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Communications

Effect of light-level geolocators on apparent survival of two highly aerial swift species

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Light-level geolocators are currently widely used to track the migration of small-sized birds, but their potentially detrimental effects on survival of highly aerial species have been poorly investigated so far. We recorded capture–recapture histories of 283 common swifts *Apus apus* and 107 pallid swifts *Apus pallidus* breeding in 14 colonies in Italy, Spain, Sweden and Switzerland that were equipped with 10 different types of geolocators ('geolocator birds'), and compared their survival with that of, respectively, 215 common and 101 pallid swifts not equipped with geolocators ('control birds'). Data were analysed using both GLMMs with return rate as a proxy for survival and mark–recapture models to estimate survival while accounting for recapture probability. In all the analyses, geolocator birds showed reduced apparent survival compared to controls. Geolocator weight was always lower than 3% of body mass, and did not affect survival per se. Geolocators with a light-stalk, which is used in some geolocator models to reduce light sensor shading by feathers, decreased apparent survival more than models without light-stalk. Apparent survival of geolocator birds significantly varied among sites, being much higher in northern Europe. Despite in our analyses we could only partly account for variable recapture probabilities among sites and for inter-annual variability in survival, our results generally showed that equipping swifts with geolocators decreased their survival prospects, but also that the magnitude of this effect may depend on species-specific traits. These conclusions are in line with those of other studies on aerial foragers. We suggest that future studies tracking the movements of aerial insectivorous birds should use devices designed to minimize drag.

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Introduction

Light-level geolocators are small data loggers that register daylight intensity during daily cycles (DeLong et al. 1992, Phillips et al. 2004). Light measures are then used to estimate sunrise and sunset times and therefore position on the Earth with a reduced error (Afanasyev 2004, Bridge et al. 2011, 2013). Since these devices can be miniaturized, they are currently widely used to track the annual migrations of even small-sized birds, including highly aerial species, like swifts (Stuchbury et al. 2009, Åkesson et al. 2012, 2016, Bairlein et al. 2012, Bridge et al. 2013, Kristensen et al. 2013, Wellbrock et al. 2017), but their impact on survival and flight performance remains to be fully explored (cf. Costantini and Møller 2013, Fairhurst et al. 2015, Matyjasiak et al. 2016, Raybuck et al. 2017). Indeed, deployment of tracking devices such as geolocators on birds may entail negative effects, including, for instance, increased drag when the device is attached on the back of the bird, which may result in higher cost of transportation (Bowlin et al. 2010, Pennycuick et al. 2012). Carrying a geolocator may also determine negative effects on clutch size, time of breeding and fitness in some species (Rodriguez et al. 2009, Arlt et al. 2013, Gómez et al. 2013, Scandolara et al. 2014). For instance, in the aerially foraging barn swallow *Hirundo rustica*, geolocators negatively affected fitness traits (Scandolara et al. 2014). Similarly, northern weathears *Oenanthe oenanthe* equipped with geolocators had reduced survival, delayed migration and lower breeding success than control birds (Arlt et al. 2013). However, barn swallows equipped with geolocators seemed to have the same flight performance as control individuals (Matyjasiak et al. 2016). Small passerines equipped with geolocators may also perform similar to controls during breeding, but suffer increased inter-annual mortality (Raybuck et al. 2017). Overall, it seems established that smaller species and aerial foragers suffer the most from carrying geolocators (Fairhurst et al. 2015; but see Matyjasiak et al. 2016 for lack of short-term effects on flight performance). On the other hand, evidence exists that several small-sized, highly migratory species did not suffer detectable effects of carrying a geolocator (Pakanen et al. 2015, Peterson et al. 2015, Blackburn et al. 2016, van Wijk et al. 2016, Bell et al. 2017). These contrasting findings suggest that species-specific traits and features of the devices can determine large variation in the size of the detrimental effects of tracking devices. Specifically, in all species where the device is attached on the back of the individual by a leg-loop or a full-body harness, the presence of a so-called 'light stalk', a feature used in some geolocator models to enhance light reception, may increase drag (Bowlin et al. 2010, Pennycuick et al. 2012) and eventually boost the detrimental effects of carrying a geolocator (Scandolara et al. 2014, Blackburn et al. 2016).

