An experimental evaluation of the effects of geolocator design and attachment method on between-year survival on Whinchats *Saxicola rubetra*

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Tweetable abstract: Migrant birds are declining; location tags can tell us why but have survival costs; we show how they can be used safely

Data from location logging tags have revolutionised our understanding of migration ecology, but methods of tagging that do not compromise survival need to be identified. We compared resighting rates for 156 geolocator-tagged and 316 colour ringed-only Whinchats on their African wintering grounds after migration to and from Eastern Europe in two separate years. We experimentally varied both light stalk length (0, 5 and 10 mm) and harness material (elastic or non-elastic nylon braid tied on, leg-loop ‘Rappole’ harnesses) in the second year using a reasonably balanced design (all tags in the first year used an elastic harness and 10 mm light stalk). Tags weighed 0.63 g (0.01SE), representing 4.1 % of average body mass. There was no overall significant reduction in between-year resighting rate (our proxy for survival) comparing tagged and untagged birds in either year. When comparing within tagged birds, however, using a tied harness significantly reduced resighting rate by 53 % on average compared to using an elastic harness (in all models), but stalk length effects were not statistically significant in any model considered. There was no strong evidence that the fit (relative tightness) or added tag mass affected survival, although tied tags were fitted more tightly later in the study, and birds fitted with tied tags later may have had lower survival. Overall, on a precautionary principle, deploying tags with non-elastic tied harnesses should be avoided because the necessary fit, so as not to reduce survival, is time-consuming to achieve and does not necessarily improve with experience. Geolocator tags of the recommended percentage of body mass fitted with elastic leg-loop harnesses and with short light stalks can be used without survival effects in small long-distance migrant birds.

Information from individual animals on their identity, location, survival, social interactions, condition and much more, can now be obtained by tagging, allowing large amounts of novel information to be gathered to inform physiological, behavioural, ecological and conservation studies (Burger and Shaffer 2008, Cooke et al. 2004, Ropert-Coudert and Wilson 2005, Rutz and Hays 2009). Recently, miniaturisation of geolocators (tags that record light levels across time, enabling estimates of sunrise and sunset, and hence location, to be calculated) has enabled their deployment on passerine birds (Bridge et al. 2013, Stutchbury et al. 2009). The results of these studies have been revolutionary and much valuable data has been obtained from them, which can greatly contribute to our understanding of migration ecology and the conservation of declining species (e.g. Bairlein et al. 2012, Delmore et al. 2012, Lemke et al. 2013). Although these tags may be superseded by more accurate GPS tags in due course (Tomkiewicz et al. 2010, Bouten et al. 2013) as with radio tags before them (Kenward 2000), the range of options of attachment for any tag and its characteristics such as tag mass and protruding sensors or antennae remain as issues that can potentially affect the fitness of tagged animals (Pennycuick et al. 2012).

The attachment of a tag may affect the behaviour (Barron et al. 2010) and survival (Murray and Fuller 2000) of animals by altering their condition, energetics or movement (Walker et al. 2012). These “tag effects” apply particularly for taxa where travel speed or efficiency depends on their reducing hydrodynamic (Bannasch et al. 1994) or aerodynamic effects (Scandolara et al. 2014), and when taxa are small so that the weight of the tag itself may constrain the animal (Bowlin et al. 2010, e.g. Zenzal et al. 2014). Small birds (<15 g) present the current limit for field attachment of tags because battery limitations mean that tags are relatively large and at the 3-5 % of body weight limit that is widely regarded as the threshold for significant effects (Caccamise and Hedin 1985, Cochran 1980, Kenward 2000). The use of geolocators on small passerines has so far produced equivocal results with respect to whether their use impacts fitness (Fairhurst et al. 2015, Peterson et al. 2015, Bridge et al. 2013) or substantially reduces survival rate (Gomez et al. 2014, Costantini and Moller 2013), although a meta-analysis concluded that deleterious effects are widespread (Barron et al. 2010). A key issue is that the majority of geolocator studies do not have a formal control group, nor do they adopt an experimental approach to measure variation in effects due to tag design.

Size, weight, design and method of attachment largely determine the extent of any tag-effect. Tags and harnesses may change a flying bird’s centre of gravity (Vandenabeele et al. 2014) constraining flight or manoeuvrability, may become snagged on vegetation (e.g. Dougill et al. 2000), or snag limbs or bills during grooming or preening (Hill et al. 1999, Kenward 2000). Geolocator tags can vary in the presence of and length of a light stalk, which may carry the additional trade-off of less noisy light data versus a potential reduction in aerodynamic efficiency or chance of becoming snagged (Peterson et al. 2015). How tags are attached to birds can vary not only in the choice of harness design but also in the flexibility of the harness material used and the final tightness of tag on the bird (Naef-Daenzer 2007).

Determining the impact of tags on migrant birds is particularly important given the rapidly increasing number of studies now using tracking devices to map the migration routes of small migrants (Hedenstrom and Lindstrom 2014), many of which are in decline (Vickery et al. 2014). In this study, we aimed to determine whether some elements of geolocator tags and the methods of their attachment influence annual survival for a small, long-distance migrant. We compared tag effects on 156 whinchats (body mass c.15 g) with 316 colour-ringed only controls wintering in Jos, Nigeria. Whinchats were caught and tagged, or controls colour-ringed (or resighted if ringed during previous seasons) in February and March. Returning individuals were then recaptured or resighted the following wintering season (September – March) after migration to and from Eastern Europe. We experimentally varied both the light stalk length (0, 0.5 and 10 mm) and attachment method and material of attachment (pre-made elastic or adjustable but non-elastic tied nylon leg-loop harness) in the second year using a reasonably balanced design (tags in the first year were all deployed with an elastic harness and 10 mm light stalk). Total load (tag + harness) varied between 2.5 and 5.3 % of body mass. All harnesses had an acceptable fit but we also tested harness fit and order of application in case experience altered fit. Tag mass was also a potentially confounding variable in our study but this was mostly determined by whether the tags had light stalks. Nevertheless, lighter tags and larger birds would likely lead to lower tag effects so we considered added wing loading (tag and harness mass/wing length, see Norberg and Rayner 1987, Rayner 1990), the extra percentage that any tag and harness added in all analyses. We also considered the confounding effects of body mass and time of year because these may also influence resighting and survival rates. We therefore tested:

1. How tags affected between-year return rates of tagged versus control birds by comparing probability of return.

2. How tag and harness characteristics affected between-year return rates of tagged birds by comparing probability of return dependent on harness material and light stalk length.

3. If any effects of tag design depended on harness material, order of attachment, or the fit of the tag.

4. Whether condition and body mass varied between returning tagged birds and newly caught controls.

Methods

The study took place between February 2013 and November 2013 (Year 1) and February 2014 until April 2015 (Year 2) during the dry season (early September to late April) on the Jos Plateau in the guinea savannah zone of central Nigeria, West Africa (N09°53', E08°59', approximately 1250 m altitude). Note that each Year encompassed two wintering periods. Some control colour-ringed only Whinchats were captured outside of these months (i.e. earlier in the wintering period or were colour-ringed birds that had returned from previous winters); but see below for which birds were included in the control cohort. Whinchats were captured within an area of approximately 5 x 8 km; full site details are described in Blackburn and Cresswell (2015c). Capture areas were principally open scrubland with varying degrees of habitat degradation from human habitation, arable farming and livestock grazing, the latter increasing in intensity over the dry season (see Hulme and Cresswell 2012, Blackburn and Cresswell 2015a). The study area represents typical wintering habitat for this species in the area (open savannah) and had high densities of Whinchats.

