

Weak effects of geolocators on small birds

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

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Manuscripts

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

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- 136
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- 138
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140

141 **Abstract**

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147 meta-analyses did not evaluate unpublished data and impact of multiple life-history traits,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 We quantitatively reviewed 549 records extracted from 74 published and 48 unpublished studies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

163 geolocators on small bird species but the ethical aspects and scientific benefits should always be
164 considered.

165

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

168

169 **Introduction**

170 Tracking devices have brought undisputed insights into the ecology of birds. Use of these tags has
171 enabled researchers to gather valuable information about the timing of life events across annual cycles,
172 the year-round geographic distribution of populations and other important ecological patterns in many
173 species whose movement ecology was widely unknown (e.g. Patchett, Finch, & Cresswell, 2018; Stanley,
174 MacPherson, Fraser, McKinnon, & Stutchbury, 2012; Weimerskirch et al., 2002). A significant proportion
175 of recently published tracking studies use light-level geolocators on small bird species (body mass up to
176 100 g; Bridge et al., 2013; McKinnon & Love, 2018); however, the increasing use of these tags on small
177 birds raises questions about ethics of tagging and how representative the behaviour of tagged
178 individuals is (Jewell, 2013; Wilson & McMahon, 2006).

179 Studies using tracking devices such as archival light-level geolocators (hereafter 'geolocators')
180 frequently report the effect of tagging. The published results on the effects of geocator tagging are
181 equivocal: some found reduced apparent survival, breeding success and parental care (Arlt, Low, & Pärt,
182 2013; Pakanen, Rönkä, Thomson, & Koivula, 2015; Scandolara et al., 2014; Weiser et al., 2016) while
183 others report no obvious effects (Bell, Harouchi, Hewson, & Burgess, 2017; Fairhurst et al., 2015;
184 Peterson et al., 2015; van Wijk, Souchay, Jenni-Eiermann, Bauer, & Schaub, 2015). Recent meta-analyses

185 evaluating the effects of geolocators (Costantini & Møller, 2013) and other tracking devices (Barron,
186 Brawn, & Weatherhead, 2010; Bodey et al., 2018) showed slightly negative effects on apparent survival,
187 breeding success and parental care. These studies also discussed relative load as an aspect affecting the
188 tagged birds (Costantini & Møller, 2013), or suggested multiple threshold values of relative load on birds
189 (Barron et al., 2010; Bodey et al., 2018). However, these studies involved mainly large bird species
190 where the same additional relative load will more negatively affect surplus power and thus the flight
191 performance than in smaller species (Caccamise & Hedin, 1985). Moreover, previous studies did not
192 control for the effect of small-sample studies, or phylogenetic non-independence and its uncertainty.
193 There is thus a lack of systematic and complex evaluation of geocator effects on small birds including
194 species' life-history and ecological traits, geocator design, and type of attachment.

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

205 The number of studies tagging small birds is rapidly increasing each year even though our
206 understanding of tag effects is incomplete. In this study, we evaluated the effects of tagging on apparent
207 survival, condition, phenology, and breeding performance for small bird species (<100 g) in a robust
208 dataset of both published and unpublished studies to minimize the impact of publication bias.

209 Moreover, we assess whether the tagging effects are related to species' ecological and life-history traits,
210 type of control treatment as well as geolocator and attachment designs. We build on the most recent
211 advances in meta-analytical statistical modelling to get unbiased estimates of the geolocator
212 deployment effects controlled for phylogenetic non-independence and its uncertainty (Doncaster &
213 Spake, 2017; Guillaume & Healy 2017; Hadfield, 2010; Viechtbauer, 2010).

214

215 **Predictions**

- 216 i) Geolocators will negatively affect apparent survival, condition, phenology and breeding
217 performance of small birds.
- 218 ii) Negative effects will be stronger in unpublished studies than in published studies.
- 219 iii) Deleterious effects will be most prominent in studies establishing matched control groups compared
220 to studies with potentially-biased control groups.
- 221 iv) Geolocators which constitute a higher relative load will imply stronger negative effects.
- 222 v) Geolocators with a longer light stalk/pipe will cause stronger negative effects because of increased
223 drag in flight and thus increased energetic expenditure (Bowlin et al., 2010; Pennycuik, Fast,
224 Ballerstädt, & Rattenborg, 2012). These effects will be stronger in aerial foragers than in other
225 foraging guilds (Costantini & Møller, 2013).
- 226 vi) Non-elastic harnesses will cause stronger negative effects than elastic harnesses, which better
227 adjust to intra-annual body mass changes and avoid flight restriction (Blackburn et al., 2016).

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230

231 **Material and Methods**

232 *Data search*

233 We conducted a comprehensive search for both published and unpublished studies deploying
234 geolocators on bird species with body mass up to 100 g. We searched the Web of Science Core
235 Collection (search terms: TS = (geoloc* AND (bird* OR avian OR migra*) OR geologg*)) and Scopus
236 databases (search terms: TITLE-ABS-KEY (geoloc* AND (bird* OR migra*) OR geologg*)), to find
237 published studies listed to 18 February 2018. Moreover, we searched reference lists of studies using
238 geolocators on small birds and included studies from previous comparative studies (Bridge et al., 2013;
239 Costantini & Møller, 2013; Weiser et al., 2016). In order to obtain information from unpublished studies,
240 we inquired geocator producers and the Migrant Landbird Study Group to disseminate our request for
241 unpublished study details among their customers and members, respectively. In addition, we asked the
242 corresponding authors of the published studies to share any unpublished data. The major geocator
243 producers – Biotrack, Lotek, Migrate Technology and the Swiss Ornithological Institute – sent our
244 request to their customers. To find whether the originally unpublished studies were published over the
245 course of this study, we inspected their status on 1 December 2018. The entire process of search and
246 selection of studies and records (described below) is presented in a flow-chart (Fig. S1).