Generally, studies aiming at assessing the potential detrimental effects of geolocators have used inter-annual return rate as a proxy of survival (Arlt et al. 2013, Scandolara et al. 2014, Blackburn et al. 2016, Raybuck et al. 2017). However, return rate may not correctly represent true survival whenever inter-annual recapture probability is much lower than 100% (Cooch and White 2017), for instance in species with low breeding site fidelity or when capture and manipulation at the nest promote colony desertion in the following year, as it may be the case for swift species, and for species that need to be recaptured to assess whether they have returned or not. In these cases, inter-annual recapture probability should be estimated prior to estimating survival. In addition, it can be argued that birds deployed with geolocators may have different recapture probability than control individuals e.g. because of longer manipulation or because they suffered more stress by carrying a device, so this parameter should be estimated separately for either group of birds. In such cases, mark–recapture models (White and Burnham 1999), which have been designed specifically to estimate both survival and recapture probabilities simultaneously (van Wijk et al. 2016), may be applied. However, mark–recapture models have been seldom used in these studies, probably because they require data from at least three consecutive recapture occasions (i.e. three breeding seasons), while most geolocator studies last only the year when geolocators are deployed and the subsequent year when they are recovered (Rodriguez et al. 2009, Peterson et al. 2015, but see Sergio et al. 2015 for a longer study based on mark–recapture models).

The aim of the present study is to assess the effect of carrying a geolocator on two closely-related small-sized and long-distance migratory birds, the common swift *Apus apus* and the pallid swift *A. pallidus.* We used data collected in 14 colonies from different parts of Europe where swifts were equipped with geolocators. Swifts are among the bird species that spend the largest proportion of their lifetime on the wings, as they land only in the nest to attend eggs and chicks (Liechti et al. 2013, Hedenström et al. 2016). For instance, common swifts fly for almost 10 months per year (Hedenström et al. 2016). Such an aerial behaviour makes swifts among the most interesting birds to be tracked, but also those that may suffer the largest detrimental effects from carrying geolocators (Bowlin et al. 2010, Pennycuick et al. 2012).

As a first step in our analyses, we used the data from two swift colonies where mark–recapture data were available for three or more years. These data therefore allowed comparing recapture probability and survival between geolocator and control birds using MARK (White and Burnham 1999). Second, we used return rate in the following breeding season as a proxy of actual survival, and we tested whether it differed between sites, species and geolocator/control birds. This analysis allowed using data collected on a larger number of colonies where only two years of data were available. Third, given that different geolocator models were used in different colonies and years, we compared return rates of birds equipped with different models to assess which geolocator features were important in affecting apparent survival.

Material and methods

Study species and general methods

Both common and pallid swifts perform long-distance migrations toward wintering quarters in sub-Saharan Africa and spend most of their time on the wing (Lack 1951, Cramp 1998, Åkesson et al. 2012, 2016, Liechti et al. 2013, Hedenström et al. 2016). However, the geographical distribution of the two species markedly differs: the common swift has a wide breeding range including Europe up to 70°N, most of Asia and northern Africa, while the breeding range of the pallid swift is limited to the Mediterranean basin (Cramp 1998). Migration distances also markedly differ between species: common swifts reach the south-eastern extreme of Africa in mid-winter (Åkesson et al. 2012, 2016, Hedenström et al. 2016), while pallid swift are traditionally believed to overwinter in the Sahel region (Cramp 1998), as confirmed also by preliminary migratory tracks from geolocation (SEO/Birdlife 2017).

Overall, we used data from eleven common swift and three pallid swift colonies (Fig. 1) located either in historical 'swift towers', which allow easy access to the nests (colonies 1, 2, 12 in Fig. 1) or in other buildings. In swift towers, breeding adults were captured in their nests, while in the other colonies, where nests were not accessible from inside the building, mist nets were placed at the front of the nests and swifts were captured while entering or leaving their nest site. In all the colonies, captures were mainly performed during the chick attending phase, and in all the cases after egg laying. Depending on the study site, geolocators were deployed in different years ranging from 2009 to 2015. In all colonies, capture sessions were performed in the year following geolocators deployment with the same method of the previous year with the aim of retrieving geolocators. In colonies 1 and 12 (Fig. 1), long-term population studies were ongoing and captures were performed also in the years following geolocator recovery (Boano et al. 2015). In colonies 1–5 and 12, wing chord (Svensson 1992) was recorded to the nearest 1 mm by means of a wing ruler with an end-stop, and body mass to the nearest 0.1 g by means of an electronic balance. We calculated the ratio between body mass and wing length and used this measure as a proxy for wing loading since no measure of wing area was taken at the study colonies (Pennycuick 1989, 2008).

