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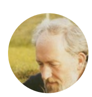

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Contrasting effects of GPS device and harness attachment on adult survival of Lesser Black-backed Gulls *Larus fuscus* and Great Skuas *Stercorarius skua*

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Telemetry has become an important method for studying the biology and ecology of animals. However, the impact of tracking devices and their method of attachment on different species across multiple temporal scales has seldom been assessed. We compared the behavioural and demographic responses of two species of seabird, Lesser Black-backed Gull *Larus fuscus* and Great Skua *Stercorarius skua*, to a GPS device attached using a crossover wing harness. We used telemetry information and monitoring of breeding colonies to compare birds equipped with a device and harness and control birds without an attachment. We assessed whether tagged birds have lower short-term breeding productivity or lower longer-term over-winter return rates (indicative of over-winter survival) than controls. For Great Skua, we also assessed whether territory attendance within the breeding season differed between tagged and control birds. As with previous studies on Lesser Black-backed Gull, we found no short-term impacts on breeding productivity or long-term impacts on over-winter return rates. For Great Skua, there was no evidence for impacts of the device and harness on territory attendance or breeding productivity. However, as found by a previous study of Great Skuas using a different (body) harness design, there was strong evidence of reduced over-winter return
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rates. Consequently, a device attached using a wing harness was considered suitable for long-term deployment on Lesser Black-backed Gulls, but not on Great Skuas. These findings will inform the planning of future tracking studies.

Keywords: Breeding productivity, foraging behaviour, return rate, seabird, telemetry, wing harness

Attaching devices to animals may affect their behaviour, physiology, reproduction and survival (Murray & Fuller 2000, Wilson & McMahon 2006, Walker *et al*. 2012). Among birds, the most serious deleterious effects include deterioration in body condition and foraging behaviour, compromised energetics and direct physical injury, which can then lead to reduced nesting success (e.g. productivity and propensity to breed) and lower adult survival (Barron *et al*. 2010, Vandanabeele *et al*. 2011). Impacts may arise from initial discomfort, subsequent abrasion, compromised plumage insulation, or the overall inability to accommodate any increased weight or drag leading to reduced manoeuvrability (Calvo & Furness 1992, Vandanabeele *et al*. 2011). Different species can vary considerably in their responses to device shape and weight, the attachment method used and the length of deployment (Barron *et al*. 2010, Vandenabeele *et al*. 2011, Bridge *et al*. 2013). Therefore, while some studies have reported negative effects, others have found no such deleterious impacts (Vandanabeele *et al*. 2011). Based on the relatively limited number of comparative studies and the wide range of metrics and effects reported, it is therefore difficult to make broad generalisations about the potential impact of a device and its attachment.

Bird-borne telemetry has been extensively used to study the ecology of bird species during their breeding seasons. For such short-term studies, telemetry devices may be attached temporarily to feathers (Wilson *et al*. 1997). However, to study birds outside the breeding season, the device must remain in place through periods of feather moult, dictating a need for alternative attachments (Kenward 1987). Monitoring species across their full annual cycle remains a key research priority for many species (Marra *et al*. 2015). Long-term attachments can be achieved through the use of leg ring attachments, e.g. for geolocators (Bridge *et al*.

2013, Bustnes *et al*. 2013), harness mounting, or surgical implantation (Meyers *et al.* 1998, White *et al*. 2013). Harnesses have been used previously on waterbirds (e.g. Pietz *et al.* 1993), seabirds (e.g. Falk & Møller 1995, Nicholls *et al* 2002, Manosa *et al*. 2004, Shamoun-Baranes *et al*. 2011, Klaassen *et al*. 2012) and birds of prey (e.g. Britten *et al*. 1999, Peniche *et al*. 2011, Steenhof *et al*. 2011, Sergio *et al*. 2015), as well as on much smaller migrant birds (e.g. Bridge *et al.* 2013). However, the reported effects of harnesses on different species have also varied widely (e.g. Peniche *et al*. 2011, Sergio *et al*. 2015). Although there have been numerous reviews of device and attachment effects across different species (see above), the effects of devices attached with a specific harness type for long-term deployment have not been examined (e.g Barron *et al.* 2010). Consequently, there is a pressing need to assess the suitability of particular harnesses and devices for different species across different time scales.

