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A meta-analysis of the effects of geolocator application on birds

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Abstract An increasing trend in use of tracking devices such as geolocators is based on the assumption that the information gathered from such devices provides reliable information about the migratory behavior of free-living birds. This underlying assumption is rarely tested, as evidenced by the absence in many studies of controls, in particular treated controls, and so far never with a reasonable statistical power. Published studies have shown reduced survival prospects or delayed breeding in some species, suggesting that there may be reason to doubt that tracking devices provide unbiased information. Therefore, we conducted a meta-analysis of studies applying geolocators to wild birds to determine whether geolocators affected fitness components. Geolocators had an overall negative effect on fitness components, in particular survival, and ecological variables. Effect size was larger for aerial foragers than for other species. Moreover the leg band attachment method was more detrimental for birds than the leg-loop backpack harness. A meta-regression model of effect size showed independent negative effects of geolocators on aerial foragers, smaller species, species with smaller migration distances and in studies where geolocators were attached with a ring. These results suggest that geolocator studies should be interpreted with caution, but also raise questions whether it is ethically defensible to use geolocators on aerial foragers or small species without carrying out robust pilot studies [*Current Zoology* 59 (6) : – ,].

Key words Aerial foraging, Aerodynamics, Fitness cost, Geolocator, Migration, Survival cost

Science is the acquisition of information about the world based on empirical evidence. While this claim may seem obvious, acquisition of such information may be less than straightforward because the method of investigation may itself affect the data being recorded. A standard scientific approach to accommodate such effects in biological, veterinary and medical sciences includes the use of treated (sham-treated) and untreated control groups, allowing for quantification of the effect of experimental treatment and the use of the method, respectively. Importantly, the method of investigation may also have detrimental effects on the study object, such as the impairment of survival and reproduction caused by flipper banding in free-ranging king penguins *Aptenodytes patagonicus* (Saraux et al., 2011), the effect of wing markers on survival, hatch and nest success (Trefry et al., 2013), and the effect of color markings on survival in tadpoles (Carlson and Langkilde, 2013). In this regard, another relevant example is the development of miniature radio transmitters, which helped ecologists overcome the challenges of tracking free-ranging animals. Decreases in transmitter size and increased battery life allowed investigators to apply such devices on a larger number of animal species and made the technology especially useful for studying birds that often travel thousands of kilometers during the annual cycle. However, application of transmitters to birds was found to significantly increase energy expenditure and reduce the probability of nesting, calling for a balance of the benefits of using these techniques against potential costs to the birds and reliability of the data obtained (Barron et al., 2010).

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Another case in point that raises conservation and methodological concerns is the recent, but increasing use of geolocators for tracking birds. Light-sensing geolocators (also known as light-level loggers or global location sensing/GLS loggers) are light recording data loggers that provide a relatively low-cost, lightweight, long-duration alternative to traditional tracking technologies. Since their initial development to study the movement of marine mammals (DeLong et al., 1992), geolocators have been used on a variety of wildlife, including pelagic fish and pinnipeds, and in birds ranging from albatrosses to songbirds (Stutchbury et al., 2009; Egevang et al., 2010; Bridge et al., 2013). Over the last years, the use of geolocators has seemingly opened windows into the lives of many bird species, such as those living in offshore marine environments, showing that such devices may provide important biological information about the movement of animals. However, it has been also shown that geolocators can significantly increase drag on the bodies of small birds (Bowlin et al., 2010; Pennycuick et al., 2012). Moreover, observations in some studies that individuals equipped with such devices deviate significantly from controls in terms of survival prospects, reproductive success or body mass (e.g., Adams et al., 2009; Stutchbury et al., 2009) suggest that caution is required for application of geolocators to wild birds and for interpretation of such data. Results of these studies have important ethical implications and suggest that care must be taken in the application of transmitting devices (e.g. radiotransmitters, geolocators) as highlighted on page 303 of ASAB guidelines (2012).

Therefore, we performed a meta-analysis of studies applying geolocators to wild birds to determine whether geolocators affect birds and if so, which traits are influenced, which species are more sensitive, and which attributes of geolocators have a stronger impact on physiology and reproduction of birds.

1 Material and Methods

1.1 Data Collection

An exhaustive literature search for studies in which geolocators have been applied to birds was conducted using 'Geolocators' or 'Geolocators*Birds' as keywords on the Web of Science as of 3 April 2013. We then included additional studies found by checking the literature quoted in each article found on the Web of Science. We also contacted authors to ask for data (e.g., sample size, control values) missing in the selected papers or for their own unpublished results.

Return rates were recalculated in cases where previously tagged birds were retrapped without geolocators by exclusion of these individuals. For example, if 8 out of 10 birds that were tagged were retrapped, but one of them was not carrying the geolocator, the return rate was calculated as 7/9 instead of 8/10. This is a more conservative approach than including in the calculation birds that lost the geolocator because it is impossible to know if birds were carrying the geolocator for almost the entire duration of the experiment or just lost the geolocator the day after they were tagged. It is unlikely that there is bias in the data included given the random selection of studies to be included based on Web of Science. An exhaustive survey of the literature is not required because a random selection of references will provide unbiased estimates of effect size (Coté et al., 2012). We extracted information on the mass of geolocators and the mode of attachment (with a harness or on a leg band) directly from the scientific papers.