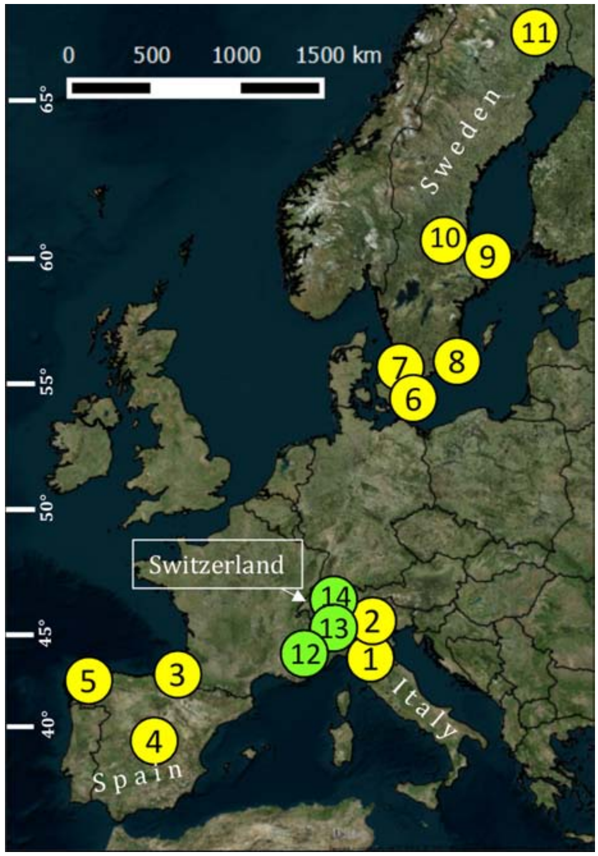

Figure 1. Location of the study colonies. Yellow dots: common swift *Apus apus*. Green dots: pallid swift *Apus pallidus*. 1: Modena (Italy); 2: San Paolo (Brescia, Italy); 3: Irún (Gipuzkoa, Spain); 4: Nuevo Batzán (Madrid, Spain); 5: Lugo (Spain); 6: Skurup (Sweden); 7: Lund (Sweden); 8: Ås (Oland, Sweden); 9: Barkö (Sweden); 10: Falun (Sweden); 11: Hakkas (Sweden); 12: Carmagnola (Torino, Italy); 13: Cannobio (Varese, Italy); 14: Locarno (Switzerland).

Geolocators characteristics

Overall, 10 different models of light-level geolocators were deployed, whose weights ranged from 0.47 to 1.20 g (Table 1). Three out of the 10 models had a light stalk. In all cases, geolocators were deployed by a full-body harness (weighting ~0.3 g) following the same standardized protocol (Åkesson et al. 2012), according to which the geolocator was finally positioned in the intra-scapular region of the bird (Fig. 2). The geolocator weight (including harness) corresponded to 2.11% to 3.04% of the individual body mass in all the cases in which both measures were taken (Table 2).

Statistical analyses

We used t-tests to compare body mass, wing length and wing loading between common and pallid swifts.

We investigated whether carrying a geolocator affected survival to the following year with two different approaches. First, we used a mark–recapture model for analysing the individual recapture histories of common swifts from colony 1 (Modena, Italy) and for pallid swifts from colony 12 (Carmagnola, Italy). These were the only two sites where captures were performed with similar effort for at least three years and where recapture data were available for both geolocator and control birds (birds captured and treated as geolocator birds, but only ringed). With respect to the analysis of return rate, mark–recapture models allow estimating apparent survival (parameter ϕ), while accounting for recapture probability (parameter p; White and Burnham 1999). To be conservative, survival will be defined as 'apparent' because

Table 1. Types and features of light level geolocators deployed in the 14 colonies between 2009 and 2015. Weight (as declared by the producer and without including the mounting harness) as well as the presence of the light stalk and its length and angle are indicated.

	Geolocator model	Producer	Weight (g)	Light stalk	Stalk length (mm)	Stalk angle (°)	Source
A	Intigeo-W55B1	Migrate Technology	0.47	No			Migrate Technology – Intigeo series Geolocator Manual – James Fox – Dec 2015 <www.migratetech.co.uk/IntigeoSummary.pdf>
B	Intigeo-W65A9	Migrate Technology	0.7	No			Migrate Technology – Intigeo series Geolocator Manual – James Fox – Dec 2015 <www.migratetech.co.uk/IntigeoSummary.pdf>
C	Intigeo-W65C1	Migrate Technology	0.67	No			Migrate Technology – Intigeo series Geolocator Manual – James Fox – Dec 2015 <www.migratetech.co.uk/IntigeoSummary.pdf>
D	MK10 (S)	British Antarctic Survey	1.2	No			BAS Geolocator Manual ver. 7 – James Fox – <www.arctictern.info/carsten/pdf/Geolocator_manual_v7.pdf>
E	MK20	British Antarctic Survey	0.9	Yes	15	30	BAS Geolocator Manual ver. 7 – James Fox – <www.arctictern.info/carsten/pdf/Geolocator_manual_v7.pdf>
F	MK5540C	Biotrack	0.6	No			Biotrack Geolocator Datasheet
G	ML6590	Biotrack	0.6	No			Bioltrack Geolocator Datasheet
H	SOI-GDL 2.11	Swiss Ornithological Institute	0.68	Yes	5	90	<www.vogelwarte.ch/en/projects/bird-migration/tracking-devices-miniaturized-geolocators.html> – and cited references
I	SOI-GDL 1.0	Swiss Ornithological Institute	0.77	Yes	10	60	<www.vogelwarte.ch/en/projects/bird-migration/tracking-devices-miniaturized-geolocators.html> – and cited references
J	Intigeo-W65B1	Migrate Technology	0.6	No			Migrate Technology – Intigeo series Geolocator Manual – James Fox – Dec 2015 <www.migratetech.co.uk/IntigeoSummary.pdf>