Harness manufacture and fitting

In Year 1 we deployed 49 geolocator tags of model MK6740, developed by the British Antarctic Survey (BAS) with a 10 mm light-stalk positioned at a fixed angle of 45°, with the tube for harness attachment placed on the back instead of the end of the tag (Figure 1). In Winter 1, average geolocator mass (without harness) was 0.69, 0.02 SE g. In Year 2 we deployed 94 geolocators of model ML6740 of the same design but in light grey instead of black to reduce heat absorption (Figure 1): 47 had long light-stalks of 10 mm (0.64, 0.02 SE g) and 47 had short light-stalks of 5 mm (0.57 0.01 SE g). We also fitted 36 black tags ML6540 with no light-stalks (0.42, 0.01 SE g). The average mass of the elastic loop harness was 0.05, 0.01 SE g and for the tied harness this was 0.03, 0.01 SE g (measured from harnesses removed from birds on recovery of the tag); sample size details are given in Table 1.

We used leg-loop harnesses, also known as ‘backpack’ or ‘Rappole-Tipton’ harnesses. We used two harness materials: an elastic leg-loop design (Rappole and Tipton 1991) which was not adjustable during fitting, and the same design but using a tied harness made from braided nylon thread which allowed the fit to be adjusted on the bird. We fitted 74 elastic harnesses (30 on long light-stalks, 30 on short light-stalks, and 14 on no light-stalk tags), and 56 tied harnesses (17 on long light-stalks, 16 on short light-stalks, and 23 on no light-stalk tags). In Year 1 only elastic harnesses were used (49 tagged birds overall) whereas in Year 2 we fitted an even spread of either elastic or tied non-elastic harnesses to the 18^{th} to 106^{th} bird tagged (of 130 birds tagged overall).

All harnesses were constructed and attached to the geolocator prior to fieldwork (see Figure 1 and Supplementary Material: Harness Construction). The relationship between final fitted span in mm and wing length was: span = ((0.16, 0.06 SE) x (maximum wing chord length in mm)) + (22.8, 4.3 SE): $F_{1,92} = 8.3$, $P = 0.0048$, adjusted $R^2 = 0.07$. The relationship between final fitted span in mm and body mass was: span = ((0.48, 0.10 SE) x (body mass in g)) + (27.8, 1.6 SE): $F_{1,93} = 21.6$, $P < 0.0001$, $R^2 = 0.18$. Including wing length in the model with body mass only contributed a further 1.3 % of overall variance.

Captures and harness fitting

Captures, harness fitting and assessment of fit are fully detailed in Supplementary Materials: Captures and harness fitting. In brief, whinchats were caught by spring traps and mist nets, aged and sexed, ringed with individual combinations of colour-rings and fitted with a geolocator. Elastic harnesses took approximately 1 minute to fit and all were fitted by EB. Tie harnesses took approximately 7 minutes to fit and all were fitted by both EB and MB working together. Two observers (EB Year 1 or both EB and MB Year 2) assessed all geolocator/harness fits before release. Fit assessment was independent of harness material. Harness fit was scored on a scale of increasing tightness from 1-3: a score of 1 indicated a looser fit with clear movement from side to side and up and down of more than 3 mm and movement of the tag without influencing the bird's position; 2 indicated a fit with displacement of 1-3 mm up or down or side to side with little resistance; 3 indicated a tighter fit with only slight movement of the tag and some resistance when attempting to move the tag away from the bird's back and moving the tag also caused the bird's body to move. Birds were released immediately after harness fit was assessed at their capture location.

Control birds, resighting and recapturing birds

Control birds were captured, handled and colour-ringed as per tagged birds, except that no tag was fitted. Control birds were mainly ringed as part of a larger study into Whinchat wintering ecology from January 2012 until March 2014 (see Blackburn and Cresswell 2015c, Blackburn and Cresswell 2015a). We resighted both tagged and control Whinchats to establish a) the degree of residency in their winter of capture, and b) whether a bird had returned the following winter. Some Whinchats in the study area had relatively short residency periods, with evidence of an increase in transient or passage individuals towards the end of the wintering period (Blackburn and Cresswell 2015c) so that a colour-ringed Whinchat might be present for one half of the wintering period. For whinchats ringed in Year 1, resighting for birds returning in the following winter was carried out systematically from October to January. Therefore in the first year, we considered only tagged and control birds that we were reasonably confident were resident on the site in their winter of capture: only control birds that were resighted, or tagged birds that were resighted after capture, during the period of fitting tags were considered. For Whinchats ringed in Year 2, resighting effort for return in the following winter increased and was carried out from September 2014 to April 2015 inclusive, several times a week so that even very short term residents or transients moving through the study area could have been resighted. This allowed us to greatly increase the sample size of control and tagged birds we could consider to analyse return rates. In Year 2, we therefore considered any colour-ringed bird resighted during the winter of 2013-14 to be a control bird for the following winter and every tagged bird caught in February-March 2014 as an experimental bird.

A Whinchat was considered to have been resighted if its colour-rings were visually recorded by a good sighting through a telescope (Zeiss Diascope 65 mm with 25x eyepiece). Whinchats perch conspicuously, allow approach to within 50 m and can be immobile for long periods allowing their rings to be easily read, particularly in the bright conditions present in the winter in Africa. Whinchats resighted in Year 2 (September-April 2014-15) were sighted on average 3.7 (0.3 SE) times. When a tagged bird was resighted attempts were made to recatch the bird to recover its geolocator as part of a wider study. Upon recapture, geolocators were removed by cutting the harness, and any negative effects such as chaffing or feather damage from the harness were noted.

Analyses

Overall sample size was 460 birds, but a small number of birds acted as controls in both years and one control bird in Year 1 was tagged in Year 2 resulting in a sample size of 472 including 156 tagged birds and 316 control birds (overall sample size details are in Table 1 and detailed sample sizes in Table S1). Some analyses had smaller sample sizes because of missing biometric and fit data not collected in the field. Two recaptured tagged birds (6 %, out of 16 recaptured from Year 1 and 21 recaptured from Year 2) were missing their tags – both with elastic harnesses – but are included because we are interested in the effects on overall survival of the tagging process not the efficiency of the technique. Analyses were nonetheless repeated throughout without these birds to determine the effect of this inclusion on the results. In Year 2, 18/39 resighted Whinchats with tags were not recaptured because many had become extremely wary of spring-traps and mist-nets: 12/18 of these birds were visually seen to be carrying tags during lengthy attempts at recapture; the remaining 6 were carrying tags without light stalks that cannot be readily observed even when a bird is in the hand.