1.2 Ecological Variables

For each study we extracted information on all ecological effects as published. If survival data for a control group were unavailable for a specific study, we compared the observed apparent survival estimate with the expectation based on literature information preferably from the same population, or in a few cases from a different population. We obtained body mass and mass of the geolocator from the studies, or if missing, we extracted information on body mass from Dunning (1993). We estimated latitudinal migration distance in units of degrees latitude by recording the northernmost and the southernmost distribution limits for the breeding season and for the winter using Cramp and

Perrins (1977–1994) and del Hoyo et al. (1992–2011) as sources. Migration distance was simply the difference between mean latitude during breeding and mean latitude during winter. Although these estimates of migration distance are bound to be imprecise, there is no reason to assume that they will cause any systematic bias. Previous studies have obtained biologically meaningful results using this estimate of migration distance as an explanatory variable (e.g., Møller and Mousseau, 2007). In contrast, if we relied entirely on migration distances as estimated by the use of geolocators, this could cause systematic bias if geolocators increased the cost of migration. We used the same sources to classify all species as aerial foragers or other categories of foragers.

1.3 Statistical Analyses

For each study (see Supplementary Material), we calculated effect size from test statistics reported in the original papers by using the equations given by Rosenthal (1991, 1994: Table 16.1) and Rosenberg (2010). When test statistics were not included in the paper, we used means, standard errors/deviations or P-values and sample sizes to estimate effect sizes. We calculated an overall effect size for each study assigning a sign to the effect size depending on whether it was detrimental (i.e., had a negative effect on the animal, such as reduced survival compared to controls) or not (e.g., survival or body mass were lower in controls; in these cases the sign of the effect size is positive, but this does not imply a beneficial effect of carrying a geolocator).

Effect size was estimated by comparing birds with geolocator (treated birds) and birds without a geolocator (controls). As response variables, we used data on physiology (e.g., stress hormones, immune cells), body mass, reproductive performance (e.g., clutch size, fledging success), or survival (e.g., return rate). As explanatory variables, we used species, weight of geolocator, body mass, attachment type, foraging behavior (aerial or not) and migration distance. The group 'aerial foragers' included all species that spend large amounts of time on the wings independently of whether they eat flying insects or dive for fish or invertebrates. For body mass we predicted that effect sizes would be greater for species with small body mass and for large geolocators. In a few cases we did not have an expected adult survival estimate for control birds, and then we instead used published estimates from the literature (Alnås, 1974; Cramp and Perrins, 1977–1994; Poole, 2005). Given that scientists are likely to have made every effort possible to re-trap any bird with a geolocator, we consider that the survival estimates reported for geolocator birds are over-estimates relative to that of controls, and, therefore, that our estimated effect sizes are conservative.

The measure of effect size used in the meta-analyses was Pearson's correlation coefficient, which was subsequently transformed by means of Fisher's transformation to z-values for further statistical analysis. This measure of effect size was adjusted for sample size using N-3 as an adjustment factor (Rosenthal 1991, pp. 27–28), based on the assumption that a larger sample size should provide a more reliable estimate of the unknown true relationship. We used data reported in the scientific publications or data reported by the authors upon request. Therefore, we also used the control samples from untreated birds as reported in the literature, but we did not include their sample size because we used control information for estimating expected values that were then used for comparison with the observed values. Again, the underlying reasonable assumption is that a larger control sample will provide a more reliable estimate of the effect in this group simply because sampling variance decreases with sample size. We calculated an overall effect using mean effect size adjusted for sample size after Fisher's z-transformation. The mean weighted zr values were tested against the null hypothesis of no effect by examining the significance of their associated r's. This was done by back-transforming the mean weighted effect size to a correlation coefficient and testing the significance of this coefficient given the total sample size (Rosenthal, 1991). An estimate of heterogeneity in effect sizes among samples was subsequently calculated using the formula provided by Rosenthal (1991, pp. 73–74), which has a χ^2-distribution with K-1 degrees of freedom, where K is the number of analysis units. To estimate the possibility for publication bias, we calculated the fail-safe number, which refers to the number of unpublished null studies needed to eliminate the observed global effect size. We obtained that estimate by relying on the equations reported by Rosenthal (1991, p. 104). All analyses were made using the software Meta-Win.

