONE*, *7*, e34886. https://doi.org/10.1371/journal.pone.0034886

Sechrist, J., Paxton, E., Ahlers, D., Doster, R., & Ryan, V. M. (2012). One year of migration data for a western yellow-billed cuckoo. *Western Birds*, *43*, 2–11.

Smith, M., Bolton, M., David, J., Summers, R. W., Ellis, P., & Wilson, J. D. (2014). Short communication Geolocator tagging reveals Pacific migration of Red-necked Phalarope *Phalaropus lobatus* breeding in Scotland. *Ibis*, *156*, 870–873. https://doi.org/10.1111/ibi.12196

Stutchbury, B. J. M., Gow, E. A., Done, T., MacPherson, M., Fox, J. W., & Stutchbury, B. J. M. (2010). Effects of post-breeding moult and energetic condition on timing of songbird migration into the tropics. *Proceedings of the Royal Society B: Biological Sciences*, *278*, 131–137. https://doi.org/10.1098/rspb.2010.1220

Stutchbury, B. J. M., Tarof, S. A., Done, T., Gow, E., Kramer, P. M., Tautin, J., … Afanasyev, V. (2009). Tracking long-distance songbird migration by using geolocators. *Science*, *323*, 896. https://doi.org/10.1126/science.1166664

Szép, T., Liechti, F., Nagy, K., Nagy, Z., & Hahn, S. (2017). Discovering the migration and non-breeding areas of sand martins and house martins breeding in the Pannonian basin (central-eastern Europe). *Journal of Avian Biology*, *48*, 114–122. https://doi.org/10.1111/jav.01339

Tøttrup, A. P., Klaassen, H. G., Strandberg, R., Thorup, K., Kristensen, M. W., Jørgensen, P. S., … Alerstam, T. (2012). The annual cycle of a trans-equatorial Eurasian–African passerine migrant: different spatio-temporal strategies for autumn and spring migration. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 1009–1016. https://doi.org/10.1098/rspb.2011.1323

van Oosten, H. H., Versluijs, R., & van Wijk, R. (2014). Twee Nederlandse Tapuiten in de Sahel: trekroutes en winterlocaties ontrafeld. *Limosa*, *87*, 168–172.

van Wijk, R. E., Schaub, M., Tolkmitt, D., Becker, D., & Hahn, S. (2013). Short-distance migration of Wrynecks *Jynx torquilla* from Central European populations. *Ibis*, *155*, 886–890. https://doi.org/10.1111/ibi.12083

van Wijk, R. E., Souchay, G., Jenni-Eiermann, S., Bauer, S., & Schaub, M. (2015). No detectable effects of lightweight geolocators on a Palaearctic-African long-distance migrant. *Journal of Ornithology*, *157*, 255–264. https://doi.org/10.1007/s10336-015-1274-6

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. *Movement Ecology*, *4*, 12. https://doi.org/10.1186/s40462-016-0077-6

Wellbrock, A. H. J., Bauch, C., Rozman, J., & Witte, K. (2017). “Same procedure as last year?” – Repeatedly tracked swifts show individual consistency in migration pattern in successive years. *Journal of Avian Biology*, *48*, 897–903. https://doi.org/10.1111/jav.01251

Woodworth, B. K., Newman, A. E. M., Turbek, S. P., Dossman, B. C., Hobson, K. A., Wassenaar, L. I., … Norris, D. R. (2016). Differential migration and the link between winter latitude, timing of migration, and breeding in a songbird. *Oecologia*, *181*, 413–422. https://doi.org/10.1007/s00442-015-3527-8

Xenophontos, M., Blackburn, E., & Cresswell, W. (2017). Cyprus Wheatears *Oenanthe cypriaca* likely reach sub-Saharan African wintering grounds in a single migratory flight. *Journal of Avian Biology*, *48*, 529–535. https://doi.org/10.1111/jav.01119

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		
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