247 *Inclusion criteria; additional data requesting*

248 We included studies that met the following criteria:

- 249 1. The study reported response variables (e.g. return rates, body masses) necessary for effect size
250 calculation.
- 251 2. The study included a control group of birds alongside the geocator-tagged individuals or reported
252 a pairwise comparison of tagged birds during geocator deployment and recovery.

- 253 3. As a control group, the study considered birds marked on the same site, of the same sex and age
254 class without any indication of a difference in recapture effort between tagged and control groups.
- 255 4. For pairwise comparisons, the study presented correlation coefficients or raw data.
- 256 5. The variable of interest was presented outside the interaction with another variable.

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

265 *Trait categories; effect size calculation; explanatory variables*

266 We divided all collected data into four trait categories: apparent survival, condition, phenology and
267 breeding performance based on the response variables reported (e.g. inter-annual recapture rates, body
268 mass changes, arrival dates, or clutch sizes; Table S2). These categories represent the main traits
269 possibly affected in the geolocator-tagged individuals. Subsequently, analyses were run separately for
270 each trait category. We calculated the effect sizes for groups of tagged birds from the same study site
271 and year of attachment, of the same sex (if applicable) and specific geolocator and attachment type
272 accompanied with the corresponding control groups. For simplicity, we call these units *records*
273 throughout the text. For each record, we extracted a contingency table with the treatment arm
274 continuity correction (Schwarzer, Carpenter, & Rucker, 2014) or mean, variance, and sample size, to
275 calculate the unbiased standardised mean difference – Hedges' *g* (Borenstein, Hedges, Higgins, &

276 Rothstein, 2009) – and its variance with correction for the effect of small sample sizes (Doncaster &
277 Spake, 2018). We used the equation from Sweeting et al. (2004) to calculate variance in pairwise
278 comparisons. When raw data were not provided, we used the reported test statistics (F , t or χ^2) and
279 sample sizes to calculate the effect size using the R package compute.es (Del Re 2013). Besides the
280 effect size measures, we extracted additional variables of potential interest – ecological and life-history
281 traits per species, methodological aspects of the study, geolocator and attachment designs and harness
282 material elasticity (Table 1).

283 *Accounting for dependency*

284 We accounted for data non-independence on several levels. When multiple records shared one control
285 group (e.g. several geolocator types and attachment designs used in one year), we split the sample size
286 in the shared control group by the number of records to avoid a false increase in record precision. When
287 multiple measures were available for the same individuals, we randomly chose one effect size measure
288 in each trait category ($n = 8$). If the study provided both recapture and re-encounter rates, we chose the
289 re-encounter rate as a more objective measure of apparent survival. Re-encounters included captures
290 and observations of tagged birds and thus the bias towards the tagged birds caused by the potentially
291 higher recapture effort to retrieve the geolocators should be lower. Finally, we accounted for
292 phylogenetic non-independence between the species and the uncertainty of these relationships using
293 100 phylogenetic trees (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) downloaded from the
294 BirdTree.org (www.birdtree.org) using the backbone of Hackett et al. (2008). Moreover, we used the
295 random intercepts of species and study sites in all models, the latter to account for possible site-specific
296 differences (such as different netting effort or other field methods used by particular research teams).

297 *Overall effect sizes and heterogeneity*

298 We calculated the overall effect size for each trait category from all available records using meta-
299 analytical null models. We employed the *MCMCglmm* function from the *MCMCglmm* package (Hadfield,
300 2010) to estimate overall effect sizes not controlled for phylogeny (model 1, Table S3). We then used the
301 *mulTree* function from the *mulTree* package (Guillerme & Healy, 2017) to automatically fit a
302 *MCMCglmm* model on each phylogenetic tree and summarized the results from all these models to
303 obtain phylogenetically controlled overall effect size estimates (model 2, Table S3). We used weakly
304 informative inverse-Gamma priors ($V = 1$, $\nu = 0.002$) in all models. All fitted *MCMCglmm* models
305 converged and Gelman-Rubin statistic was always <1.1 for all parameters. As our data contained many
306 effect sizes based on small sample sizes, which could lead to a biased estimate of the overall effect size
307 variance, all effect sizes were weighted by their mean-adjusted sampling variance (Doncaster & Spake,
308 2018). We considered effect sizes (Hedge's g) of 0.2, 0.5 and 0.8 weak, moderate and large effects,
309 respectively. Moreover, we calculated the amount of between-study heterogeneity in all null models
310 using the equation described in Nakagawa and Santos (2012). Phylogenetic heritability (H^2) expressing
311 the phylogenetic signal was estimated as the ratio of phylogenetic variance ($\sigma^2_{phylogeny}$) against the sum
312 of phylogenetic and species variance ($\sigma^2_{species}$) from the models (Table S3; Hadfield & Nakagawa, 2010):

$$313 H^2 = \sigma^2_{phylogeny} / (\sigma^2_{phylogeny} + \sigma^2_{species})$$

314 *Multivariate meta-analysis*

315 To unveil the most important dependencies of the geolocator effects, we calculated three types of
316 multivariate models: a full trait model (model 3), an ecological model (model 4) and models of
317 publication bias (model 5, Table S3). In the full trait model, we used methodological, species, geolocator
318 specification and attachment variables (Table 1) to estimate their impact on apparent survival (model 3).
319 We did not compare the tagging effects of different attachment types due to their use in specific groups
320 of species (e.g. the leg-flagged attachment in shorebirds or the full-body harnesses in nightjars and