2 Results

Effect size of statistical outcomes varied considerably among studies from -0.74 to 0.48 with more studies with negative effects differing significantly from the value of zero than studies with positive effects (Fig. 1). We found a significant effect size of -0.098 (95% bootstrap CI = -0.154, -0.041) in a random effects meta-analysis weighted by sample size (Table 1). Variation in individual effect sizes was no larger than expected due to sampling error (Table 1). This effect was significant and could not readily be eliminated by unpublished studies as reflected by Rosenthal's fail-safe number (Table 1). There was a significant effect size independent of whether external information was included (Table 1). We tested for a significant effect of the category of effect (condition, survival, other life history traits). Mean effect size was significantly different from zero for survival estimates, but not for other life history traits or condition (Table 1). The mean effect of geolocators for aerially foraging birds was significantly negative (Table 1). Attachment method had a significant negative effect for leg band, while the effect for leg-loop backpack harness was not significant (Table 1). Whether species migrated shorter or longer distances affected effect size (Table 1). Species with a smaller or larger body mass had a significant negative effect (Table 1).

In a meta-regression weighted by N-3 we found a significant model that accounted for 24% of the variance (Table 2). This model fitted the data as shown by a test for lack of fit ($F_{46, 15}$ = 0.94, P = 0.58). Effect size was more negative for aerially foraging species than for other species (Fig. 2a). In addition, effect size increased with body mass (Fig. 2b). Furthermore effect size increased with migration distance (Fig. 2c). Finally, effect size was significantly more negative for studies with geolocators attached to rings than with a harness (Table 2). There were no additional significant effects of whether external data for controls were used, geolocator mass or category of effect size.

We found no significant evidence of publication bias regardless of whether the rank correlation for estimating bias was performed between standardized effect size estimates and their variances (r_{bias} = -0.0008, n = 69, P = 0.98), between effect size estimates and study sample size (r_{bias} = -0.121, n = 69, P = 0.93), or between effect size and year of publication (r_{bias} = -0.066, n = 69, P = 0.59).

3 Discussion

The main result of this meta-analysis of the effects of geolocators was an overall negative effect on fitness components such as survival. Effect size was larger for aerial foragers than for other species. Attachment method had a significant negative effect for leg band, while the effect for harness was not significant. Finally, there were significant additional effects of body mass and migration distance. We found no evidence of publication bias as reflected by non-significant funnel plots, a non-significant relationship between standardized effect sizes and their variances, or between effect size and publication year.

Geolocators are useful devices for identifying the migration routes and winter quarters of migratory birds and other animals, but also for describing migratory behavior and staging behavior in the annual cycle of migrants. However, this information may be biased if the behavior of birds with geolocators differs significantly from that of controls. Comparison of geolocator and control birds depends on large sample sizes in order to achieve a reasonable statistical power, and such large sample sizes are rare in most field studies. Until such verification studies have been performed we caution against the use of information derived from application of geolocators on aerial foragers, but also other categories of birds as described below. For example, the physiological cost (e.g., higher stress or energy expenditure) of carrying additional mass, as represented by the geolocator, could limit the migration distance normally achieved or induce a bird to use alternative migration routes and staging areas that might exacerbate such a cost.

Although the effect on survival was statistically significant, that was not the case for body condition or other life history traits. We highlight, however, that there is no general consensus on whether higher stress hormones or lower levels of immune cells indicate a poor condition. We also highlight that the estimates of effects on body condition and other life history traits may have been under-estimated because mortality is unlikely to have been random with respect to these variables. It could be possible, for example, that for some species only high quality individuals are able to carry the geolocators, and hence any information gathered from these species would be biased toward a specific fraction of the population.

We are aware of at least ten additional unpublished studies not included in our analyses, and several of these studies apparently showed strongly negative effects of geolocators on migratory birds, although we were not allowed to report this information in our survey. Moreover, given that scientists are likely to have made every effort possible to re-trap any bird with a geolocator, we consider that the survival estimates reported for geolocator birds are over-estimates relative to that of controls. There are therefore several good reasons to believe that the effect sizes reported here are conservative.

Møller and Jennions (2001) have shown for all meta-analyses in biology that mean effect size typically accounts for 5%–7% of the variance. Although our mean estimate in this study is small, there were still significant effects on survival, especially for aerially foraging species and small birds. Small effects are difficult to document because of the large sample sizes required to achieve a power of 80% with a significance level of 5%. Thus it is impossible to make claims about statistical significance with a reasonable statistical power in most of the studies reviewed here due to small sample sizes. Here we have conducted a meta-analysis based on 7851 individuals, providing a high level of statistical power for evaluating the null hypothesis of no effects of geolocators.

We found a significant effect of aerial foraging on effect size, with no negative effect remaining among non-aerial insectivores after eliminating aerial foragers. We suggest that this major dichotomy can be attributed to the impact of geolocators on aerodynamics as reported in other studies (Barron et al., 2010; Bowlin et al., 2010; Pennycuick et al., 2012). This finding also questions whether it is ethically defensible to use geolocators on aerial foragers because of the high mortality in the absence of any certainty that findings derived from such studies will be representative of performance under natural conditions. This is a very important point, as testified, for example, by the growing attention of committees to the impact of experimental procedures (e.g., marking and radiotagging on page 303 in ASAB guidelines 2012) on the welfare of wild animals.