914 * only used for harness attachments

915 [1] Cramp & Perrins, 1977–1994

916 [2] Rodewald, 2015

917 [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

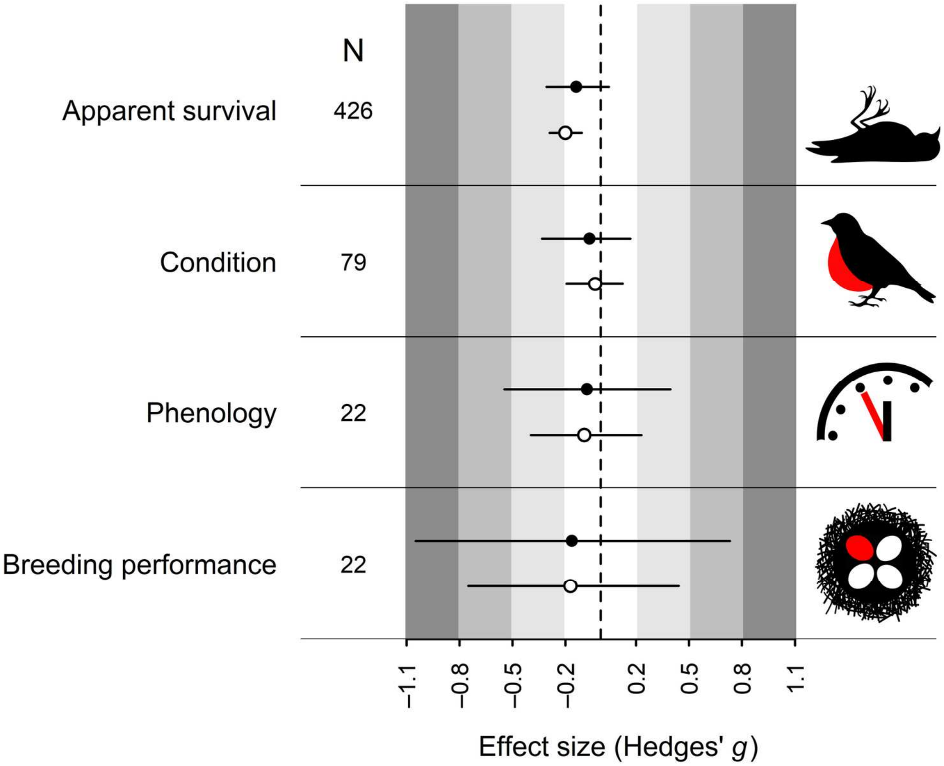

Figure 1. Overall effects of geolocators in the four trait categories, circles give means, horizontal lines represent 95% CrI. Filled symbols present the phylogenetically controlled overall effects, open symbols give the value from null models not accounting for phylogeny. N presents the number of effect sizes analysed. For the detailed description of the trait categories see Methods and Table S2.

85x68mm (600 x 600 DPI)

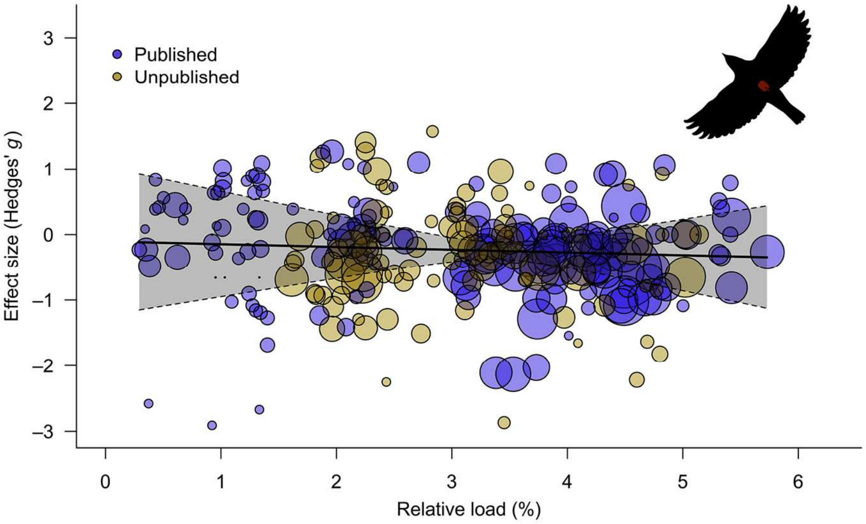

Figure 2. Relationship between relative load and the effect of geolocator deployment on the apparent survival of tagged birds. Size of the circles reflects the precision (1 / mean-adjusted SE) of the effect sizes, the shaded area and dashed lines depict the 95% CI of the regression.