there is no way to distinguish permanent desertion to the breeding colony due to change of breeding site from death. With this test, we aimed at assessing whether inter-annual recapture probability differed between geolocator and control birds, based on the hypothesis that individuals equipped with geolocators are more prone to desert the colony in the following years. In the mark–recapture analytical framework this difference in recapture probability, if real, is taken into account when estimating survival. In contrast, models using return rate as the response variable do not account for such difference and therefore may inflate the estimate of the negative effect of geolocators because all individuals that 'disappear' from the breeding colony are considered as dead. Hence, in our analyses, mark–recapture models served not only to accurately estimate survival, but also to assess the possible extent of biases in the analyses performed with models that use return rate as a proxy for survival. We stress that the highest the recapture probability, the more accurate the estimation of 'true' survival is (Cooch and White 2017).

Figure 2. A pallid swift *Apus pallidus* equipped with an Intigeo-W55B1 light-level geolocator at the colony of Carmagnola (Italy), September 2013. Geolocators were mounted in the same way (a 'full body harness', see Methods) in all colonies and years.

We compared in MARK ver. 8.1 (White and Burnham 1999) four different models testing alternative hypotheses: 1) survival did not differ between species or geolocator/control birds; 2) survival differed between geolocator and control birds, but not between species; 3) survival of control birds was equal among species, but that of geolocator birds differed between species (i.e. carrying a geolocator reduced survival of the two species differently); 4) survival differed both between geolocator and control birds and between species. Furthermore, we tested for the possibility that recapture probability differed between geolocator and control birds by re-running the four models above while also estimating recapture probabilities separately for geolocator and control birds. Overall, we ran eight models, ranked them based on AICc scores, and discarded all models with a ΔAICc $>$ 2 from the best model (i.e. the model with the lowest AICc) (Symonds and Moussalli 2011). We assessed the goodness-of-fit of our models by the means of the global

Table 2. Summary table of localities, sample size and basic biometrics. Rows indicate capture localities (cf. Fig. 1). For each study year, number of birds equipped with light level geolocators is indicated, as well as the number of control birds ringed but not equipped with geolocators. The mean proportion of geolocator weight with respect to body mass was calculated by dividing the weight of the device declared by the producer and adding a standard 0.3 g for the mounting harness by the weight of each equipped birds for the colonies where weight was measured and individually calculated in the other cases (Swedish colonies).

Site ID	Locality name	Lat.	Long.	Country	Species	Sample size geolocator-birds	Geolocator type (cf. Table 1)	Sample size control-birds	Deploying years	Mean wing chord (mm ± SD)	Mean body mass (g ± SD)	Mean proportion of geolocator weight with respect to body mass (% ± SD)
1	Modena	44.65	10.93	Italy	*A. apus*	28	B-D-E	161	2010–2012	174.55 ± 15.80	44.80 ± 4.05	2.51 ± 0.14
2	San Pietro	45.38	10.03	Italy	*A. apus*	20	H	54	2012	175.64 ± 28.48	42.78 ± 6.93	2.35 ± 0.03
3	Irún	43.34	−1.79	Spain	*A. apus*	16	C-G	–	2015	173.28 ± 44.73	40.37 ± 1.04	3.04 ± 0.08
4	Nuevo Batzán	40.37	−3.24	Spain	*A. apus*	30	C-F-G	–	2012, 2014	175.12 ± 32.51	43.85 ± 8.13	2.11 ± 0.03
5	Lugo	43.01	−7.56	Spain	*A. apus*	32	G	–	2015	177.41 ± 25.70	44.45 ± 2.37	2.03 ± 0.11
6	Skurup	55.47	13.50	Sweden	*A. apus*	12	D-J	–	2009–2010	n.a.	n.a.	< 3%*
7	Lund	55.71	13.21	Sweden	*A. apus*	34	J	–	2010–2013	n.a.	n.a.	< 3%*
8	Ås	56.24	16.45	Sweden	*A. apus*	31	J	–	2011–2012	n.a.	n.a.	< 3%*
9	Bärko	60.28	18.26	Sweden	*A. apus*	21	J	–	2009, 2010, 2012	n.a.	n.a.	< 3%*
10	Falun	60.55	15.78	Sweden	*A. apus*	26	J	–	2012, 2013	n.a.	n.a.	< 3%*
11	Hakkas	66.92	21.55	Sweden	*A. apus*	36	J	–	2010, 2012	n.a.	n.a.	< 3%*
12	Carmagnola	44.86	7.72	Italy	*A. pallidus*	44	A-B-I	56	2011–2014	173.25 ± 15.13	38.55 ± 3.36	3.04 ± 0.08
13	Cannobio	46.06	8.70	Italy	*A. pallidus*	11	I	11	2013	n.a.	n.a.	n.a.
14	Locarno	46.17	8.79	Switzerland	*A. pallidus*	34	I	34	2011, 2013, 2014	n.a.	n.a.	n.a.