We also found that the attachment method had a significant negative effect for leg band, while the effect for leg-loop backpack harness was not significant. This finding suggests that using leg-loop backpack harness might reduce any detrimental effects on the birds. However, there is variation in design of geolocators that is not simply related to geolocator mass or attachment, but also to other characteristics like light stalk length. It is therefore important to test the effects of the multiple components of a geolocator rather than just a few. Our data also challenge the rule of thumb of 5%, which recommends that the use of geolocators with an upper size limit of 5% of bird body mass would not harm the birds. In fact, almost all studies included in the present meta-analysis respected this rule.

There was an independent significant effect of body mass on effect size with more strongly negative effects (i.e., higher fitness costs) in small-sized species. Finally, there was a significant effect of migration distance, with effect size approaching zero at longer migration distances. We hypothesize that longer distance migrants may incur smaller costs of carrying a geolocator due to their physiology having been selected to carry varying amounts of fuel without being penalized in terms of fitness.

The use of geolocators without any treated experimental controls is surprising because their absence deviates from the design of experiments in all biological sciences, and because their absence may suggest that any findings at least for small bird species are biased. Here we suggest three possible methods for determining whether information about the whereabouts of individual birds provided with tracking devices is reliable. The argument relies on repeated measures of treated and control individuals in two subsequent years. Given that many migrants molt in the winter quarters or during migration, and that such migrants incorporate trace elements and stable isotopes permanently into their feathers (e.g., Szép et al., 2003), any change in composition of feathers will arise as a consequence of change in location at the time of molt, as long as birds move among isotopically distinct locations. Therefore, feathers collected from control birds and individuals equipped with the tracking device before and after the device is attached might provide information about change in winter location.

A second approach would rely on the fact that corticosterone is deposited in feathers during molt (Bortolotti et al., 2008), and that the use of a tracking device might permanently increase the level of circulating corticosterone (see Supplementary Material), if an individual was stressed by the presence of the tracking device. However, a lower corticosterone level in tagged birds than in controls might also indicate a potential detrimental effect on the animal, such as a deregulation of the physiological response mediated by the HPA axis (Cyr and Romero, 2007; Dickens and Romero, 2013). Again, samples from the control group could form the baseline for evaluating the biological meaning of corticosterone level of the geolocator group. Additional physiological measures (e.g., oxidative damage level; Costantini et al., 2011) might help our assessment of the effects of stress hormones.

A third approach would rely on arrival date being recorded in individuals with and without geolocators in the year when the geolocators were first attached and in the subsequent year. A treatment effect would result in a delay in arrival in the second year relative to the arrival date in the first year for geolocator individuals, but not for controls, if geolocators had a negative effect on research findings.

To conclude, excessive mortality in aerially foraging bird species (i.e., those species that spend most foraging time on the wings before catching insects or diving for fish or other types of food) and small birds provided with geolocators suggests that there are reasons to treat conclusions about the biological significance of findings concerning migration and migratory behavior of those species with caution. Our data also challenge the claim of a recent review suggesting that geolocators do not influence birds (Bridge et al. 2013). Discrepancies between studies arose likely because Bridge et al. (2013) did not provide any statistical analyses of the reviewed studies to support their conclusions.

Our data also show that the leg band attachment method was more detrimental for the birds than the leg-loop backpack harness. Finally, results from our study highlight the need for robust pilot studies with proper experimental controls as is done in all other fields of the biological sciences.