160x91mm (300 x 300 DPI)

SUPPLEMENTARY MATERIALS S1–S8

Figure S1. Flow-chart showing the study selection process and the number of records used for the effect size calculation for both published and unpublished studies. Records are 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.

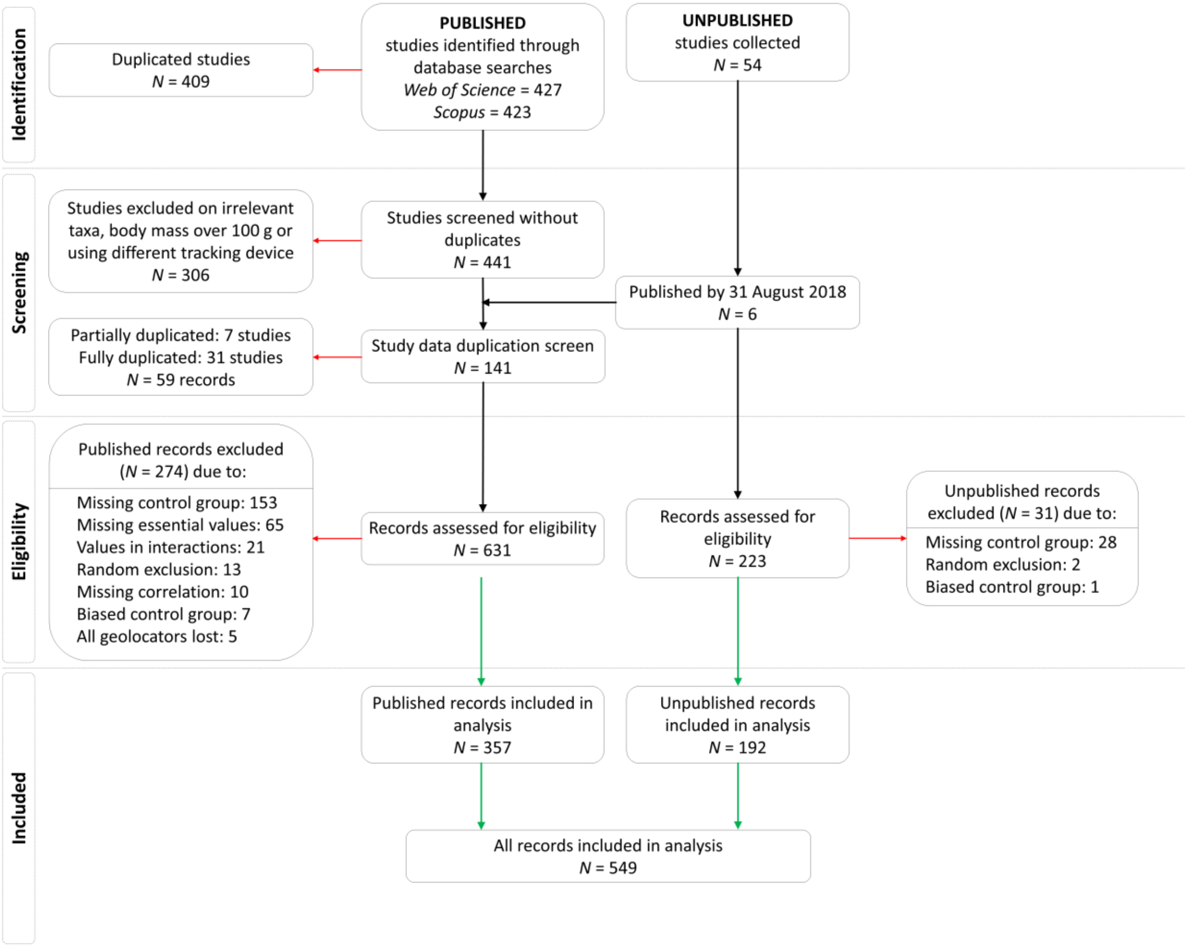

Table S2. Overview on trait categories, the corresponding response variables and their description as well as the number of studies and the number of records (specified as groups of tagged birds from the same study site, year of attachment, of the same sex, and the specific geolocator and attachment type having corresponding control groups).

Trait	*Response variables*	*Description*	*# studies*	*# records*
Apparent survival	Recapture rate	Ratio of recaptured individuals between years	59	287
	Re-encounter rate	Ratio of recaptured or re-sighted individuals between years	40	139
Condition	Change in body mass	Inter-annual changes	36	66
	Feather corticosterone level		1	11
	Arrival body condition	Body condition index (body mass/wing length)	1	1
	Flight speed		1	1
Phenology	Arrival date		7	13
	First egg laying date		6	9
Breeding performance	Clutch size		4	5
	Number of fledglings		4	4
	Hatching success		3	10
	Brood success (nest with at least one fledgling)		2	2
	Inter-annual site fidelity	Inter-annual breeding dispersal distances	1	1

Figure S3. The two most important ordination axes from a principal component analysis (PC1 and PC2), explaining the largest proportion of variability among continuous life-history traits (male and female body mass, egg mass, clutch mass, number of broods per year, clutch size and distance travelled between the breeding and non-breeding grounds; Table 1) for all 69 species included in the analysis. PC1 and PC2 explained 54.4 % and 18.7 % of the variability, respectively.