*geolocators in Swedish study sites weighted less then 3% of the body mass in all the cases (Åkesson et al. 2016).

test in U-CARE ver. 2.3.4 considering as general case the Cormack–Jolly–Seber parameterization (Choquet et al. 2009). The global test includes the results of a series of tests exploring the possibility that data are significantly violating the implicit assumption of the mark–recapture framework (see Choquet et al. 2009 for details), so that a non-significant result of this test allows to proceed in the analyses. Furthermore, the global test in U-CARE also measures the dispersion of the data with a parameter called $\hat{c}$, whose values above 1 indicate overdispersion in the data and the need to correct for it (Choquet et al. 2009). We did not run models considering the possibility that survival and recapture probability differed between years (Cormack–Jolly–Seber parametrization) because the actual sample size was only 20 in this analysis since each group of birds per colony and year (e.g. common swifts equipped with geolocators in Modena in 2010) contributed one datum and a MARK model accounting for variation in survival among sites and years would have estimated as many as 32 parameters. In addition, sample size was highly unbalanced among years and colonies. We therefore assumed that both capture and survival probability were constant among years within each group of birds (i.e. within species and within geolocator or control birds). However, we explored whether apparent survival differed among years and sites in a further analysis run on a larger dataset.

In a second step, we used data from all colonies where both geolocator and control birds were captured and marked in at least two consecutive years (colonies 1, 2, 12, 13, 14 in Fig. 1) and ran a binomial generalized linear mixed model (GLMM) to assess whether the proportion of birds that were recaptured in the year following geolocator deployment (return rate used as a proxy of apparent survival) differed between geolocator and control birds, species (common or pallid swift) and the interaction between these two variables. To account for the fact that recapture probability may vary among sites and among years (van Wijk et al. 2016), we entered 'colony' and 'year of geolocator deployment' as crossed random effects in this model. This analysis was based on 263 common swifts and 190 pallid swifts from 5 colonies captured and recaptured during breeding seasons 2010–2014.

Finally, we tested for the effect of geolocator weight and of the presence of a light stalk on return rate (number of recaptured birds over the number of birds equipped with geolocator in a specific colony and year) by fitting a binomial GLMM where species, geolocator weight (excluding harness weight, which was the same in all sites) and the presence of the light stalk (dichotomous variable) were entered as fixed effects. As for the previous model, 'colony' and 'year of geolocator deployment' were entered as crossed random effects. This analysis was based on 283 common swifts and 90 pallid swifts from all 14 colonies where captures and recaptures were performed during the breeding seasons 2010–2016. We also assessed whether the random factors colony and year explained a significant proportion of variance by the means of a likelihood ratio test between models fitted with the REML procedure and including or excluding the random effects. Significant likelihood ratio test would indicate significant variation among years and colonies in the dependent variable (i.e. return rate). GLMMs were fitted with the 'glmer' function of the lme4 package (Bates et al. 2015) for R ver. 3.1.2 (R Core Team). We also calculated marginal and conditional pseudo-R^2 with the function r.squared.GLMM in the package MuMIN (Barton 2016). Marginal pseudo-R^2 is considered a measure of variation in the dependent variable due to fixed effects only (i.e. geolocator weight and presence of a light stalk in the present study) while conditional pseudo-R^2 is considered a measure of variation in return rate due to both fixed and random effects (Barton 2016).

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.b1t42> (Morganti et al. 2017).

Results

Inter-specific differences in morphology and wing loading

Body mass ranged between 36.2 and 58.0 g in common swifts (mean ± SE: 43.8 ± 0.3 g, n = 192) and between 29.0 and 44.0 g in pallid swifts (38.5 ± 0.3 g, n = 151). Common swifts were significantly heavier than pallid swifts ($t_{216} = 13.2$, $p < 0.001$). Wing length ranged from 16.5 to 19.2 cm in common swifts (17.5 ± 0.1 cm, n = 240) and from 16.3 to 18.2 cm in pallid swifts (17.3 ± 0.1 cm, n = 132), and was significantly smaller for pallid swifts ($t_{308} = 3.8$, $p < 0.001$). Wing loading (body mass/wing length) was significantly larger for common swifts (2.49 ± 0.01 g cm^{-1}, n = 192) than pallid swifts (2.22 ± 0.02 g cm^{-1}, n = 130, $t_{262} = 11.3$, $p < 0.001$).

Effects of geolocators on return rate and survival

Global goodness-of-fit test in U-CARE was non-significant ($\chi^2_{24} = 17.3$; p = 0.834) and $\hat{c}$ value was below 1 ($\hat{c} = 0.722$), thus indicating the absence of overdispersion in the data. We could therefore proceed to model selection based on the AICc values in MARK.