321 swifts only). Prior to fitting the ecological model, we employed a principal component analysis of the
322 inter-correlated log continuous life-history traits and extracted the two most important ordination axes
323 – PC1 and PC2 (Table 1). The PC1 explained 54.4% of the variability and expressed a gradient of species
324 characterised mainly by increasing body mass, egg mass and clutch mass (Fig. S4). The PC2 explained
325 18.7% of variance and was characterised mainly by increasing clutch sizes, number of broods and
326 decreasing migration distances (Fig. S4). These axes together with the categorical ecological traits (Table
327 1) were then entered into the ecological model to estimate their effect on apparent survival (model 4).
328 Finally, we tested for differences in effect sizes between published and unpublished results in each trait
329 category using all available records (model 5). In these models, we employed the *rma.mv* function from
330 the R package metafor (Viechtbauer, 2010) weighted by the mean-adjusted sampling error (Doncaster &
331 Spake, 2018). Continuous predictors were scaled and centred. None of the model residuals violated the
332 assumptions of normal distribution. Because the phylogenetic relatedness of the species explained only
333 a small amount of variation and the phylogenetic relatedness correlates with the life-history and
334 ecological traits, we did not control for phylogeny in the multivariate models but incorporated the
335 random intercepts of species and study site. We calculated R^2 for the full trait and ecological models
336 using the residual between-study variability (τ^2_{residual}) and the total between-study variability (τ^2_{total})
337 according to the equation (López-López, Marín-Martínez, Sánchez-Meca, Van den Noortgate, &
338 Viechtbauer, 2014):

$$339 \quad R^2 = (1 - \tau^2_{\text{residual}} / \tau^2_{\text{total}}) \times 100$$

340 *Publication bias; body mass manipulation*

341 We used funnel plots to visually check for potential asymmetry caused by publication bias in each trait
342 category (Fig. S5). To quantify the level of asymmetry in each trait category, we applied the Egger's
343 regression tests of the meta-analytical residuals from all null models of the trait categories (calculated

344 using the *rma.mv* function) against effect size precision ($1 / \text{mean-adjusted standard error}$; Nakagawa &
345 Santos, 2012). An intercept significantly differing from zero suggests the presence of publication bias. In
346 order to find differences in log body mass between the tagged and control individuals during the tagging
347 and marking, we applied a linear mixed-effect model with species and study site as a random intercept
348 weighted by the sample sizes. We considered all effect sizes significant when the 95% credible interval
349 (CrI; using *MCMCglmm* function) or confidence interval (CI; using *rma.mv* function) did not overlap zero.
350 All analyses were conducted in R version 3.3.1 (R Core Team, 2016).

351

352 **Results**

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

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

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

375 We did not find any evidence for publication bias in any of the trait categories, either visually in
376 the funnel plots (Fig. S5), or using Egger's regression tests (Table 2). Moreover, there were no
377 statistically significant differences in tagging effects between published and unpublished studies (model
378 5, Table S9). The geocator-tagged birds were on average 3.8% heavier than control individuals prior to
379 the geocator deployment and marking (LMM: estimate 0.008 ± 0.003 , $t = 2.47$, $P = 0.014$).

380

381 **Discussion**

382 Geocator deployment has a potential to reduce a bird's apparent survival, condition, breeding
383 performance, or may delay events of the annual cycle leading to biases in movement data. By
384 conducting a quantitative review of published studies deploying geolocators on small bird species and
385 incorporating unpublished data, we revealed only a weak overall effect of geolocators on apparent
386 survival of tagged birds while we found no clear overall effect on condition, phenology and breeding
387 performance. Moreover, we found no statistically significant effects of tagging in any of trait categories
388 when accounting for phylogenetic relationships. Tagging effects on apparent survival were stronger with

389 a higher relative load, when the geolocators were attached with elastic harnesses and in small-bodied
390 species.

391 *Overall tag effects*

392 A negative overall effect of geocator tagging on apparent survival found in this study seems to be
393 prevalent across previous comparative studies of tagging effects (Barron et al., 2010; Bodey et al., 2018;
394 Costantini & Møller, 2013; Trefry, Diamond, & Jesson, 2012; Weiser et al., 2016). However, unlike
395 previous comparative (Barron et al., 2010; Bodey et al., 2018) and primary studies (e.g. Adams et al.,
396 2009; Arlt et al., 2013; Snijders et al., 2017), we found no overall negative effects of tagging on variables
397 associated with breeding performance in our analysis. We also did not find evidence for overall effects
398 of tagging on body condition and phenology, which was consistent with equivocal results of previous
399 studies: some found reduced body condition (Adams et al. 2009, Elliott et al., 2012) or delayed timing of
400 annual cycle events (Arlt et al., 2013, Scandolara et al., 2014), while others found no evidence for
401 tagging effects on these traits (Bell et al., 2017; Fairhurst et al., 2015; Peterson et al., 2015; van Wijk et
402 al., 2015).

403 Tagged individuals that returned to the study site are potentially in better condition than the
404 tagged individuals that did not return – this potentially contributes to the weak tagging effects on
405 condition, phenology and breeding performance. However, the lack of effect we found on phenology
406 and breeding performance could also be an artefact of the small sample sizes, as collecting these data is
407 probably more challenging in small avian species, which are more difficult to re-sight and recapture and
408 have shorter life-spans than the relatively heavier species included in the previous studies. Similarly,
409 effects of tagging on condition could be underestimated in our analysis due to the initial differences we
410 found between the body mass of tagged and control birds. Additionally, the intra-annual body mass
411 changes could be biased in studies where timing of geocator deployment and geocator recovery

412 differs. Unfortunately, the timing of captures and recaptures was rarely reported and could not be
413 analysed in our study. Overall, the weak effects of tagging we found support several primary studies
414 (e.g. Bell et al., 2017; Fairhurst et al., 2015; Peterson et al., 2015; van Wijk et al., 2015), indicating that
415 geolocator tagging is both ethical and provides credible information on bird movements. On the other
416 hand, care should be taken as the tagging effect may be specific to populations or species. For example,
417 Weiser et al. (2016) found a negligible overall effect but significant reduction of return rates in the
418 smallest species in their meta-analysis. The negative effect of geolocators can also vary between years
419 (Bell et al., 2017, Scandolara et al., 2014), or be induced by occasional bad weather conditions (Snijders
420 et al., 2017), or food shortages (Saraux et al., 2011; Wilson et al., 2015).