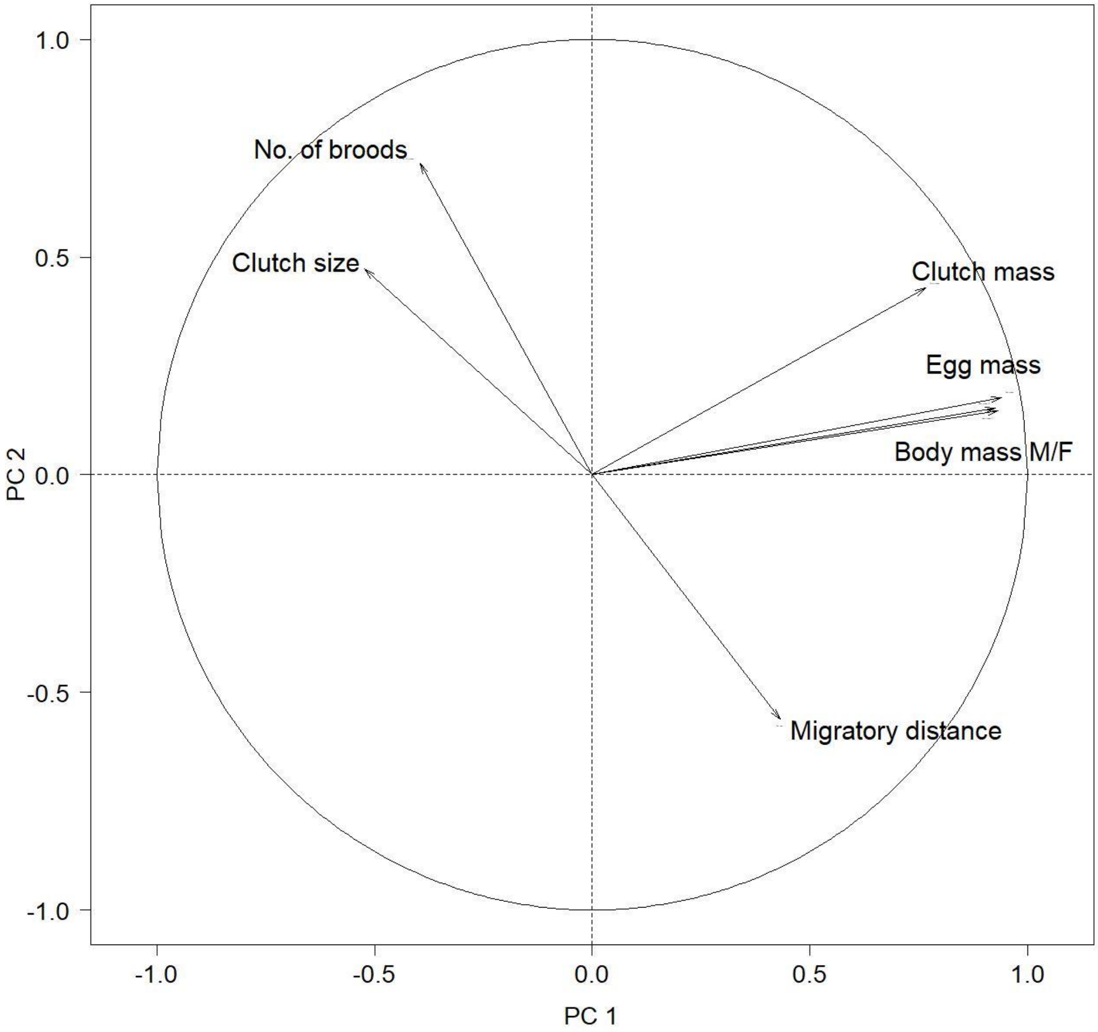

Figure S4. Funnel plots presenting the effect size (Hedges' *g*) against the inverse of the mean-adjusted sampling error in four trait categories. Solid lines present phylogenetically controlled overall effect size and dotted lines 95% CrI. Publication bias in the dataset is indicated by asymmetry of the funnel-shaped scatterplot (Koricheva, Gurevitch, & Mengersen, 2013).