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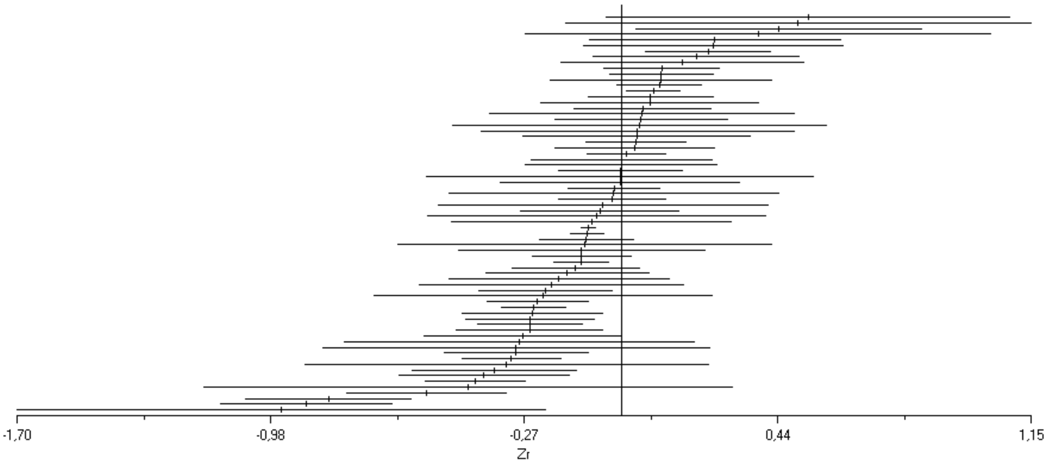
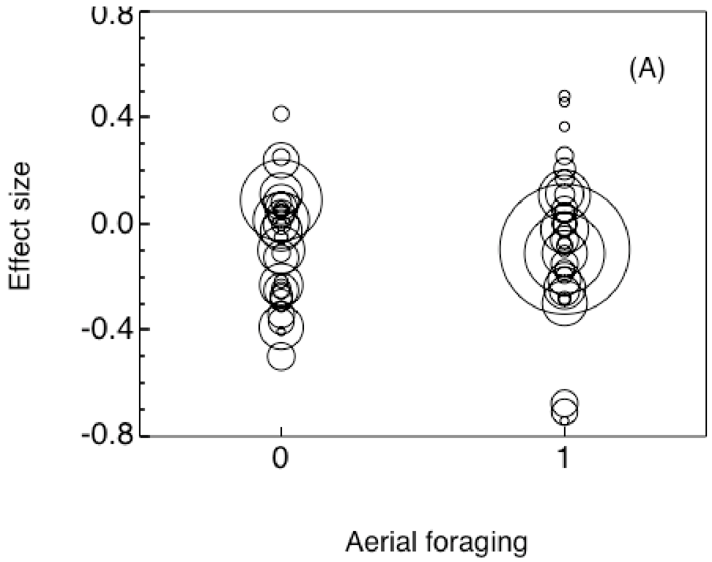
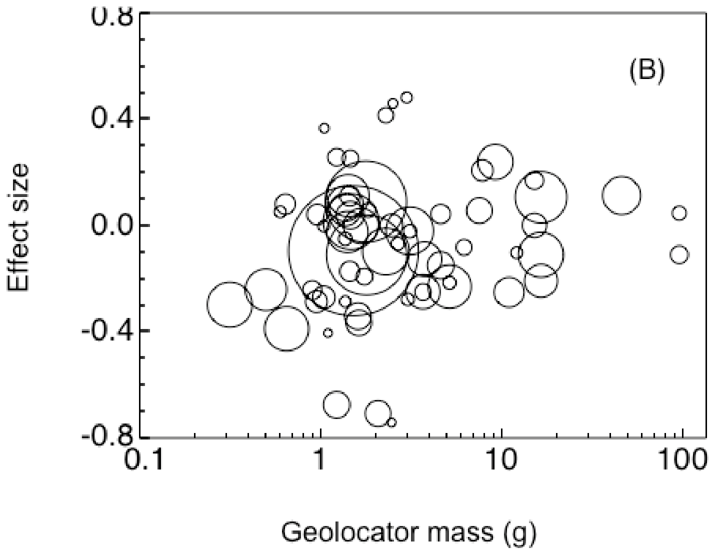


Fig. 1 Effect size (z-transformed Pearson r) and 95% confidence intervals for different estimates ranked by effect size

Notice that many more negative than positive estimates do not overlap with zero (the vertical line).


0.8
(A)
0.4
Effect size
0.0
-0.4
-0.8
0
1
Aerial foraging


0.8
(B)
0.4
Effect size
0.0
-0.4
-0.8
0.1
1
10
100
Geolocator mass (g)

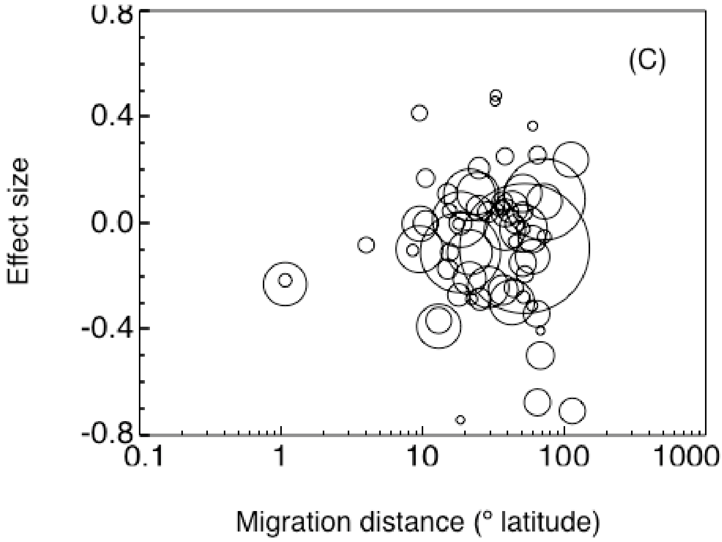


Fig. 2 Effect size for impact of geolocators on birds in relation to (A) aerial foraging, (B) body mass (g) and (C) migration distance (º latitude)

The size of symbols reflects sample size.