The mean body mass of Whinchats in the study was 15.2 g (0.05 SE; N = 471); the mean body mass of birds selected for tagging was 15.3 (0.08 SE; N = 156). The mean mass of tag and harness was 0.63 g (0.01 SE, N = 156), representing an average percentage of body mass for tagged birds of 4.13 % (0.05 SE) calculated as the average mass of tag and harness mass added/mass at capture. The percentage body mass that the tags represented varied from a minimum of 2.5 % to a maximum of 5.3 % dependent on the tag design and harness method and the body mass of the bird (range 13.2 – 19.0 g). In both years, the mass of birds selected for tagging was slightly, but significantly higher than control birds (tagged birds weighed 0.25, 0.10 SE g more than control birds, $t_{1,468}$ = 2.4, P = 0.015; year $t_{1,468}$ = 0.7, P = 0.47; year*tag presence added to the model, $t_{1,467}$ = -0.9, P = 0.33). In the first year only, wing length of tagged birds was slightly, but significantly higher than control birds (wing length, first year, control 77.1, 0.3 SE mm versus tag presence 78.3, 0.5 SE mm, $t_{1,60}$ = 2.6, P = 0.012; wing length second year, control 78.2, 0.1 SE mm versus tag presence 78.0, 0.2 SE mm, $t_{1,404}$ = -1.1, P = 0.24; year*tag presence interaction in overall model, $t_{3,464}$ = -2.6, P = 0.009). We therefore consider the potential confounding effects of biases in body size in detail in the following analyses and also repeat all analyses using only control birds with wing lengths of >= 77 mm and without very low muscle scores to remove the bias that we introduced by only tagging larger birds (see Supplementary Material: Supporting results examining the effects of missing values and Table S1 detailing the sample sizes in these analyses).

In general, we tested how between year resighting rate, as a proxy for true survival, after a complete migration cycle varied with respect to tag presence and characteristics controlling for a number of confounding variables. The probability of resighting was a binomial (1 = resighted the following winter, 0 = not), and was our dependent variable in most cases. Predictors of interest were: harness material (factor, elastic or tied), and light stalk length (continuous scale, 0, 5 or 10 mm length). Confounding variables considered were the harness fit (on a continuous scale, loose to tight, looser=0, neither loose nor tight=1, tighter=2) because although we attempted to fit all tags as optimally as possible there was some slight variation in fit; the order of attachment (where 1 was the first tag fitted and 20 the 20th etc., with separate counts for each harness material) because increased experience of the fitters for a harness material might be expected to reduce tag effects associated with fitting and handling; Julian date (where 1 = 1st Feb) because the first 16 and last 25 birds in Year 2 were fitted solely with elastic harnesses; year because annual survival rates were expected to vary regardless of tagging; tagged bird mass because condition may affect survival rates; and the added wing loading imposed by a tag if present (mean mass of the tag and harness/wing length of the individual, with values of 0 % for control birds) because relative tag mass may also influence survival. We also examined whether the tag effects of interest (harness material, stalk length) might have an interactive effect on survival and whether they were dependent on the fit. We do not consider sex and age in any models because previous analysis has shown that neither affects survival in untagged birds in this population (Blackburn and Cresswell 2015b) and to avoid over parameterising models. Full details of the models tested are given in the Supplementary Material: Model structures.

All analyses were carried out using R version 3.1.1 (R Development Core Team 2014). Because we were likely to have overparameterised starting models we used model reduction on the basis of AIC (Burnham and Anderson 2002). To avoid subjectivity in model selection we considered all possible models using the Dredge function in the MuMIn library (Bartoń 2012) to identify and rank the most important variables in terms of the proportion of predictive models that they occurred in. When presenting top models from Dredge analyses, we included models within 2 ΔAICc of the top model to give a representative range of models to illustrate that there was no clear "top" model. Cases with missing values were removed from the dataset as required for Dredge analyses (i.e. any birds with a missing value for any of the variables in the full model were removed from all possible models). Model fits were evaluated from diagnostic model plots and models were presented if assumptions were reasonably met (Crawley 2007). Collinearity among variables in models was examined using the Variance Inflation Factor command VIF in the R library Car: no variables exceeded thresholds of acceptability. Mean values are presented as means followed by one standard error (SE) in all cases.

Results

1. No tag effect when comparing controls and tagged birds

Simple frequency analyses of resighting rates showed no obvious tag effect (Year 1: 16/37 = 43.2 % control vs 10/26 = 38.4 % tagged; Year 2: 74/279 = 26.5 % control vs 39/130 = 30.0 % tagged) and the proportion of control birds resighted compared to the proportion of tagged birds resighted was not significantly different in each year (2013: $\chi^2_1 = 0.01$, $P = 0.99$; 2014: $\chi^2_1 = 0.2$, $P = 0.66$). The ratio of resighting rates for control compared to tagged birds was not significantly different between years ($\chi^2_1 = 0.1$, $P = 0.70$). The proportion of control birds compared to tagged birds resighted was not significantly different when years were pooled ($\chi^2_1 = 0.\ 1$, $P = 0.70$).

The probability of resighting a bird the following winter was independent of almost all variables, combinations of variables and interactions considered (Table 2). Resighting rate was lower overall in the second year of the study and there was a slight trend for heavier birds to have a higher likelihood of resighting (top model, Table 2). The null model was only 0.6 ΔAICc points below the highest ranking model that included tag presence.

2. Harness material but not light stalk length reduced between-year resighting rate of tagged birds

The probability of resighting a tagged bird was dependent on whether it had an elastic or tied harness, with a lower probability of resighting if the tag was tied on (Figure 2): attachment method was present in all models with a significant effect in the full and all top models (Table 3). Stalk length was present in 47 % of 15 top models with a decrease in resighting rate with increasing stalk length (Figure 3) but this was not statistically significant in any model. There was only very weak evidence for effects of body mass, added wing loading, harness fit, and order of attachment affecting resighting rate and there were no confounding effects of year; however, birds that were tagged later (i.e. in March rather than February) were more likely to be resighted (Table 3). In terms of biological effects, the top model (Table 3) predicted a resighting rate of 0.48 for an elastic harness, no light stalk, median date of tagging compared to 0.23 for the same bird with a tied harness (a decrease in resighting rate of 53 %), compared to 0.40 and 0.31 for the same bird with a 5 mm and a 10 mm light stalk respectively.

When analysis was restricted to birds fitted only with elastic harnesses and 10 mm light stalk tags, to look at any effect of relative tag mass, added wing loading was not a significant predictor of resighting probability (-298.3, 166 SE, z = -0.2, P = 0.86), controlling for body mass, year, order and fit; interactions with year substantially worsened the model in terms of much higher AIC values.

3. The effects of harness material may have been dependent on harness fit

The only potential interaction identified was an effect of harness material depending on order of attachment, with tied tags possibly reducing resighting rates if they were fitted later (Table S2 Supplementary Material, Figure 3A). The interaction of harness material with order was retained in 42 % of top models and was marginally significant, both as a model averaged parameter estimate and in the top model (Table S2 Supplementary Material). We found that harness fit changed with order of attachment dependent on harness material, becoming marginally significantly looser for elastic harnesses and significantly tighter for tied harnesses for tags fitted later in the study (Table S2 Supplementary Material, Figure 3B).