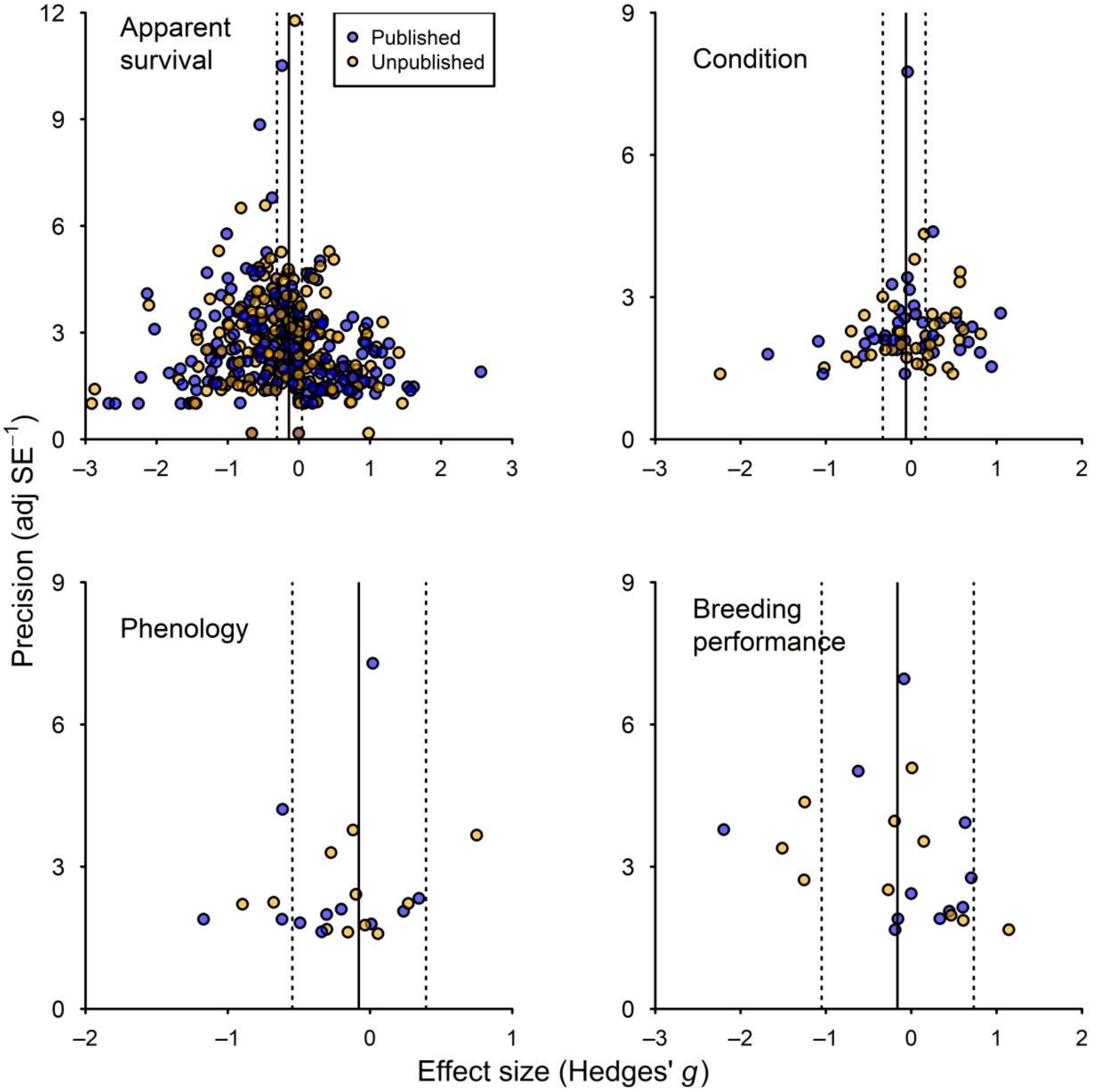

Figure S5. Location of the study sites included in the analysis.