Table 1 Summary statistics for mean effect sizes, 95% bootstrap confidence intervals, Rosenthal's fail-safe number, heterogeneity test and the associated *P* value

Effect	Category	*N*	Mean effect	Lower 95% CI	Upper 95% CI	Rosenthal's fail-safe number	Q_{total}	*P*
Overall effect		69	-0.098	-0.154	-0.041	241	87.86	0.053
External information	No	47	-0.047	-0.097	-0.001	301	101.86	0.005
	Yes	22	-0.241	-0.387	-0.099			
Effect size category	Survival	42	-0.134	-0.216	-0.057	250	88.08	0.043
	Condition	15	-0.098	-0.195	0.007			
	Life history	11	0.052	-0.026	0.135			
Aerial foraging	No	34	-0.094	-0.173	-0.020	231	85.36	0.076
	Yes	35	-0.101	-0.197	-0.016			
Attachment	Harness	20	-0.111	-0.231	-0.0001	229	84.91	0.081
	Ring	49	-0.092	-0.159	-0.030			
Migration		68	-0.098	-0.156	-0.046	234	86.21	0.067
Body mass		68	-0.098	-0.153	-0.043	240	87.51	0.056

Table 2 Meta-regression model of effect size in relation to aerial foraging and geolocator mass (g)

Variable	Sum of squares	*d.f.*	*F*	*P*	Estimate (SE)
Intercept		1	15.29	0.0002	-0.355 (0.091)
Aerial foraging	20.543	1	6.09	0.016	-0.054 (0.022)
Geolocator mass	32.687	1	9.69	0.0028	0.152 (0.049)
Migration distance	25.200	1	7.47	0.0082	0.154 (0.056)
Error	205.716	61			

The model was weighted by *N*-3. The model had the statistics $F = 6.52$, $d.f. = 3, 61$, adjusted $r^2 = 0.24$, $P = 0.0007$.

Supplementary Table: Summary information on species, response variable, mean signed effect size, sample size, aerial foraging, attachment type, migration distance (º latitude), species body mass, proportion of body mass for geolocator and references

Species	External sources	Response variable	Signed effect size	z Signed effect size	Aerial foraging	Attachment type	Migration distance	Body mass	Prop. body mass	Total sample size	Sample size geolocators	Article
Acrocephalus paludicola	No	Survival	0.080	0.080	No	**Harness**	36.5	12.5	0.0515	44	14	Salewski et al., 2013, J. Ornithol., 154, 549-552
Alle alle	No	Survival	-0.367	-0.385	No	Leg band	13	163	0.01	70	52	Mosbech et al., 2012, Pol. Biol., 35, 305-311
Apus apus	Yes	Survival	-0.061	-0.061	Yes	Harness	59.39	39.65	0.03	80	80	Åkesson et al., 2012, PLoS One, 7, e41195
Arenaria interpres	Yes	Survival	-0.342	-0.356	No	Leg band	63.875	107.5	0.015	75	75	Minton et al., 2011, Wader Study Group Bull., 118, 40-49
Calidris canutus	No	Survival	0.089	0.089	No	Leg band	72.41	137	0.013	669	47	Niles et al., 2010, Wader Study Group Bull., 117, 123-130
Calidris canutus rufa	No	Condition	-0.051	-0.051	No	Leg band	72.41	137	0.01	21	8	Burger et al., 2012, Condor, 114, 302-313
Calidris canutus rufa	No	Survival	0.082	0.082	No	Leg band	72.41	137	0.01	129	40	Burger et al., 2012, Condor, 114, 302-313
Calonectris diomedea	No	Condition	-0.209	-0.212	Yes	Leg band	21.5	945.5	0.0175	113	24	Igual et al., 2005, Mar. Biol., 146, 619-624
Calonectris diomedea	No	Life history	0.106	0.107	Yes	Leg band	21.5	945.5	0.0175	272	13	Igual et al., 2005, Mar. Biol., 146, 619-624
Calonectris diomedea	No	Survival	-0.111	-0.111	Yes	Leg band	21.5	945.5	0.0175	207	20	Igual et al., 2005, Mar. Biol., 146, 619-624
Calonectris leucomelas	No	Condition	0.207	0.210	Yes	Leg band	25	581	0.0135	49	34	Yamamoto et al., 2008, Anim. Behav., 76, 1647-1652
Calonectris leucomelas	No	Survival	0.055	0.055	Yes	Leg band	25	581	0.013	69	11	Takahashi et al., 2008, Ornithol. Sci., 7, 29-35
Catharacta lonnbergi	No	Condition	0.046	0.046	No	Leg band	15.5	1922	0.05	23	7	Phillips et al., 2007, Mar. Ecol. Progr. Series, 345, 281-291
Catharacta lonnbergi	No	Life history	-0.111	-0.111	No	Leg band	15.5	1922	0.05	35	7	Phillips et al., 2007, Mar. Ecol. Progr. Series, 345, 281-291
Catharacta maccormicki	No	Survival	0.239	0.243	No	Leg band	111.5	1156	0.008	128	58	Kopp et al., 2011, Mar. Ecol. Progr. Series, 435, 263-267
Catharus fuscescens	Yes	Survival	-0.311	-0.322	No	Harness	59.5	31.2		15	15	Heckscher et al., 2011, The Auk, 128, 531-542
Catharus ustulatus	Yes	Survival	-0.244	-0.249	No	Leg band	44	30.58	0.0227	103	39	Delmore et al., 2012, Proc. R. Soc. Lond. B, 279, 4582–4589
Charadrius leschenaultii	Yes	Survival	0.060	0.060	No	Leg band	43	91.4	0.015	108	30	Minton et al., 2011, Wader Study Group Bull., 118, 40-49
Crex crex	Yes	Survival	-0.499	-0.548	No	Leg band	67.915	146.5		80	80	Christiansen S. S. Ehrenberg, 2011, Bläcku, 37, 40-41
Cypseloides niger borealis	Yes	Survival	-0.287	-0.295	Yes	Harness	22.2	45.6	0.03	16	4	Beason et al., 2012, Wilson J. Ornithol., 124, 1-8
Dumetella carolinensis	No	Survival	0.014	0.014	No	Harness	18.5	36.9	0.04	316	22	Ryder et al., 2011, The Auk, 128, 448-453
Falco naumanni	No	Condition	-0.021	-0.021	Yes	Leg band	51.5	152	0.0205	232	36	Rodríguez et al., 2009, J. Field Ornithol., 80, 399-407
Falco naumanni	No	Life history	-0.022	-0.022	Yes	Leg band	51.5	152	0.0205	21	8	Rodríguez et al., 2009, J. Field Ornithol., 80, 399-407
Falco naumanni	Yes	Survival	-0.279	-0.286	Yes	Leg band	51.5	152	0.02	19	19	Catry et al., 2011, Ibis 153, 154-164
Fratercula arctica	Yes	Life history	0.415	0.441	No	Leg band	9.5	383	0.006	27	27	Guilford et al., 2011, PLoS One, 6, e21336
Fratercula arctica	Yes	Survival	-0.099	-0.099	No	Leg band	9.5	383	0.006	225	27	Guilford et al., 2011, PLoS One, 6, e21336
Gallinago media	Yes	Survival	-0.406	-0.430	No	Leg band	68	193.5		10	30	Klaassen et al. 2013, Biol. Lett., in press
Hylocichla mustelina	No	Survival	0.112	0.112	No	Harness	24.5	47.4	0.03	182	47	Stutchbury et al., 2011, Proc. R. Soc. Lond. B, 278, 131-137