421 *Inferring unbiased overall effect sizes*

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

428 Moreover, we found no support for stronger tag effects in studies with matched control
429 individuals compared to studies with less strict control treatments. However, this result is potentially
430 confounded by the fact that tagged birds were on average larger and in potentially better condition than
431 control birds, which would underestimate the negative effects of tagging. We thus suggest establishing
432 carefully matched control groups in all future studies to enable a more reliable estimation of tagging
433 effects. Such a control group should include: i) randomly selected individuals of the same species, sex
434 and age class; ii) individuals caught at the same time of the season and year; iii) at the same time of the

435 day; iv) of similar size and condition as tagged individuals, and v) exclude non-territorial birds or
436 individuals passing through the site.

437 *Influence of relative load and species' life-histories*

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

449 *Harness material*

450 Contrary to our prediction, we found higher apparent survival in birds tagged with harnesses made of
451 non-elastic materials. Non-elastic harnesses are usually individually adjusted on each individual,
452 whereas elastic harnesses are often prepared before attachment to fit the expected body size of the
453 tagged individuals according to allometric equations (e.g. Naef-Daenzer, 2007). As pre-sized elastic
454 harnesses cannot match perfectly the size of every captured individual, they may be in the end more
455 frequently tightly fitted as some researches might tend to tag larger individuals or avoid too loose
456 harnesses to prevent geolocator loss. Non-elastic harnesses may also be more frequently looser than
457 elastic harnesses as researchers try to reduce the possibility of non-elastic harness getting tight when

458 birds accumulate fat. Tight harnesses significantly reduced the return rates in whinchat (*Saxicola*
459 *rubetra*; Blackburn et al. 2016), and it may be difficult to register whether elastic harnesses are
460 restricting physical movement of birds when deploying tags. In contrast, non-elastic harnesses, which
461 are more commonly tailored according to the actual size, are often made sufficiently loose to account
462 for body mass changes of each individual. Prepared elastic harnesses are usually used to reduce the
463 handling time during the geolocator deployment (Streby et al. 2015) but this advantage may be
464 outweighed by the reduced apparent survival of geolocators with tied elastic harnesses. We thus
465 suggest to consider stress during geolocator deployment together with the potentially reduced apparent
466 survival and the risk of tag loss when choosing harness material.

467 *Variables without statistically significant impact on tagging effect*

468 Migratory distance did not affect the magnitude of the effect sizes, contrasting with some previous
469 findings (Bodey et al., 2018; Costantini & Møller, 2013). However, none of these studies used
470 population-specific distances travelled; instead, they used latitudinal spans between ranges of
471 occurrence (Costantini & Møller, 2013) or travelled distance categorised into three distances groups
472 (Bodey et al., 2018). These types of distance measurements could greatly affect the results especially in
473 species that migrate mainly in an east-west direction (Lislevand et al., 2015; Stach, Kullberg, Jakobsson,
474 Ström, & Fransson, 2016) or in species whose populations largely differ in their travel distances (Bairlein
475 et al., 2012; Schmaljohann, Buchmann, Fox, & Bairlein, 2012). Moreover, light-level geolocators were
476 most frequently deployed to the long-distance migrants in our study and the result can be thus
477 applicable to these species only.

478 Additionally, we found no overall effect of species' foraging strategy, contrary to the strong
479 overall negative effect found for aerial foraging species (Costantini and Møller 2013). Despite the tag
480 shape altering the drag and thus energy expenditure during flight (Bowlin et al., 2010; Pennycuick et al.,

481 2012), apparent survival tended to be better in individuals fitted with stalked geolocators and we found
482 no interaction between stalk length and foraging strategy on the tagging effect size. Geolocators with
483 longer stalks have been more frequently used in heavier birds with low relative load where the expected
484 tag effect is weak. Moreover, previous results of strong negative effects in aerial foragers led to a
485 preferential use of stalkless geolocators in these species and probably minimised the tagging effect in
486 this foraging guild (Morganti et al., 2018; Scandolara et al., 2015). However, the evidence for the
487 negative effects in non-aerial foragers is low as there is only one field study focusing on stalk length
488 effects on the return rates (Blackburn et al., 2016).

489 *Future considerations*

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

497

498 **Authors' contributions**

499 VBr, JK and PP conceived the idea and designed the methodology. VBr reviewed the literature and
500 collected data, JK and PP checked the data extracted for analysis. VBr and PP analysed the data. VBr led
501 the writing of the manuscript with significant contributions from JK and PP. MB, SH, DH, MK, JO and EW
502 contributed with unpublished data and their comments and suggestions significantly improved the
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506 manuscript. All authors gave final approval for publication.

507

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524

525 **Data accessibility**

526 Data described in this article are available at <https://doi.org/10.5281/zenodo.1886530> (Brlík et al.,
527 2018).

528

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

Methodological aspect	<i>Description</i>	<i>N</i>
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 – elasthan, 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

935 * only used for harness attachments

936 ¹Cramp & Perrins, 1977–1994

937 ²Rodewald, 2015

938 ³Schönwetter, 1960–1992

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

<i>Trait category</i>	<i>Unpublished (%)</i>		<i>Egger's regression</i>			
	<i>Effect sizes</i>	<i>N</i>	<i>Intercept</i>	<i>t</i>	<i>SE</i>	<i>P</i>
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

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950 Table 3. Summary of the full trait model (n = 281; model 3) and the ecological model (n = 426; model 4)
 951 of the geolocator effects on apparent survival. Levels contrasted against the reference level are given in
 952 parentheses.