4. No apparent effects of tags on condition or body mass

Apart from a small bald patch of featherless, calloused skin around 4 mm in diameter directly underneath the tag and some dry skin where the harness material contacted the thigh, all recaptured tagged birds were indistinguishable on visual inspection from untagged birds that were inadvertently caught during the recapture mist-netting. Seventeen tagged birds recaptured in Year 2 were matched with new birds captured within 15 minutes at the same location: there was no significant difference in body mass (matched pairs t test, t_{16} = -0.7, P = 0.48, tagged birds 15.0, 0.2 SE g versus untagged birds 15.2 +/- 0.2 g).

Discussion

In our study, tagging a bird with a geolocator over a full migratory cycle had no influence on between-year resighting rate, provided that geolocators were fitted with elastic harnesses. Our results therefore show that with careful choice of study birds, tag weight, harness material and possibly light stalk length it is possible to achieve apparent survival rates that do not differ from the population average. Geolocator tags may, however, have negative effects when they are attached using a non-elastic harness material and tie attachment method, for which the fit appears to be much more important. In contrast, the fit of elastic harnesses appears to be less important. Light stalk length does not seem to have any significant effect on survival, although longer stalks may tend to lower survival. There was weak statistical evidence to suggest that, if light stalks had any effect, stalks of 5 mm or less had little biological effect compared to 10 mm length stalks. Consequently, geolocator tags on Whinchats should be attached with flexible elastic leg-loop harnesses and on the basis of a precautionary principle, should be fitted with short (c. 5 mm or less) light stalks. Tags should, of course, minimise weight: our study shows that tags that varied between 2.5 and 5.3 % of body mass can have no effect on apparent survival.

The mechanism for the reduction in survival caused by attaching tags with tied, non-elastic harnesses is likely due to the lack of stretch and flexibility in the material, making it more important to achieve the correct fit when attaching the geolocator. Whinchats are typical passerine migrants and may increase their body mass by over 50 % during pre-migratory fattening (Risely et al. 2015), and so non-elastic harnesses may become tighter and potentially prohibitively constricting as birds increase in size. Fat stores are deposited in areas that would cause harness fit to become tighter, especially when large amounts of fat are deposited such as during pre-migratory fattening (e.g. see Fig. 1 5-8 in Kaiser 1993, Dunn 2003). Flight muscle mass often increases also during pre-migratory fattening (Piersma 1990, Lindstrom and Piersma 1993), which could also cause harnesses to become tighter. The flexible characteristic of elastic harnesses may reduce the consequences of these effects. Relevant to this was the better relationship we found between the span of the elastic harness that was fitted and the size of the bird when this was measured by body mass rather than wing length. This suggests that variation in body mass rather than skeletal size of the bird determines the harness fit and so body mass gains post fitting may be an important consideration when using non-elastic harnesses. Alternatively, differences in attachment time and procedure may have caused the tag effect.

Attachment of geolocators using tied harness took at least four times as long, involved two people handling the bird and glue in very close proximity to the bird, and increased handling time has been shown to reduce survival in tagging studies (Ponjoan et al. 2008, Sharpe et al. 2009). Whether our handling times when fitting tied harnesses exceeded any threshold for harm is unknown. There was, however, probably no effect of harness material on the probability of resighting a tagged bird during the marking period, i.e. an immediate effect of tagging of any type (the null model was the top model with a weight of 0.30 and harness material appeared in none of the six top models with the same starting structure as in Table 3 except predicting probability of resighting at least once after capture during the tagging period, and considering only Year 2 data). We did not, however, systematically record handling time, nor did we systematically attempt to resight all birds with equal effort making this analysis only suggestive. Furthermore, in Year 2, 41 of the tagged birds and 34 control birds were resighted systematically until their departure: no obvious effects were seen on any birds and departure date was not significantly different for tagged and untagged birds (Risely et al. 2015).

It is important to note that our study only considers part of the annual cycle for Whinchats; nevertheless we consider both migration periods, which represent the most likely times that tags would exert a detrimental effect on survival. It is also important to consider that we selected larger birds for tagging in both years, and heavier birds in the first. However, analyses comparing tagged birds to equivalently large control birds gave essentially identical results. Our wider study of Whinchats shows no effects of body size (wing length and body mass at capture), and age or sex, on apparent annual survival rates (Blackburn & Cresswell unpublished).

Other results have some bearing on the hypothesis that differences in survival due to harness method may be due to the difference in fits, although these results are contradictory. We established reasonable evidence for a change in fit with handler experience (Fig. 3B) and suggestive evidence for a change in between-year resighting probability with handler experience (Fig. 3B), both that were dependent on attachment method. However, fit never appeared in any top models and did not ever significantly predict resighting rate. The logical interpretation for the first set of results is that later tied fits were tighter, leading to a decrease in survival for birds tagged later, but then the interpretation arising from the second result is that resighting effects as a consequence of order must be independent of fit. One possible reason for the contradiction is that the majority of fits for both harness materials was 'good', so that fit would have correspondingly much lower leverage in any model than order of attachment. Tags were also all fitted before the period of pre-migratory fattening for whinchat with most birds being close to their lean mid-winter body mass (Risely et al. 2015). Despite the contradiction we can still draw some reasonably supported conclusions. Elastic harnesses can likely compensate where a tighter harness may negatively impact the bird, and certainly grant more flexibility in the event of large body mass gains. With no effect of fitting experience, it also seems more likely that both naive and experienced single researchers can more quickly and safely use the technique.

The mechanism for reduction in survival caused by light stalks, if this occurs – and it should be stressed at this point that there is only very limited statistical evidence for an effect – is likely to be aerodynamic. Longer, light stalks that protrude above the feathers will increase drag and the energy needed to fly and migrate (Bowlin et al. 2010). There was no indication of an interaction between attachment method and stalk length that might indicate that snagging in vegetation was a problem. There is, of course, a trade-off between the utility of a geolocator without a light stalk because light records are less accurate when the light sensor (located at the end of a light stalk for stalked geolocators) is covered with feathers, and so fewer reliable positions may be obtained (but see Peterson et al. 2015 where the presence of stalks made no difference to data quality).

Overall the of use of geolocators and of elastic leg-loop harnesses for their attachment, in instances where the durability of inflexible nylon harnesses is not required, seems compelling: geolocators can have no or limited impacts on survival, and elastic harnesses are quicker and easier to fit and also probably do not reduce survival (see also Streby et al. 2015). It should be noted, however, that inflexible nylon harnesses have been applied successfully in other studies, including some with ringed-only control cohorts where no effect on return rate was noted (C Hewson, unpublished data). Our results may suggest that non-elastic harnesses could be used if fitted looser than elastic harnesses. We recommend using elastic leg-loop harnesses and minimising light stalk length. Our results suggest that for a fairly typical, small, long-distance migrant passerine, fitting geolocators or similar tags need not have any detrimental effect on survival – it is possible, however, that our results could have been different in another year, with more severe environmental conditions. A key point is that only through experiment can we determine our effects and ultimately minimise them, and so answer the vital population dynamic questions that can only be addressed through marking and tagging animals. Future geolocator studies should, at the very least, have a control cohort and report tag effects properly, and carefully measure any variation in tag and harness parameters to explore the reason for any emergent tag effects.