Lanius collurio	No	Condition	0.256	0.262	Yes	Harness	64.725	30.7	0.04	34	10	Tøttrup et al., 2012, Proc. R. Soc. Lond. B, 279, 1008-1016
Lanius collurio	Yes	Survival	-0.676	-0.821	Yes	Harness	64.725	30.7	0.04	74	74	Tøttrup et al., 2012, Proc. R. Soc. Lond. B, 279, 1008-1016
Limosa lapponica	No	Survival	-0.127	-0.128	No	Leg band	59.92	301	0.0125	122	24	Conklin and Battley, 2010, Wader Study Group Bull., 117, 56–58
Oenanthe oenanthe	No	Condition	0.251	0.257	No	Harness	38.175	23.95	0.061	32	6	Schmaljohann et al., 2012, Behav. Ecol. Sociobiol., 66, 915-922
Oenanthe oenanthe	No	Life history	0.038	0.038	No	Harness	38.175	23.95	0.061	80	5	Schmaljohann et al., 2012, Behav. Ecol. Sociobiol., 66, 915-922
Oenanthe oenanthe	No	Survival	-0.025	-0.025	No	Leg band	38.175	23.95	0.059	175	15	Bairlein et al., 2012, Biol. Lett., 8, 505-507
Pachyptila belcheri	No	Condition	-0.173	-0.175	Yes	Leg band	15	145	0.01	43	20	Quillfeldt et al., 2012, Mar. Biol., 159, 1809–1824
Pachyptila belcheri	No	Life history	0.111	0.111	Yes	Leg band	15	145	0.01	43	12	Quillfeldt et al., 2012, Mar. Biol., 159, 1809–1824
Passerina ciris	Yes	Survival	-0.389	-0.411	No	Harness	13	15.55	0.04	200	200	Contina et al., 2013, Auk, 130, 265-272
Phoebastria immutabilis	No	Life history	0.169	0.171	Yes	Leg band	10.5	3041.5	0.005	36	14	Young et al., 2009, PLoS One, 4, e7623
Phoebastria immutabilis	No	Survival	0	0	Yes	Leg band	10.5	3041.5	0.005	63	28	Young et al., 2009, PLoS One, 4, e7623
Phoenicurus phoenicurus	Yes	Survival	0.051	0.051	No	Harness	33.93	15.9	0.04	17	17	Kristensen et al., 2013, Auk, 130, 258-264
Pluvialis fulva	Yes	Survival	0.057	0.057	No	Leg band	37	153	0.012	24	24	Johnson et al. 2011, Wader Study Group Bull., 118, 26-31
Procellaria aequinoctialis	No	Condition	-0.103	-0.103	Yes	Leg band	8.5	1213	0.01	17	6	Phillips et al., 2006, Biol. Conserv., 129, 336-347
Progne subis	No	Survival	-0.096	-0.096	Yes	Harness	52.5	49.4	0.025	1705	20	Stutchbury et al., 2009, Science, 323, 896
Pterodroma cookii	No	Life history	-0.069	-0.069	Yes	Leg band	45	178.5	0.015	20	10	Rayner et al., 2008, Mar. Ecol. Progr. Series, 370, 271-284
Puffinus griseus	Yes	Condition	-0.252	-0.258	Yes	Leg band	37	787	0.014	93	18	Adams et al., 2009, New Zealand J. Zool., 36, 355-366
Puffinus pacificus	No	Survival	-0.083	-0.083	Yes	Leg band	4	388	0.016	28	16	Catry et al., 2009, Mar. Ecol. Progr. Series, 391, 231-242
Puffinus puffinus	Yes	Survival	0.459	0.496	Yes	Leg band	32.5	419	0.006	12	12	Guilford et al., 2009, Proc. R. Soc. Lond. B, 276, 1215-1223
Puffinus tenuirostris	No	Condition	-0.150	-0.152	Yes	Leg band	51	543	0.0085	76	9	Carey et al., 2011, Wildlife Res,, 38, 740-746
Puffinus tenuirostris	No	Life history	0.043	0.043	Yes	Leg band	51	543	0.0085	41	11	Carey et al., 2011, Wildlife Res,, 38, 740-746
Puffinus tenuirostris	No	Survival	0.112	0.113	Yes	Leg band	51	543	0.085	147	27	Carey et al., 2009, Emu, 109, 310-315
Riparia riparia	No	Survival	-0.299	-0.308	Yes	Harness	42.725	13.15	0.024	206	33	Tibro Szep, pers. comm.
Seiurus aurocapilla	No	Survival	-0.287	-0.295	No	Harness	25.5	19.2		97	51	Hallworth et al., 2013, Auk, 130, 273-282
Stercorarius longicaudus	Yes	Survival	0.481	0.524	Yes	Leg band	32.9	276	0.006	15	15	Gilg et al., 2013, PLoS One, 8, e64614
Sterna dougallii	No	Condition	-0.742	-0.955	Yes	Leg band	18.5	120	0.02	10	5	Carolyn Mostello and Ian Nisbet, unpublished data; do not use without permission
Sterna dougallii	No	Life history	0	0	Yes	Leg band	18.5	120	0.02	56	19	Carolyn Mostello and Ian Nisbet, unpublished data; do not use without permission
Sterna dougallii	No	Survival	-0.111	-0.112	Yes	Leg band	18.5	120	0.014	651	20	Carolyn Mostello and Ian Nisbet, unpublished data; do not use without permission
Sterna hirundo	No	Life history	-0.193	-0.196	Yes	Leg band	52.75	135	0.014	31	15	Nisbet et al., 2011, Waterbirds, 34, 32-39
Sterna paradisaea	Yes	Survival	-0.708	-0.884	Yes	Leg band	114.17	109.5	0.019	70	50	Egevang et al., 2010, PNAS 107, 2078-2081
Tachycineta bicolor	Yes	Survival	-0.242	-0.247	Yes	Harness	29	20.1		482	177	Laughlin et al., 2013, Auk, 130, 230-239