Full trait model

<i>Trait</i>	<i>Estimate</i>	<i>SE</i>	<i>Z</i>	<i>95% CI</i>	<i>P</i>
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

<i>Trait</i>	<i>Estimate</i>	<i>SE</i>	<i>Z</i>	<i>95% CI</i>	<i>P</i>
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

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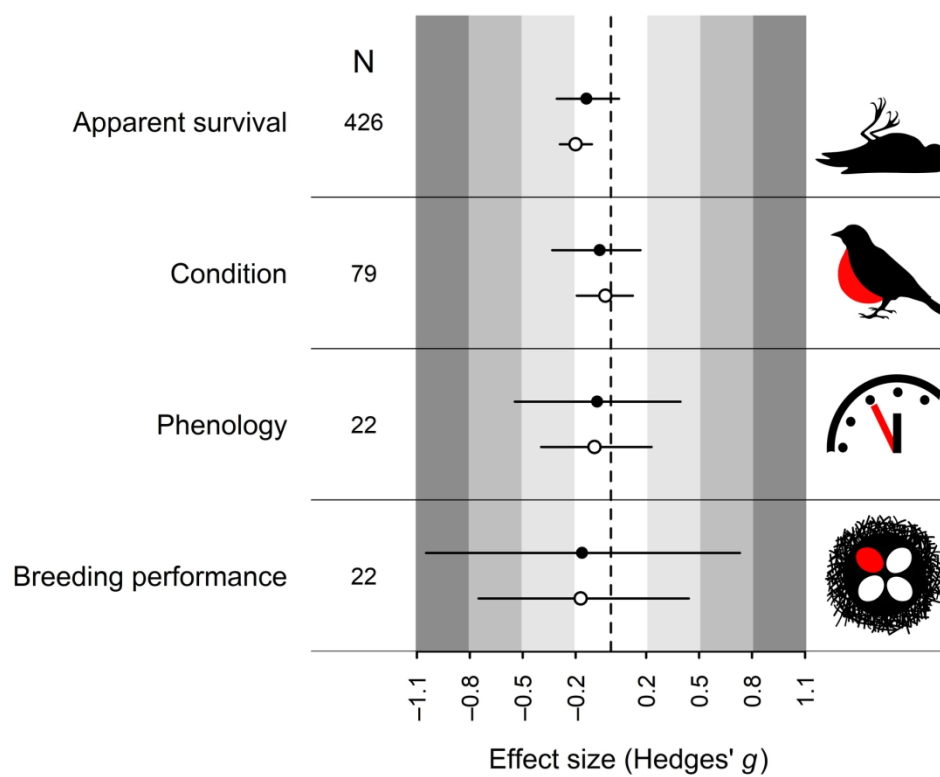


Figure 1. Overall effects of geolocators in the four trait categories, circles give means, horizontal lines represent 95% CrI. Filled symbols present the phylogenetically controlled overall effects, open symbols give the value from null models not accounting for phylogeny. N presents the number of effect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

85x68mm (600 x 600 DPI)

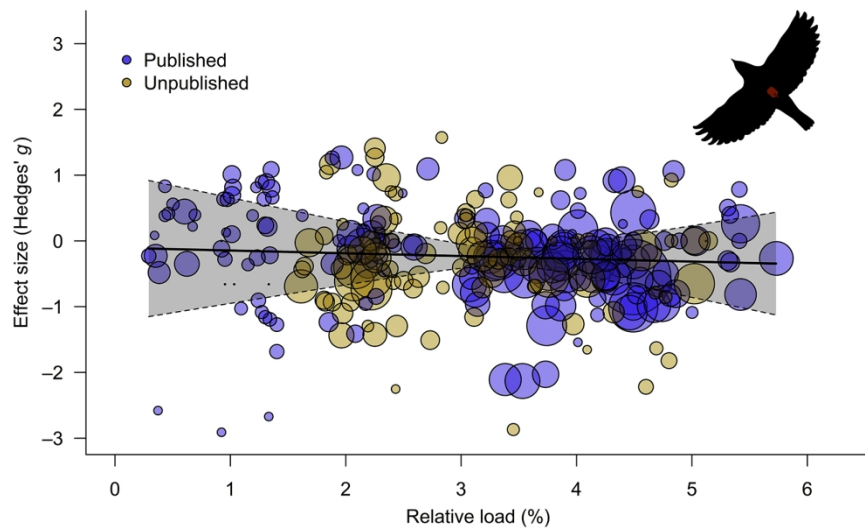


Figure 2. Relationship between relative load and the effect of geolocator deployment on the apparent survival of tagged birds. Size of the circles reflects the precision ($1 / \text{mean-adjusted SE}$) of the effect sizes, the shaded area and dashed lines depict the 95% CI of the regression.

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.