Acknowledgements

The study was carried out in Nigeria where no licences are required for the procedures used. Nevertheless this study was carried out under the ethical guidelines of the AP Leventis Ornithological Research Institute Scientific Committee (APLORI is the only ornithological research institute in Nigeria) based on the Association for the Study of Animal Behaviour guidelines and those of the British Trust for Ornithology's ringing scheme. All personnel involved in fieldwork – either catching, colour-ringing or tagging birds had BTO ringing licences. MB and CH had been previously licensed to fit geolocators in the UK. This work was supported by the Chris Goodwin, A.P. Leventis Conservation Foundation, AP Leventis Ornithological Research Institute, the British Ornithologists' Union and the Linnean Society. This is paper number 105 from the AP Leventis Ornithological Research Institute.

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Table 1: Sample sizes of tagged and control birds split by year of study, tag and attachment type.

	2013		**2014**							**Overall**	
	Control	Long Elastic	Control	Long Elastic	Long Tie	Short Elastic	Short Tie	None Elastic	None Tie	Control	Tagged
Ringed	37	26	279	30	17	30	16	14	23	316	156
Resighted	16	10	74	10	1	13	4	6	5	90	49

Table 2: Model evaluation of the most important variables predicting resighting rate for tagged and control birds (N = 468). Models were ranked by AIC and total weight calculated (proportion of top models where a variable was present) within ΔAIC = 2 of the top model (N = 6). The coefficients for the initial full model and the coefficients for the top model (AIC weight 0.31) are also given. Note interactions including tag * added wing loading are not included in the table because there was no variation because of the experimental design (i.e. added wing loading is a function of tag design).

	Total	No.	Full model				Top model r^2 = 0.01		
	weight	models	Est.	SE	Z	P	Est.	SE	P
Intercept[1]			-1.4	5.6	-0.3	0.80	-2.8	1.5	0.058
Year	0.88	5	-0.96	5.8	-0.2	0.87	-0.57	0.28	0.042
Body Mass	0.88	5	0.073	0.37	0.2	0.85	0.16	0.097	0.098
Tag	0.12	1	0.74	38.1	0.02	0.98			
Mass*Year	0.12	1	0.017	0.39	0.05	0.96			
Added Wing loading	0.12	1	-120.7	370.4	-0.3	0.75			
Year*Tag			7.7	3.2	0.2	0.81			
Mass*Tag			-0.17	1.5	-0.1	0.91			
Wing load*Mass			90.2	140.0	0.6	0.52			
Wing load*Year			-219.3	296.2	-0.1	0.94			
Mass*Year*Tag			-0.34	-0.75	-0.5	0.65			

[1]Intercept = Year 1, No tag

Table 3: Model evaluation of the most important variables predicting resighting rate for tagged birds (N = 149). Models were ranked by AIC and total weight calculated (proportion of top models where a variable was present) within ΔAIC = 2 of the top model (N = 15). The coefficients for the initial full model and the coefficients for the top model (AIC weight 0.12) are also given.

	Total	No.	Full model				Top model R^2 = 0.08			
	Weight	models	Est.	SE	Z	P	Est.	SE	z	P
Intercept[1]			-4.7	4.5	-1.0	0.30	-0.59	0.50	-1.2	0.24
Tied	1	15	-1.9	0.94	-2.0	0.043	-1.2	0.5	-2.5	0.013
Julian date[2]	0.65	9	0.040	0.025	1.6	0.11	0.029	0.015	1.9	0.056
Stalk length	0.47	7	--1.3	1.3	-1.0	0.33	-0.76	0.51	-1.5	0.13
Body Mass	0.34	5	0.24	0.22	1.1	0.26				
Harness fit	0.22	4	-0.35	0.30	-1.2	0.24				
Added Wing loading	0.18	3	128.4	409.9	0.3	0.75				
Attachment order	0.05	1	-0.017	0.015	-1.1	0.27				
Year 2	0	0	1.1	1.2	0.9	0.36				

[1]Intercept = Elastic, Year 1

[2]Julian date 1 = 1st Feb

Table 4: The effect of order of attachment, year and harness material (elastic or tied) on fit of the tag (N = 150). More negative values indicate a looser fit. Overall model $F_{4,145} = 2.7$, $P = 0.033$, Adj. $R^2 = 0.04$.

	Estimate	SE	t	P
[1]Intercept	0.84	0.15	5.5	<0.0001
Attachment order	-0.0057	0.0032	-1.8	0.077
Year 2	0.50	0.26	1.9	0.059
Tied	-0.47	0.34	-1.4	0.16
Order * Tied	0.013	0.0062	2.0	0.046