Model ranking in MARK selected a single best model, which accounted for the hypothesis that survival differed both between species and between geolocator or control birds, and that recapture probability also differed between geolocator and control birds (Table 3). Model parameters showed that survival of common swifts equipped with geolocators ($\Phi_{AA.GL1} = 0.453 \pm 0.080$) was 26.69% lower than that of control birds ($\Phi_{AA.GL0} = 0.618 \pm 0.045$). Survival of pallid swift equipped with geolocators ($\Phi_{AP.GL1} = 0.557 \pm 0.076$) resulted 35.45% lower than that of control birds ($\Phi_{AP.GL0} = 0.863 \pm 0.087$) (Fig. 3). Recapture probability was considerably higher for geolocator ($p_{GL1} = 0.698 \pm 0.097$) than for control-birds ($p_{GL0} = 0.455 \pm 0.051$).

Results of the binomial GLMM comparing return rates of geolocator and control birds showed a significant detrimental effect of geolocator on survival (Table 4, Fig. 3). Pseudo R^2 of this model showed that the variance explained by fixed effects (marginal psuedo $R^2 = 0.107$) was comparable to those explained by random effects (difference between marginal and conditional pseudo R^2=0.96). In both GLMM and MARK models a significant interaction effect between species and geolocator deployment emerged, but with opposite directions in either model (Fig. 3).

Effects of geolocator features on return rate

The model testing the effect of geolocator features on return rates revealed that the presence of the light stalk significantly decreased return rate of geolocator birds (Table 5). In contrast, geolocator weight did not affect return rate (Table 5). For this model, pseudo R^2 showed that the variances explained by fixed effects was relatively low (marginal pseudo $R^2 = 0.039$) if compared to those explained by random effects (difference between marginal and conditional pseudo $R^2 = 0.101$).

A comparison between models including or excluding colony as a random effect showed significant heterogeneity in return rates among sites (likelihood ratio test: $\chi^2_1 = 5.2$, p = 0.023). Inspection of coefficients of the random part of the model (i.e. colony-specific intercepts) revealed that such variability was mainly due to larger return rates of common swifts from Swedish colonies (Fig. 4).

Table 3. Models testing alternative hypotheses about differences in survival (ϕ) of common swift (AA) and pallid swift (AP) equipped with geolocator (GL1) or not (GL0). Each model was run both by assuming that recapture probability (p) was equal among groups and assuming that p differed for geolocator and control birds (p_{GL1} and p_{GL0} respectively). Sample sizes are: AA.GL0: 125; AA.GL1: 28; AP.GL0: 43; AP.GL1:45.

Model rank	Parameters in the model	AICc	Δ AICc	AICc weight
1	$\Phi_{AA.GL0} + \Phi_{AA.GL1} + \Phi_{AP.GL0} + \Phi_{AP.GL1} + p_{GL0} + p_{GL1}$	780.34	0	0.458
2	$\Phi_{AA.GL0} + \Phi_{AA.GL1} + \Phi_{AP.GL0} + \Phi_{AP.GL1} + p$	782.63	2.29	0.146
3	$\Phi_{GL0} + \Phi_{GL1} + p_{GL0} + p_{GL1}$	782.90	2.55	0.128
4	$\Phi_{GL0} + \Phi_{AA.GL1} + \Phi_{AP.GL1} + p_{GL0} + p_{GL1}$	783.89	3.55	0.078
5	$\Phi + p$	784.05	3.71	0.072
6	$\Phi + p_{GL0} + p_{GL1}$	784.33	3.99	0.062
7	$\Phi_{GL0} + \Phi_{GL1} + p$	785.69	5.34	0.032
8	$\Phi_{GL0} + \Phi_{AA.GL1} + \Phi_{AP.GL1} + p$	786.16	5.82	0.025

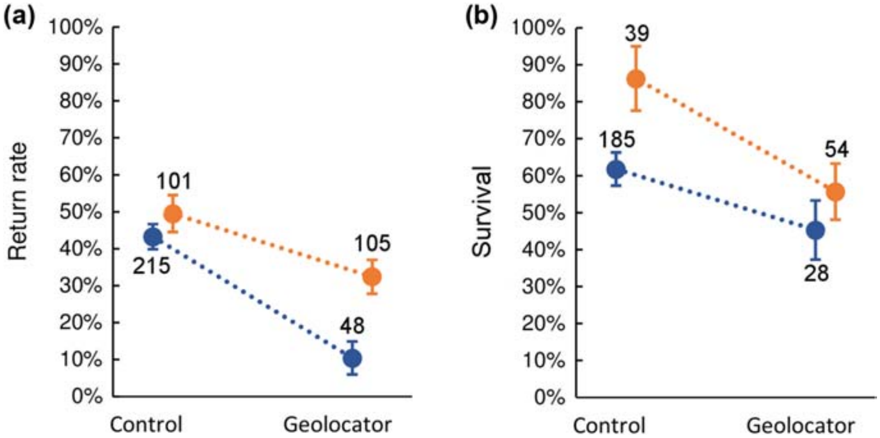

Figure 3. Mean inter-annual return rates (a) compared to survival estimates derived from MARK (b) of control and geolocator common swifts (blue) and pallid swifts (orange). Numbers indicate sample size and bars represent standard errors.