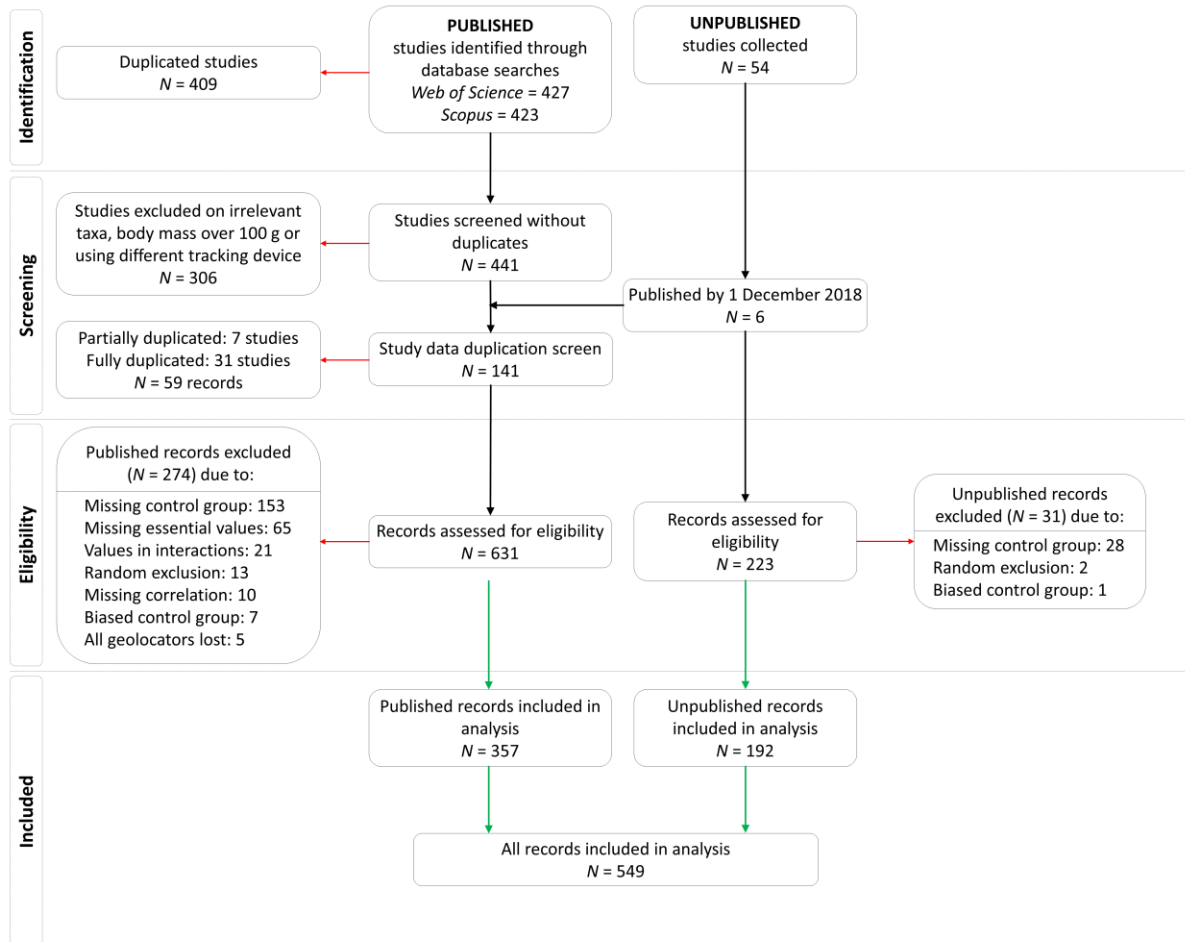


Table S2. Overview on trait categories, the corresponding response variables and their description as well as the number of studies and the number of records (specified as groups of tagged birds from the same study site, year of attachment, of the same sex, and the specific geolocator and attachment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

<i>Trait</i>	<i>Response variables</i>	<i>Description</i>	<i># studies</i>	<i># records</i>
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

Table S3. Description of model types used in our analysis and a script to extract the variance explained by the random effect terms. Models 1, 2 and 5 were fitted for each trait category, models 3 and 4 for apparent survival only.

Model 1	Null model not controlled for phylogeny	<code>MCMCglmm(smd.g ~ 1, random = ~species.tree + lon.lat, data = survival, prior = priors1.mev, nitt = 250000, burnin = 21000, thin = 10, mev = survival\$adj.vi)</code>
Model 2	Null model controlled for phylogeny	<code>multTree(multTree.data = multTree_data_survival, formula = formula_survival, priors = mult_priors_survival, parameters = parameters, mev=multTree_data_survival\$data\$adj.vi, output = "Survival_SpPhSi", chains = 2)</code>
Model 3	Full trait model	<code>rma.mv(yi = smd.g, v = adj.vi, mods = ~ factor(publ) + factor(control.type) + factor(aerial) + sex.final + scale(load) + scale(stalk.length) + elasticity + factor(aerial):scale(stalk.length), data = data.full, random = list((~1 data.full\$species.tree), (~1 factor(data.full\$lon.lat))), test = "z", level = 95, method = "ML")</code>
Model 4	Ecological model	<code>rma.mv(yi = smd.g, v = adj.vi, mods = ~ m\$scores[,1] + m\$scores[,2] + reed.shrub + nest.type, data = survival, random = list((~1 survival\$species.tree), (~1 factor(survival\$lon.lat))), test = "z", level = 95, method = "ML")</code>
Model 5	Model of publication bias	<code>rma.mv(yi = smd.g, v = adj.vi, mods = ~ factor(publ), data = survival, random = list((~1 survival\$species.tree), (~1 factor(survival\$lon.lat))), test = "z", level = 95, method = "ML")</code>

Script for heterogeneity extraction:

```
Anim.survival <- (posterior$phylogeny)
Spec.survival <- (posterior$species)
Site.survival <- (posterior$site)
Wei.survival <- (posterior$wei)
Res.survival <- (posterior$res)
sum.survival.het <- (Anim.survival+Site.survival+Spec.survival+Res.survival) /
(Anim.survival+Site.survival+Spec.survival+Res.survival+Wei.survival)
summary(sum.survival.het)
Sum.survival <- (Anim.survival+Site.survival+Spec.survival+Res.survival+Wei.survival)
summary(Anim.survival/Sum.survival)
summary(Site.survival/Sum.survival)
summary(Spec.survival/Sum.survival)
summary(Res.survival/Sum.survival)
Heritability.survival <- Anim.survival / (Anim.survival + Spec.survival)
mean(Heritability.survival)
quantile(Heritability.survival, probs = c(0.025, 0.975))
```


Figure S4. 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.