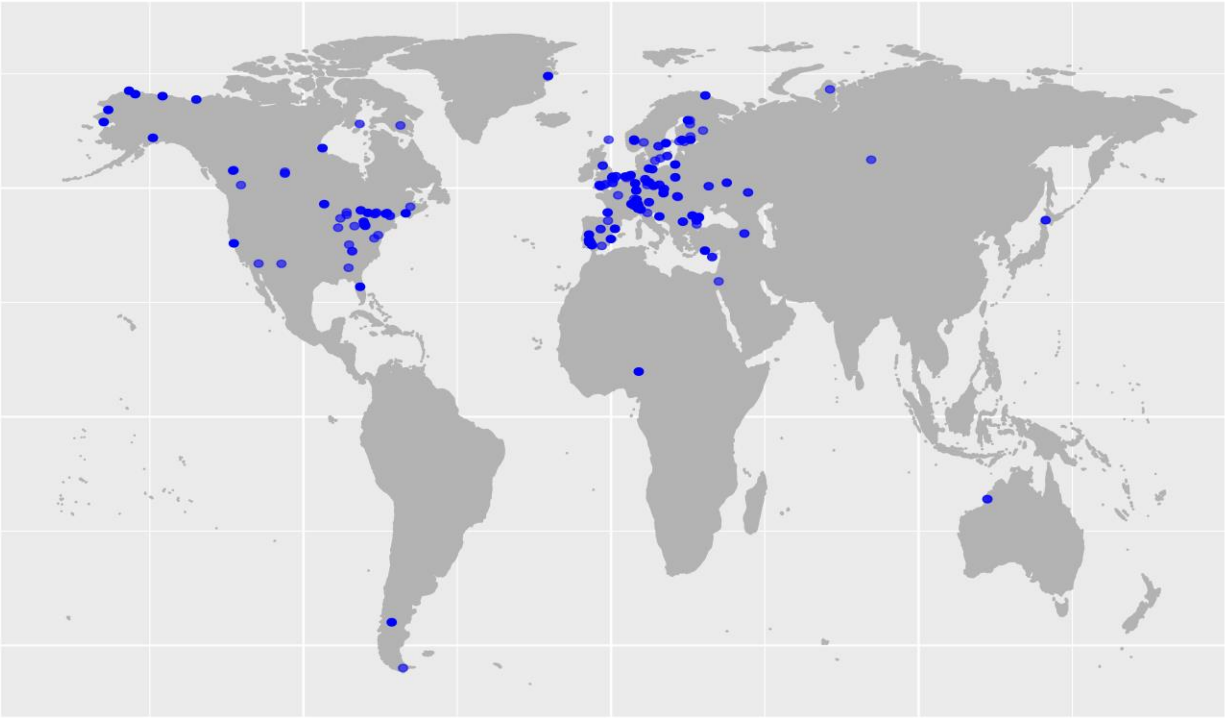

Table S6. Orders, families, species (Hackett et al. 2008) and number of records in each trait category for each species included in our analysis. Records are specified as the groups of tagged birds from the same study site, year of attachment, of the same sex, and the specific geolocator and the attachment type with the corresponding control group.

Order	*Family*	*Species*	*Survival*	*Condition*	*Phenology*	*Breeding perform.*
Caprimulgiformes	Apodidae	*Apus apus*	14	3	0	0
		Tachymarptis melba	64	5	0	0
	Caprimulgidae	*Caprimulgus europaeus*	2	1	0	0
Cuculiformes	Cuculidae	*Coccyzus americanus*	2	0	0	0
Charadriiformes	Charadriidae	*Charadrius hiaticula*	2	1	0	0
		Charadrius leschenaultii	2	0	0	0
	Scolopacidae	*Calidris alba*	5	0	0	0
		Calidris alpina	16	2	2	3
		Calidris mauri	3	0	0	1
		Calidris pusilla	16	0	0	5
		Calidris temminckii	4	1	0	0
		Phalaropus lobatus	1	0	0	0
Bucerotiformes	Upupidae	*Upupa epops*	2	1	1	1
Coraciiformes	Meropidae	*Merops apiaster*	15	3	0	0