[1]Intercept = Year 1, Elastic

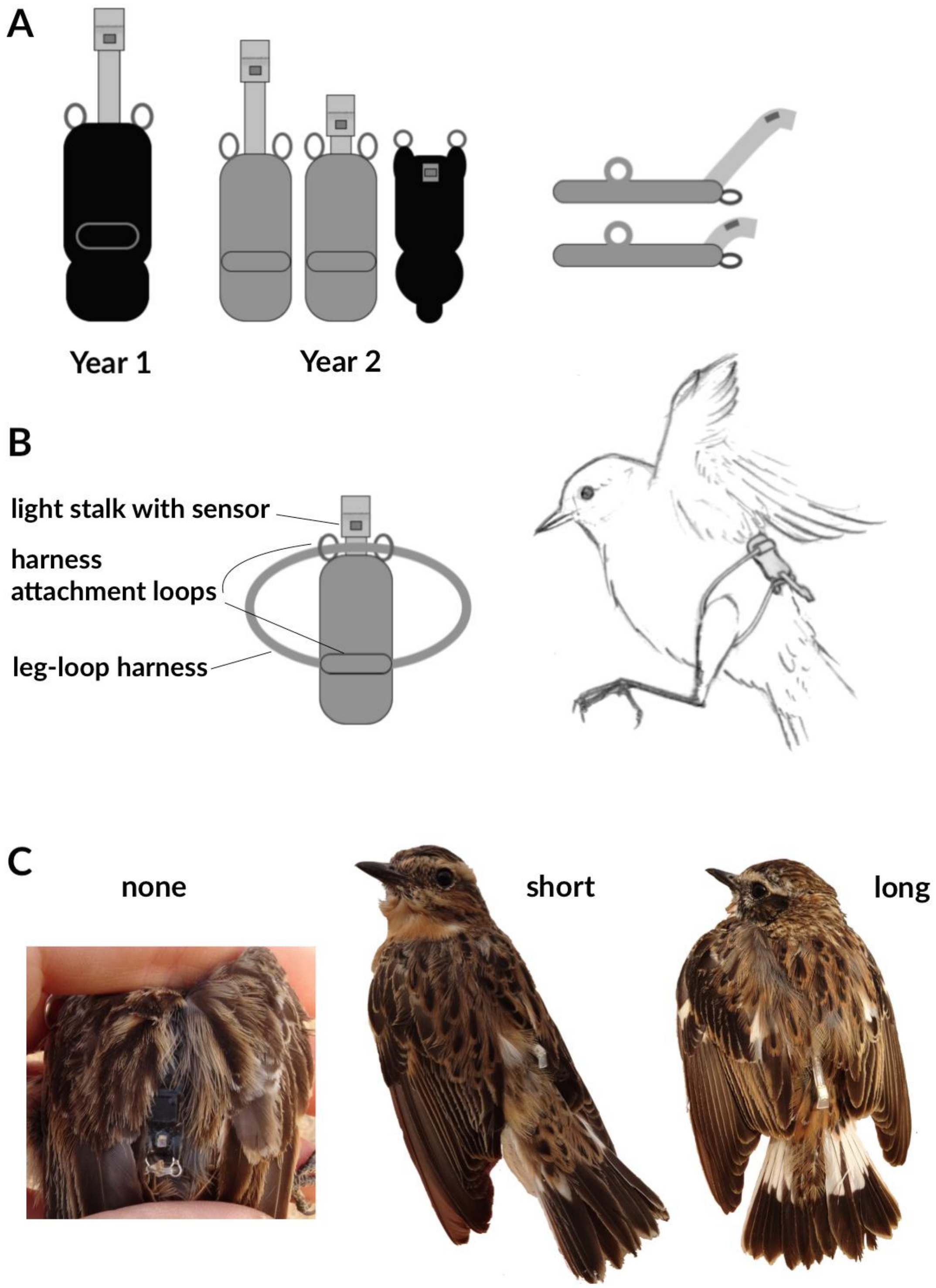
Figure legends

Figure 1: Geolocator design and attachment. A: variation in geolocator design and light-stalk length between years; B: geolocator with leg-loop 'backpack' harness, illustrating of leg-loop attachment and geolocator position once fitted (note that the position of the geolocator is angled for purposes of illustration, refer to C for correct position in the centre of the back); C: fitted geolocators showing each light stalk length and extent of protrusion and geolocator position once attached.

Figure 2: Plot of predicted values for the probability of resighting a bird tagged at the median Julian date of the study dependent on stalk length and harness material. The predicted values are from the best model identified (Table 3); only harness material shows a statistically significant effect on resighting rate.

Figure 3: A. Plot of predicted values for the probability of resighting a bird tagged at the median Julian date of the study, with a 0 mm length light stalk dependent on order of attachment and harness material. The predicted values are from the best model identified (Table S2); the interaction is borderline significant. B. Plot of predicted values for the fit of a tagged bird in Year 1 of the study, dependent on order of attachment and harness material. The predicted values are from the model in Table 4; the interaction is borderline significant.

601 Figure 1:



602

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Figure 2:

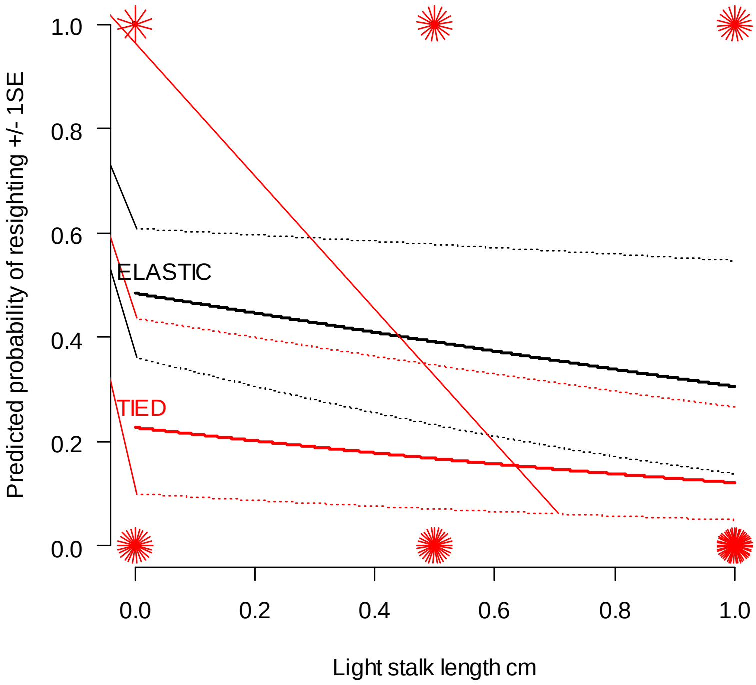
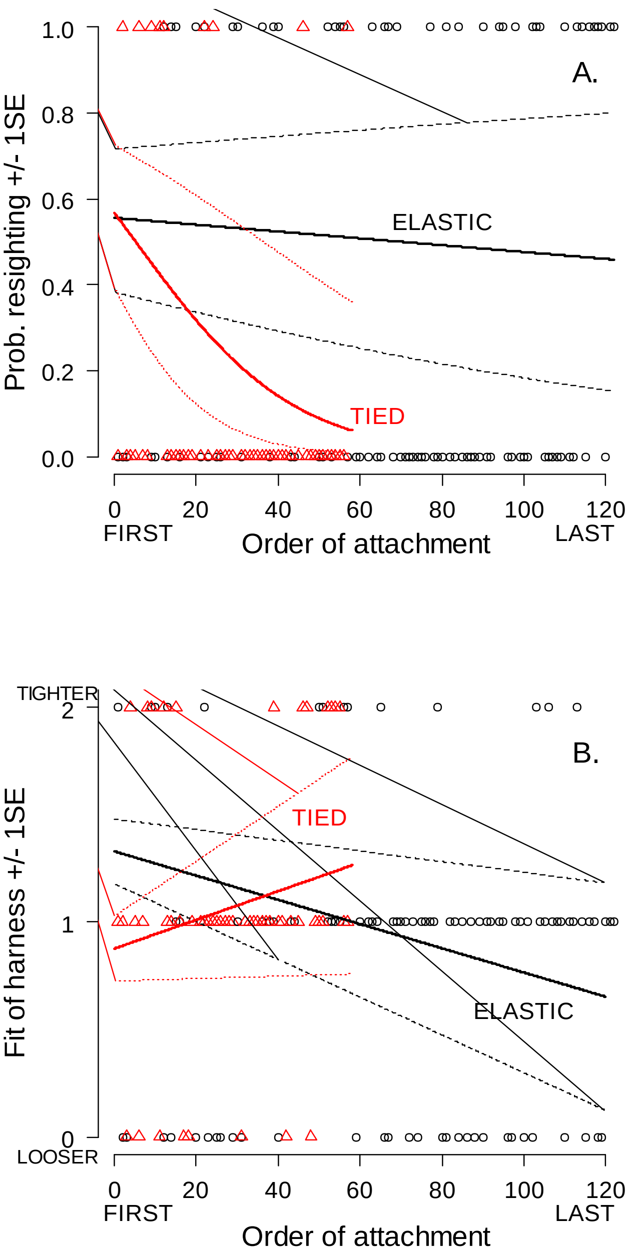

Predicted probability of resighting +/- 1SE
1.0
0.8
0.6
0.4
0.2
0.0
ELASTIC
TIED
0.0
0.2
0.4
0.6
0.8
1.0
Light stalk length cm

Figure 3:


A.
Prob. resighting +/- 1SE
1.0
0.8
0.6
0.4
0.2
0.0
ELASTIC
TIED
0
20
40
60
80
100
120
FIRST
LAST
Order of attachment
B.
Fit of harness +/- 1SE
TIGHTER
LOOSER
2
1
0
TIED
ELASTIC
0
20
40
60
80
100
120
FIRST
LAST
Order of attachment

SUPPLEMENTARY MATERIAL

Harness construction

Elastic harnesses were made from a single length of 0.8 mm diameter clear elastic beading thread (Beads Unlimited 'Elasticity') that was threaded through the geolocator loops and fused into a single loop with a battery-operated soldering iron (Figure 1). The soundness of the fused join was tested by attempting to pull the harness apart with reasonable force either side of the join, and any harnesses which showed signs of failing were rejected and remade using new elastic thread. The harness was then glued inside the rear harness tube on the geolocator with superglue because this prevented the harness being completely free running with respect to the tag and asymmetrical once fitted. We found this made fitting quicker and easier but still then allowed some correction for asymmetry once on the bird. The span of each harness was then measured as per Fig.1 in Naef-Daenzer (2007) to 0.5 mm accuracy. We measured the span of each harness twice, or until the same span was measured in two consecutive attempts. The optimal elastic harness span (size) was determined with prior field tests in which we fitted a range of harness sizes to whinchats before the study began and assessed their fit on different sized birds (see below): all the test fitting tags were then removed and the test birds released with only colour rings on. We found that the allometric function developed by Naef-Daenzer (2007) did not give useful fits for our study species or harness design, possibly due to our minor modifications to the standard geolocator design (Figure 1). Through these prior tests we established the common harness span associated with each wing length and used this to best determine which span to first attempt to fit on a captured bird. We made a large number of harnesses across the range of sizes to maximise the chances of fitting the correct harness span to a bird on the first attempt: final span size was determined empirically by trying several, if necessary, until the optimum fit was achieved. Average span fitted was 35.3, 0.1 SE mm (N = 95).

Tie harnesses were made from black nylon braid that was threaded through the attachment loops and tubes as per elastic harness, and loosely tied with a reef knot secured with a small clip during attachment, but then adjustable in the field to achieve the optimal fit for each bird. The harness was glued into the top attachment tube prior to fitting, as per the elastic harness. Final spans could not be measured because they were set only during attachment.

Captures and harness fitting

In Year 1, Whinchats were captured using mist nests and con-specific playback between 12th February and 8th March 2013. In Year 2, birds were captured using a combination of mist nets and baited spring traps with conspecific playback between 4th February and 2nd March 2014. Both capture periods were chosen to maximise geolocator recording and resighting period following capture, whilst minimising the number of transient individuals captured. Upon capture, birds were placed in cotton bags until processing: aged as adult or first winter (Jenni and Winkler 1994), sexed, biometrics recorded and a geolocator fitted. All birds were processed within 30 minutes of capture and most cases within 10 minutes. All birds captured were ringed with unique combinations of two or three colours, including a striped ring for birds with geolocators and an aluminium ring for birds with no geolocator.

In Year 1, tags were fitted to birds with a wing length ≥ 77 mm (flattened wing chord: average across birds fitted with tags = 77.4, 0.2 SE mm, range = 77 - 81 mm, N = 26). Birds with very low pectoral muscle scores were excluded regardless of wing length (fat scores were not used because these were minimal across all wintering birds captured as part of a larger study) to avoid fitting tags to individuals in poor condition. Preliminary analyses revealed no effect of wing length or bird size, nor age and sex on return rates and no interactions between these variables on birds both with and without geolocators; therefore in Year 2 we lowered the threshold for which birds we fitted with geolocators and fitted tags to birds with wings of ≥ 74 mm flattened wing chord to reduce the bias in biometrics between control vs. geolocators, again provided that these individuals had sufficient pectoral muscle scores. These individuals made up a small proportion of those fitted with geolocators in Year 2, with 11 birds (8.5 %) having a wing of < 76 mm and 25 birds (19 %) of < 77 mm.

Only a single observer was required to fit elastic harnesses. Approximately 80 % of elastic harnesses were fitted during the first attempt (i.e. the correct harness span was selected for an individual based on wing length, see above) and all were fitted by the second attempt. When a harness was too small or large for a bird (see below for assessing harness fit), the harness was removed by simply cutting it off to reduce handling time. Elastic harnesses were fitted by holding the bird with the legs facing upwards and slipping the bird's right leg through the left harness loop and up over the thigh with the free hand. The bird was then rotated to make the other leg easily accessible whilst securing the tag in place on the back, the remaining harness loop slipped over the foot and leg, and a colour-ringing shoe was used to slip the loop over the thigh and into position. This final step required some tension to be applied. With minimal experience it was possible to establish a sub-optimal fit and choose a different harness size before the final step.

For tied harnesses, the legs were placed through the leg-loops by Observer A in exactly the same way as for elastic harness. Once the geolocator and harness was in the correct position, Observer B adjusted the harness and re-tied the knot. Once fit was assessed (see below) Observer B glued the knot in place with superglue using a piece of paper between the geolocator and the bird to prevent glue touching the bird, and trimmed the surplus harnesses ends with scissors. Water was applied to rapidly activate the glue.

Two observers (EB Year 1 or both EB and MB Year 2) assessed all geolocator/harness fits before release. Fit assessment was independent of harness material. With the bird held by the tibia-tarsi, we released any feathers trapped or in abnormal alignment from harness fitting and checked that leg-loops were above both thighs in the correct position. The geolocator was then grasped without touching the harness and we attempted to gently pull the tag away from the bird's body and from left and right and up and down to assess 1: how tight the harness was (by the amount of movement, the amount of force needed to 'pull' the geolocator away from the bird's back without stretching the elastic, if present, and the amount of space between the tag and the back); 2: whether the tag was sitting symmetrically on the back (visually and by whether the geolocator could move to one side more easily than another), and 3: that the geolocator was in the correct position on the lower back with any light-stalk protruding through the feathers. A metal clip spacer inserted between the geolocator and the bird's body was also used in Year 2 to aid consistency in assessment. We discussed harness fit until we were in agreement that the geolocator was an optimal fit (i.e. we were confident that the harness was neither too loose nor too tight to risk the tag falling off or compromising comfort, movement or body mass change) and was scored correctly. Any poorly fitting harnesses were removed and a new harness fitted.

Model Structures

The analyses with respect to our four broad tests were:

1. We investigated the effect of tags on between year resighting rates comparing control and tagged birds. We looked at straightforward differences in resighting rate dependent on tag

presence. We compared resighting rates of control versus tagged birds in each year of the study, and then pooled across years using Chi-squared tests.

2. We then used a binomial logistic regression model with a log-link function to compare the probability of resighting by tag presence, controlling for body mass, added wing loading due to the tag and year of study, and including the interactions body mass * added wing loading * tag presence, body mass * tag presence * year and added wing loading * tag presence * year to test whether any effects of tag presence were dependent on the varying size of the bird and whether any such effects varied between years; all relevant two way interactions were included.