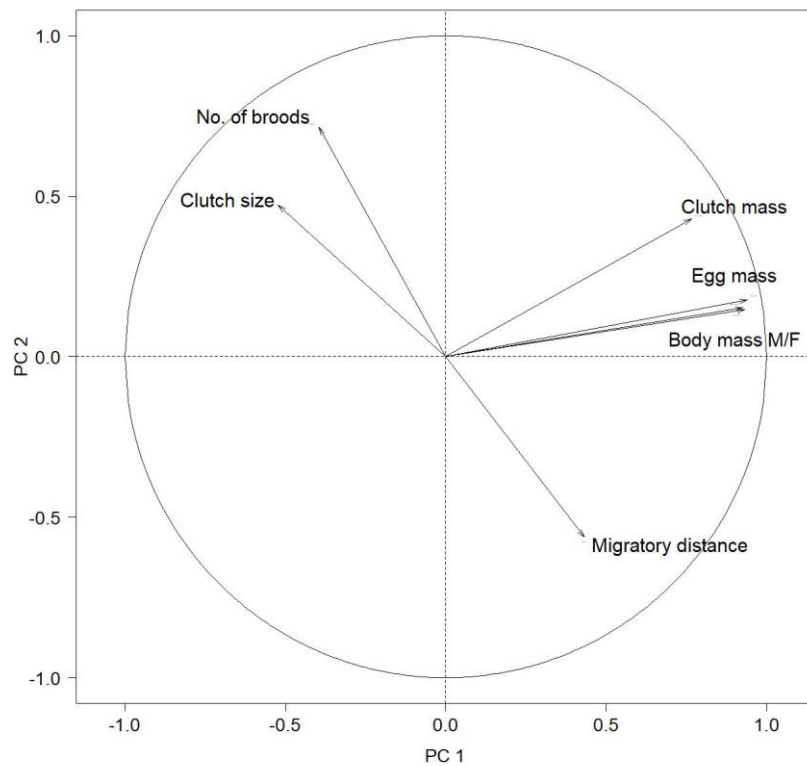


Figure S5. Funnel plots presenting the effect size (Hedges' g) against the inverse of the mean-adjusted sampling error in four trait categories. Solid lines present phylogenetically controlled overall effect size and dotted lines 95% CrI. Publication bias in the dataset is indicated by asymmetry of the funnel-shaped scatterplot (Koricheva, Gurevitch, & Mengersen, 2013).

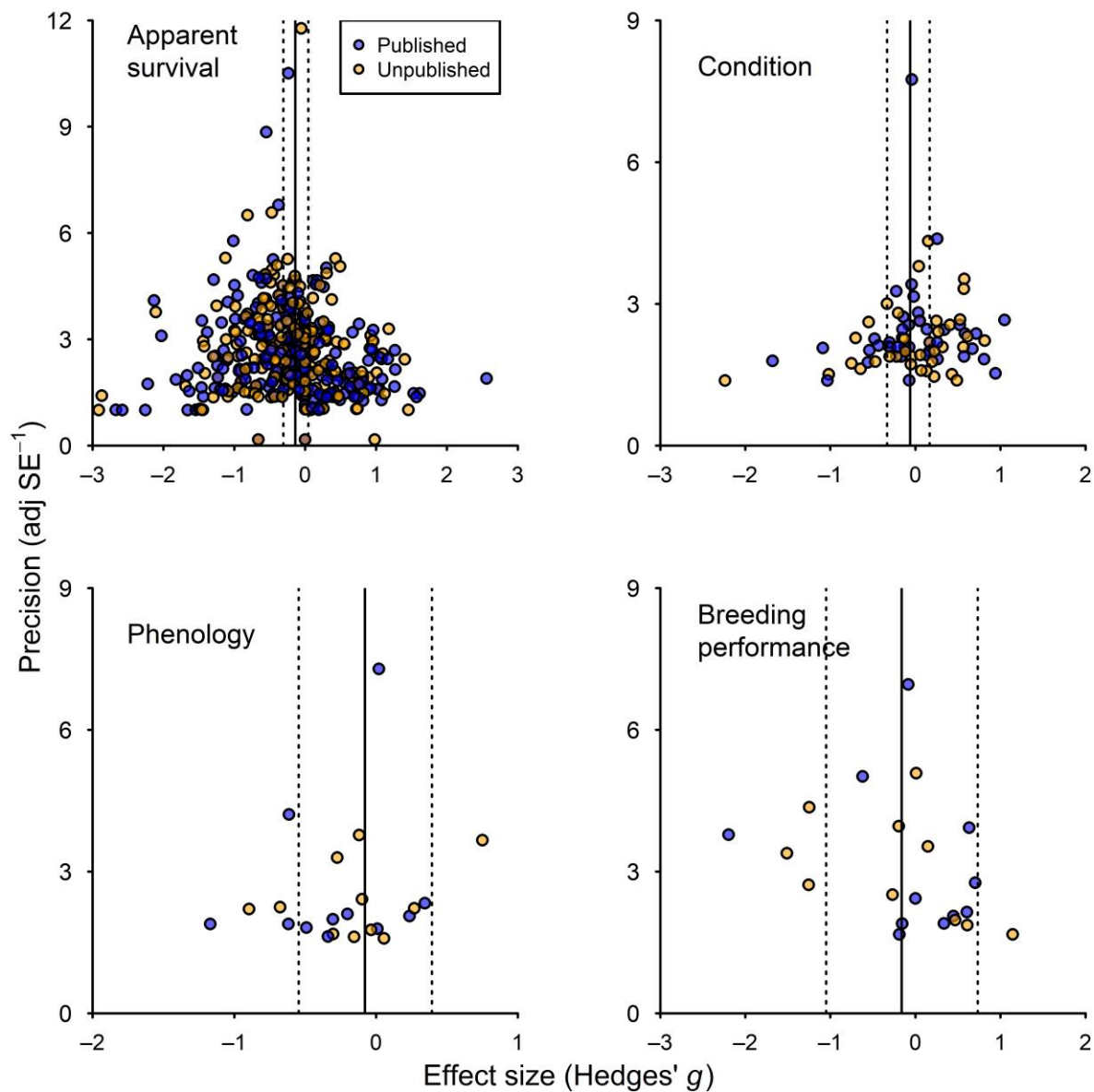


Figure S6. Location of the study sites included in the analysis.