Piciformes	Picidae	*Jynx torquilla*	4	0	0	0
Passeriformes	Acrocephalidae	*Acrocephalus agricola*	4	0	0	0
		Acrocephalus arundinaceus	27	1	6	0
		Acrocephalus paludicola	1	1	0	0
		Acrocephalus scirpaceus	15	1	0	0
	Calcariidae	*Calcarius lapponicus*	2	0	0	0
	Emberizidae	*Emberiza hortulana*	15	3	0	0
		Emberiza melanocephala	3	1	0	0
	Fringillidae	*Carpodacus erythrinus*	2	1	1	0
		Loxia curvirostra	0	1	0	0
		Plectrophenax nivalis	1	0	0	0
	Hirundinidae	*Delichon urbicum*	1	0	0	0
		Hirundo rustica	21	23	5	5
		Progne subis	11	2	0	0
		Riparia riparia	8	0	0	0
		Tachycineta bicolor	3	5	0	0
	Icteridae	*Dolichonyx oryzivorus*	8	2	0	0
		Euphagus carolinus	4	0	0	0
		Icterus bullockii	1	0	0	0
	Laniidae	*Lanius collurio*	0	1	0	0
		Lanius ludovicianus	10	0	0	1

Table S6 (continued). Orders, families, species (Hackett et al. 2008) and number of records in each trait category for each species included in our analysis. Records are 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 with the corresponding control group.