Tachycineta bicolor	No	Life history	0.041	0.041	Yes	Harness	29	20.1	0.05	198	23	Gómez et al., 2013, J. Ornithol., in press
Tyrannus tyrannus	Yes	Survival	0.366	0.383	Yes	Harness	60	43.6	0.04	12	12	Jahn et al., 2013, Auk, 130, 247-257
Upupa epops	No	Survival	-0.003	-0.003	No	Leg band	9.585	67.05	0.025	129	18	Bächler et al., 2010, PLoS One 5, e9566
Uria aalge	No	Condition	-0.231	-0.235	No	Leg band	1.07	861.5	0.0055	191	10	Hedd et al., 2011, Anim. Conserv., 14, 630-641
Uria aalge	Yes	Survival	-0.216	-0.219	No	Leg band	1.07	861.5	0.006	20	20	Hedd et al., 2011, Anim. Conserv., 14, 630-641
Uria lomvia	No	Condition	-0.250	-0.256	No	Leg band	0	919.5	0.004	121	15	Elliott et al., 2012, Mar. Ecol. Progress Series, 466, 1-7
Uria lomvia	No	Survival	-0.251	-0.256	No	Leg band	0	919.5	0.004	179	15	Elliott et al., 2012, Mar. Ecol. Progress Series, 466, 1-7
Vireo olivaceus	No	Survival	-0.004	-0.004	No	Harness	44.5	16.7	0.03	37	26	Callo et al., 2013, Auk, 130, 240-246
Zonotrichia atricapilla	No	Condition	-0.004	-0.004	No	Harness	18	29.8	0.035	16	10	Seavy et al., 2012, PLoS One, 7, e34886
Zonotrichia atricapilla	No	Survival	-0.271	-0.278	No	Leg band	18	29.8	0.035	54	26	Seavy et al., 2012, PLoS One, 7, e34886