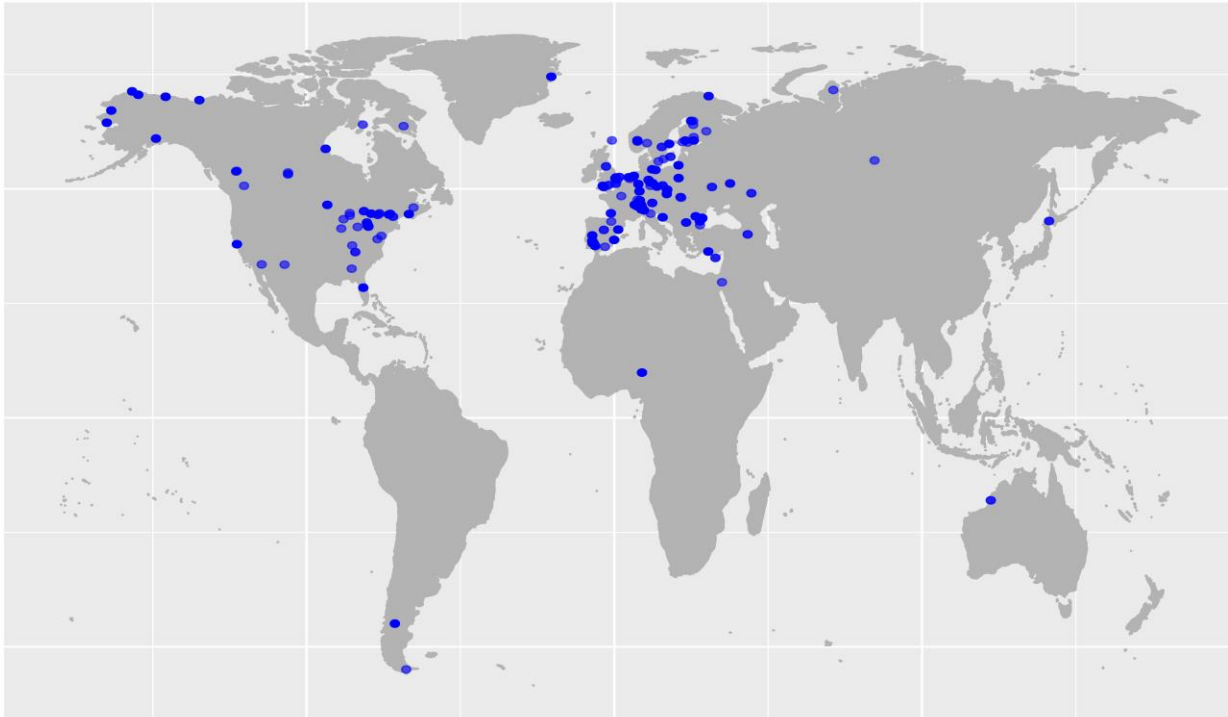


Table S7. Orders, families, species (Hackett et al. 2008) and number of records in each trait category for each species included in our analysis. Records are specified as the groups of tagged birds from the same study site, year of attachment, of the same sex, and the specific geolocator and the attachment type with the corresponding control group.

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

Table S7 (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.

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

Table S8. 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.

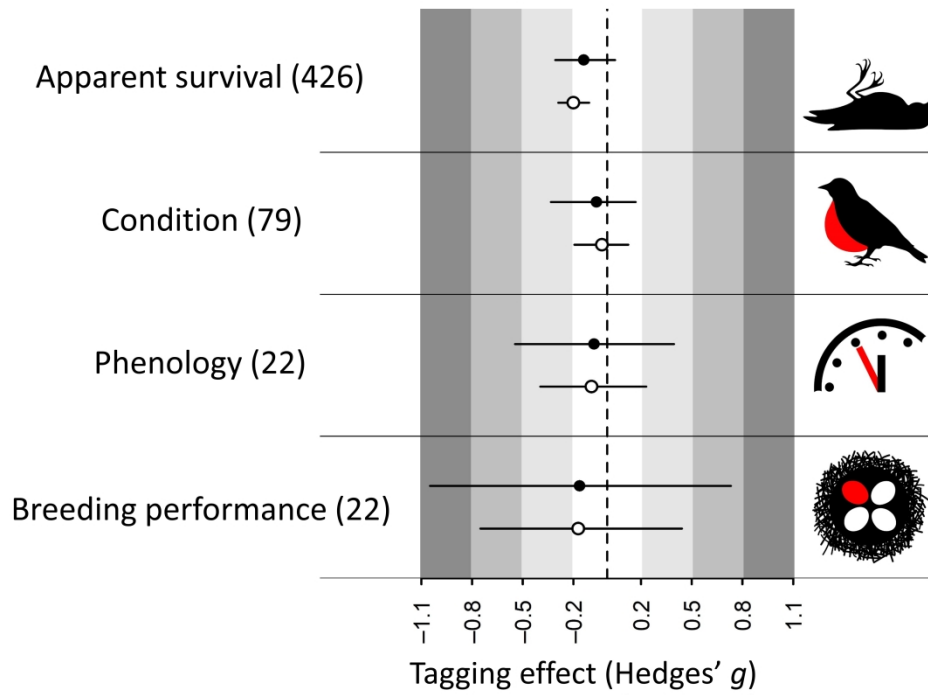
<i>Model</i>	<i>Site</i>	<i>Species</i>	<i>Phylogeny</i>	<i>Residual</i>	<i>Total</i>	<i>Heritability</i>
Apparent survival phylogeny	5.7	1.4	2.2	13.1	22.4	58.5 (15.1–92.6)
Apparent survival	6.1	1.6	–	13.5	21.2	–
Condition phylogeny	3.0	4.8	4.4	1.8	14.0	46.8 (5.1–94.1)
Condition	3.3	4.8	–	2.0	10.1	–
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 S9. Summary of the publication bias models for each trait category. Reference levels for treatment contrasts are unpublished results. Sample sizes are in parentheses.

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

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