Discussion

Overall, we found lower apparent survival of swifts equipped with a geolocator with respect to non-equipped bird. The size of the negative effect of carrying a geolocator on survival possibly differed between the two species, although the contrasting evidence from either species does not allow form conclusions on species-dependent effects. Common swifts appeared to suffer more than pallid swifts from carrying a geolocator when return rate was used as a proxy for survival, while the opposite pattern emerged in mark–recapture models. Our findings also support previous observations of larger negative effects of carrying a geolocator when this has a light stalk (Bowlin et al. 2010, Pennycuick et al. 2012, Scandolara et al. 2014, Blackburn et al. 2016), so that it is advisable to carefully consider the use of this kind of devices in future studies on swifts or other small-sized and highly aerial species.

We found a significant heterogeneity in return rates among sites, possibly due to site-specific recapture probabilities, which we could not control for. Furthermore, mark–recapture models also showed that inter-annual recapture probability was below 1, so that a fraction of returned birds was not captured and this fraction may have been different among sites. Thus, assuming that non-recaptured birds died, inflated the apparent magnitude of the effect of geolocators on survival. The high philopatry showed by swifts (Boano et al. 1993, Cramp 1998, our own data from colonies 1, 2, 12) should contribute to reduce the bias due to missed recapture of surviving birds. We note, however, that the stress of being captured and of carrying a geolocator may have prompted individuals to change breeding colony despite this rarely occurs under normal conditions. However, the results of the mark–recapture analysis (in which survival estimate accounted for any variation in recapture probability) were qualitatively consistent with those on return rate. We are therefore confident that the results of this study were generally robust to potential sources of bias.

We are aware that our large dataset, including as many as 691 individuals, was rather heterogeneous in that geolocators were deployed in different years in different colonies and not all the sites had control birds. This problem limited our possibility to fully account for all the potential confounding effects that may have caused variation in return rates and recapture probabilities among colonies and years (van Wijk et al. 2016). However, the pattern of variation in apparent survival that we observed is in line with previous results

Table 4. Binomial mixed model of the effect of geolocator application on recapture rate of common (AA) and pallid swift (AP). The model was run with common swift as reference category. Sample size was 263 common swifts (48 of which equipped with a geolocator), and 206 pallid swifts (105 with a geolocator). Marginal pseudo-R^2 represent variance explained by fixed effects while conditional pseudo-R^2 that explained by both fixed and random effects.

Factor	Estimate (SE)	z	p
Intercept	–0.394 (0.338)	–1.156	0.248
Geolocator	–1.962 (0.496)	–3.951	< 0.001
Species (AP)	–0.149 (0.317)	–0.470	0.638
Species (AP) × Geolocator	1.299 (0.571)	2.273	0.023

Marginal pseudo-R^2 = 0.107; conditional pseudo-R^2 = 0.203.

Table 5. Binomial mixed model of the effects of geolocator weight and light stalk presence on recapture rate of common (AA) and pallid swifts (AP) equipped with geolocators from 14 colonies located across Europe. The model was run with common swift as reference category. Light stalk indicates the presence (1) or absence (0) of the light stalk. Sample size was 283 common swifts equipped with a geolocator (30 with a light stalk) and 90 pallid swift equipped with a geolocator (56 with a light stalk). Marginal pseudo-R^2 represent variance explained by fixed effects while conditional pseudo-R^2 that explained by both fixed and random effects.

Factor	Estimate (SE)	z	p
Intercept	–0.819 (0.732)	–1.119	0.263
Weight	0.966 (1.058)	0.913	0.361
Light stalk (0/1)	–1.156 (0.498)	–2.324	0.020
Species (AP)	–0.309 (0.535)	–0.576	0.564

Marginal pseudo-R^2 = 0.039; conditional pseudo-R^2 = 0.140.