Order	*Family*	*Species*	*Survival*	*Condition*	*Phenology*	*Breeding perform.*
Order	*Family*	*Species*				
	Locustellidae	*Locustella luscinioides*	5	0	0	0
	Mimidae	*Dumetella carolinensis*	1	0	0	0
	Motacillidae	*Anthus campestris*	2	1	1	1
	Muscicapidae	*Ficedula albicollis*	4	3	0	0
		Ficedula hypoleuca	16	0	2	0
		Ficedula semitorquata	4	0	0	0
		Luscinia megarhynchos	7	4	0	0
		Luscinia svecica	4	2	0	1
		Muscicapa striata	3	0	0	0
		Oenanthe cypriaca	2	0	0	0
		Oenanthe oenanthe	33	1	1	3
		Phoenicurus phoenicurus	2	0	0	0
		Saxicola rubetra	9	0	0	0
	Parulidae	*Dendroica kirtlandii*	1	1	0	0
		Dendroica striata	1	0	0	0
		Seiurus aurocapilla	2	0	0	0
		Vermivora chrysoptera	4	1	1	1
	Passerellidae	*Chondestes grammacus*	1	0	0	0
		Melospiza melodia	2	0	0	0
		Passerculus sandwichensis	8	0	0	0
		Passerella iliaca	1	1	0	0
		Zonotrichia albicollis	2	0	0	0
		Zonotrichia atricapilla	3	2	0	0
	Passeridae	*Passer hispaniolensis*	1	0	0	0
	Sturnidae	*Sturnus philippensis*	2	0	0	0
	Sylviidae	*Phylloscopus sibilatrix*	2	0	0	0
	Turdidae	*Catharus bicknelli*	2	0	0	0
		Catharus fuscescens	1	0	0	0
		Catharus guttatus	2	1	0	0
		Catharus ustulatus	1	1	0	0
		Hylocichla mustelina	2	0	0	0
		Turdus migratorius	1	0	0	0
	Tyrannidae	*Elaenia albiceps*	5	2	2	0
	Vireonidae	*Vireo olivaceus*	1	0	0	0

Table S7. Heterogeneity proportions explained by the random effects (%), total between-study heterogeneity (%) and phylogenetical heritability (%; 95% CrI) for both phylogenetically controlled and uncontrolled null models of each of the four trait categories.

Model	*Site*	*Species*	*Phylogeny*	*Residual*	*Total*	*Heritability*
Apparent survival phylogeny	5.7	1.4	2.2	13.1	22.4	58.5 (15.1–92.6)
Apparent survival	6.1	1.6	–	13.5	21.2	–
Condition phylogeny	3.0	4.8	4.4	1.8	14.0	46.8 (5.1–94.1)
Condition	3.3	4.8	–	2.0	10.1	–
Phenology phylogeny	4.7	5.3	6.5	2.5	19.0	52.3 (5.0–96.5)
Phenology	5.3	5.5	–	2.7	13.5	–
Breeding performance phylogeny	19.0	12.3	12.1	10.0	53.4	45.7 (1.6–98.4)
Breeding performance	22.1	16.2	–	10.5	48.8	–

Table S8. Summary of the publication bias models for each trait category. Reference levels for treatment contrasts are unpublished results. Sample sizes are in parentheses.

Trait category	*Trait*	*Estimate*	*SE*	*Z*	*95% CI*	*P*
Apparent survival	Intercept	–0.17	0.08	–2.21	(–0.33; –0.02)	0.027
(426)	Published	–0.02	0.09	–0.20	(–0.20; 0.16)	0.838
Condition	Intercept	0.02	0.07	0.33	(–0.12; 0.17)	0.739
(79)	Published	–0.06	0.12	–0.52	(–0.29; 0.17)	0.603
Phenology	Intercept	0.03	0.18	0.14	(–0.32; 0.37)	0.888
(22)	Published	–0.20	0.21	–0.93	(–0.61; 0.22)	0.353
Breeding performance	Intercept	0.27	0.43	0.63	(–0.57; 1.11)	0.531
(22)	Published	–0.61	0.50	–1.23	(–1.58; 0.36)	0.219

References

Hackett, S., Kimball, R., Reddy, S., Bowie, R., Braun, E., Braun, M., … Yuri, T. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science*, 320, 1763–1768. doi:10.1126/science.1157704

Koricheva, J., Gurevitch, J., & Mengersen, K. (2013). Handbook of meta-analysis in ecology and evolution. Princeton University Press.