3. We investigated the main effects of harness material and stalk length on resighting rate, controlling for harness fit, order of attachment, Julian date of tagging, year, added wing loading due to the tag and harness, and the body mass of the bird at capture using the 149 tagged birds that we had complete data for (see Table 1). We used a binomial logistic regression model with a log-link function. Analyses were repeated without added wing loading or fit so that the full sample size of N = 156 tagged birds could be used to determine whether the missing data influenced final results.

4. We then investigated the effect of variation in tag mass unconfounded by variation in tag or harness material by restricting analysis to birds tagged with long light stalk tags attached with elastic harnesses (i.e. were all fitted with the same tags). The sample size was 52 birds with complete data which was the largest sample size available within a single treatment group. We used a binomial logistic regression model with a log-link function to compare the probability of resighting by order of attachment, harness fit, body mass of the bird, added wing loading and year. We also tested whether the effects of added wing loading (i.e. the tag mass relative to the size of the bird) were consistent in both years by including the interactions year * added wing loading and wing * body mass.

5. We tested if the effects of tag design depended on harness to affect return rates of tagged birds, or depended on the order of attachment, or the fit of the tag by including the interactions of stalk * harness, stalk * fit & harness * fit and stalk * order & harness * order in the main effects model in analysis 2a above. We identified a potential effect of order of attachment in this analysis so we then explored whether the harness fit might have changed through the experiment. A linear

model was used to predict the fit of the tag by the order and harness material and the interaction order * harness, including year.

6. We tested whether body mass of tagged birds was different to untagged birds by comparing the body mass of tagged birds recaptured in Year 2 (after tag removal) with the body mass of new birds captured within 15 minutes at the same location using a matched-pairs t-test.

Supporting results examining the effects of missing values

1. No tag effect when comparing controls and tagged birds

The ratio of resighting rates for control compared to tagged birds was not significantly different between years when excluding the two birds that lost their loggers between winters (χ^2_1 = 0. 05, P = 0.82). The proportion of control birds ≥ 77 mm that were resighted pooling both years was 29.1 % (N = 240) and was not significantly different from 31.4 % for tagged birds (χ^2_1 = 0. 1, P = 0.72).

Excluding the two birds that lost loggers made little difference: the probability of resighting a bird the following winter was independent of almost all variables, combinations of variables and interactions considered. The top model remained the same as in Table 2 with biological and statistical significance being almost identical. The null model was 0.5 ΔAICc points above the best model that included tag presence. The results were similar when control birds of wing length $\geq$ 77 mm (i.e. removing the size selection bias for tagged birds to be larger) were compared to tagged birds. The top model of 4 models within 2 ΔAICc had an AIC weight of 0.38 and only contained year; all models contained year, and the three others each paired year with body mass, tag presence or added wing loading; the null model was only 0.5 ΔAICc points above the best model that included tag presence.

2. Harness material but not light stalk length reduced between-year resighting rate of tagged birds

Repeating the analyses of whether the probability of resighting a tagged bird was dependent on whether it had an elastic or tied harness, excluding birds with missing data for fit and added wing loading (N = 156) gave nearly identical results, with a lower probability of resighting if the tag was tied on. Attachment method was present in all models with a significant effect in the full and all top models. Repeating the analyses excluding the two birds that lost their loggers gave nearly identical results with the statistical significance for harness material increasing slightly.

3. The effects of harness material may have been dependent on harness fit

Repeating the analyses excluding birds with missing data for fit and added wing loading (N = 156) gave nearly identical results to those presented in Table S2 and Figure 3: the only potential interaction identified was an effect of harness material depending on order of attachment, with tied tags possibly reducing resighting rates if they were fitted later. Repeating the analyses excluding the two birds that lost their loggers gave similar results, although the top model included only Julian date, harness material and stalk length; the second top model, differing in ΔAICc by only 0.06, was identical to the top model in Table S2.

Table S1: Sample sizes of tagged and control birds split by year of study, tag and attachment type. Total (without missing values) presents the total sample size for birds with complete biometric data only, required for the analysis of tag fit. 'Tag fit categories' presents sample sizes for each fit category with complete biometric data.

Winter	Treatment	Stalk	Material	Ringed Resighted	Total (all)	Tag fit			Total (without missing values)
						Fit 0	Fit 1	Fit 2	
2013	Tagged	Long	Elastic	Ringed	26	11	6	5	22
				Resight	10	5	2	1	8
	Control	-	-	Ringed	37	-	-	-	36
				Resight	16	-	-	-	15
2014	Tagged	Long	Elastic	Ringed	30	7	20	3	30
				Resight	10	1	9	0	10
			Tie	Ringed	17	5	9	2	16
				Resight	1	1	0	0	1
		Short	Elastic	Ringed	30	9	16	5	30
				Resight	13	6	4	3	13
			Tie	Ringed	16	4	8	4	16
				Resight	4	1	1	2	4
		None	Elastic	Ringed	14	3	9	1	13
				Resight	6	2	2	0	6
			Tie	Ringed	23	0	16	6	22
				Resight	5	0	3	1	4
	Control	-	-	Ringed	279	-	-	-	277
				Resight	74	-	-	-	74
Both	Tagged	All	All	Ringed	156	39	84	26	149
				Resight	49	16	23	7	46
Both	Control	-	-	Ringed	316	-	-	-	313
				Resight	90	-	-	-	89

Table S2: Model evaluation of the most important variables predicting resighting rate for tagged birds (N = 149) considering potential interactions with harness fit and attachment order. Models were ranked by AIC and total weight calculated (proportion of top models where a variable was present) within ΔAIC = 2 of the top model (N = 24). The coefficients for the initial full model and the coefficients for the top model (AIC weight 0.07) are also given.

	Total	No.	Full model				Top model R^2 = 0.10			
	weight	models	Est.	SE	z	P	Est.	SE	z	P
[1]Intercept			-5.4	5.2	-1.0	0.30	-0.60	0.70	-0.9	0.39
Tied	1	24	-0.072	2.2	-0.03	0.97	0.079	0.86	0.1	0.93
[2]Julian date	0.7	15	0.036	0.026	1.4	0.15	0.038	0.017	2.2	0.029
Stalk length	0.48	11	-0.58	3.4	-0.2	0.86	-0.91	0.55	-1.7	0.10
Attachment order	0.42	10	0.00021	0.024	0.009	0.99	-0.0012	0.0071	-0.2	0.86
Tied*Order	0.39	10	-0.053	0.030	-1.8	0.077	-0.049	0.025	-1.9	0.055
Body Mass	0.35	9	0.27	0.22	1.2	0.21				
Added Wing loading	0.2	5	-70.7	434.6	0.2	0.87				
Harness fit	0.17	5	-0.78	0.77	-1.0	0.31				
Year 2	0	0	0.69	1.6	0.4	0.67				
Fit*Stalk	0	0	0.49	0.92	0.5	0.60				
Order*Stalk	0	0	-0.011	0.034	-0.3	0.73				
Fit*Tied	0	0	0.64	0.78	0.8	0.41				
Stalk*Tied	0	0	-0.93	2.3	-0.4	0.69				

[1]Intercept = Elastic

[2]Julian date 1 = 1st Feb