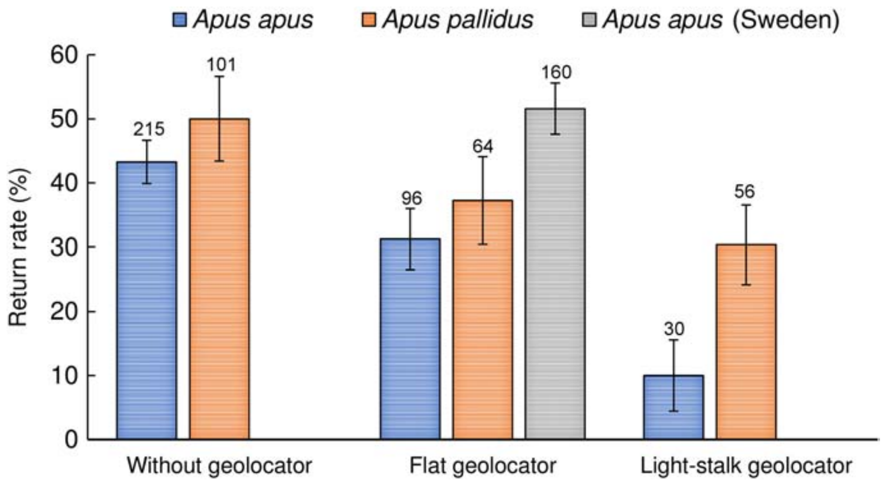

Figure 4. Mean inter-annual return rates (real values) of common and pallid swifts non-equipped with a geolocator (left), equipped with flat (i.e without light stalk) (centre) or light-stalk devices (right). Return rate of common swifts equipped with a geolocator in Swedish colony was significantly higher than that of geolocator birds from other colonies (see Results) and it is therefore represented separately. Numbers above bars indicate sample sizes. Error bars represent standard errors.

for aerial foragers. For example, Scandolara et al. (2014) showed that barn swallows equipped with a geolocator had reduced survival, and that this effect was stronger for females than from males. We are therefore confident that these potential problems did not bias our conclusions. In addition, our findings support the use of a mark–recapture approach for assessing the impact of geolocators on survival, particularly in species where recapture probability is low, like in solitarily breeding species with large dispersal.

Geolocator studies do not allow to ascertain in which part of the annual life-cycle geolocator and control birds suffered differential mortality. Differential mortality could have occurred during migration or at other energetically-demanding periods such as moult, when flight performance may be reduced. In addition, carrying extra weight may expose individuals to higher predation risk due to reduced manoeuvrability (Hedenström 1992, Kullberg et al. 2000). These effects may be expected to affect birds throughout the whole migration and wintering period. We found contrasting evidences for a differential negative effect of geolocators between the two species (Fig. 3). Morphological (i.e. wing loading) or behavioural differences (i.e. migration distance) between the two species may contribute to determine more intense negative effect on a species with respect to the other. Indeed, differential wing loading may be responsible for stronger detrimental effect of geolocators, as it is the case of barn swallow, in which higher wing loading of females was paralleled by female-biased mortality in geolocator birds (Scandolara et al. 2014).

Our dataset included ten different types of geolocators all mounted with the same harness, but differing in weight, so that the absence of a weight effect is well supported by our analyses. It is possible that low-quality individuals simply do not survive because of the extra-cost of carrying a geolocator, independently of its weight. This conclusion is supported by results obtained on two species of swallows by Fairhurst et al. (2015), who observed that, despite the clear negative effect of geolocators on return rate, returning individuals had similar stress levels (as measured by corticosterone levels in feathers) compared to control ones. Similar observations come from other studies on species where surviving geolocator birds seemed not to differ in migration or breeding performance compared to control birds (Rodriguez et al. 2009, Peterson et al. 2015, Matyjasiak et al. 2016, van Wick et al. 2016, Bell et al. 2017), although geolocator birds suffered higher inter-annual mortality (Raybuck et al. 2017). In a meta-analysis of the effect of geolocators on shorebirds, the simple presence of the device was the most significant factor affecting return rates and hatching success (Weiser et al. 2016). Overall, we may conclude that the weight of the geolocator per se (Bowlin et al. 2010, Pennycuick et al. 2012) is not the main factor responsible for the observed detrimental effect on survival, but this conclusion should be considered carefully in the light of the observed effect of the wing loading of the individuals and with respect to other features of the tracking devices (e.g. presence or absence of a light stalk, shape of device), as well as the way the device is deployed (e.g. leg-loop vs full-body harness or leg-attached device). This is not trivial, since currently the ethical norms in terms of tracking birds only give general indications about which proportion of the body weight should not be exceeded by the attached device (ASAB 2012). More detailed guidelines are, however, advisable for the future. We suggest that for future studies should not only to minimize device weight, but also their drag. In particular, the presence and the length of a light stalk should be carefully evaluated in the light of the ecological features to the species on which the devices are deployed.

We would like to stress that, despite their potential negative effect at local population level, geolocators and other tracking devices remain the best methods for collecting information on migration and on the behavioural ecology of small birds, which could eventually favour their conservation at a global level as well as provide invaluable information on movement ecology (Stutchbury et al. 2009, Åkesson et al. 2016, Hedenström et al. 2016, Bäckman et al. 2017). Their use should therefore be carefully planned by balancing costs and benefits and via pilot studies (Åkesson et al. 2012), possibly covering three or more years (i.e. allowing the estimation of survival in mark–recapture framework) before loggers are attached to large numbers of birds.

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