We compared the responses of two species of seabird, Lesser Black-backed Gull *Larus fuscus* and Great Skua *Stercorarius skua*, to the attachment of the same type/model of GPS device using a Teflon crossover wing harness, within the breeding season and across years. The combined effects of the GPS device and the wing harness were assessed. We compared information from birds equipped with a GPS device and wing harness (hereafter 'tagged birds') with information from groups of control birds without any attachment. We investigated whether, in comparison to control birds within the breeding season, tagged birds exhibited lower breeding success (short-term effects), and whether tagged birds had lower return rates between consecutive breeding seasons (long-term effects). In addition, for Great Skua, we tested whether impacts on foraging ability within the breeding season could lead to alterations in the territory attendance of tagged birds in comparison to controls. Recent studies on Lesser Black-backed and Herring Gull *Larus argentatus* have used either the same device and type of wing harness as in this study (e.g. Ens *et al*. 2008, Camphuysen 2011, Shamoun-Baranes *et al*. 2011), or a slightly heavier device and similar harness (Klaassen *et al*. 2012), with no apparent adverse effects on breeding success (Camphuysen 2011) or on over-winter return rates, which are indicative of over-winter survival (Camphuysen 2011, Klaassen *et al*. 2012). Given that the device type and wing harness attachment in this study was equivalent to that of previous studies, we predicted no effects on Lesser Black-backed Gull on these short- or long-term measures. Previous studies of Great Skuas found no detrimental short-term effects on the duration of foraging trips during breeding when a radio-tracking device (10 g) was attached to a central pair of tail feathers (Votier *et al.* 2004, 2006). In a separate study using a full body ('back-pack') harness to attach platform terminal transmitters (PTTs) to Great Skuas in Shetland, there were no short-term effects recorded on nest survival, territory attendance, body condition or foraging trip duration within the breeding season of marking (Crane 2006, Furness *et al*. 2006). However, no tagged birds returned and successfully bred the following season, suggesting that their condition may have been compromised (Furness *et al*. 2006). The full body harness uses a central breast strap and sometimes a neck loop, whereas the wing harness uses two loops under the wings, with no central breast strap. The wing harness therefore has a smaller amount of skin contact than the body harness, giving a non-constricting fit that better accommodates changes in body size (Thaxter *et al*. 2014). However, the effects of using a wing harness to attach a tracking device to Great Skuas have not previously been evaluated.

METHODS

Study sites and periods

Lesser Black-backed Gulls were studied between 2010 and 2013 at Orford Ness, part of the Alde-Ore Special Protection Area (SPA), Suffolk, UK (52° 06' N, 1° 35' E), a declining colony (23 000 Apparently Occupied Territories [AOTs] in 2000, 550-640 AOTs between

2010 and 2012; JNCC Seabird Monitoring Programme database). Great Skuas were studied between 2011 and 2013 at (i) Foula SPA, Shetland, UK (60° 08' N, 2° 05' W), a declining colony (2 293 AOTs in 2000, 1 657 AOTs in 2007; JNCC Seabird Monitoring Programme database), and (ii) Hoy SPA, Orkney, UK (58° 52' N, 3° 24' W), also a declining colony (1 973 AOTs in 2000, 1 346 AOTs in 2010; JNCC Seabird Monitoring Programme database). Both species were studied during the breeding season. This was defined as the period from the first return of individuals to the colony during pre-breeding to when chicks fledged, the latter either observed or estimated using species' breeding durations (Robinson 2005) and hatching dates (Lesser Black-backed Gull, 15 February to 1 August; Great Skua, 10 April to 15 August).

Catching and harness attachment methods

Adult birds were captured at the nest during incubation using a wire mesh walk-in cage trap (Bub 1991) for Lesser Black-backed Gulls and a remote-controlled nest-snare trap for Great Skuas. In 2010, solar-powered data storage GPS devices (weighing 19 g; Bouten *et al.* 2013) were attached to four Lesser Black-backed Gulls at Orford Ness using a crossover Teflon® wing harness (see Thaxter *et al.* 2014 for more details). A small piece of neoprene was attached underneath the tag to provide additional comfort to the bird (Thaxter *et al.* 2014). In 2011, GPS devices of the same type and model were attached to a further 14 Lesser Black-backed Gulls (Thaxter *et al.* 2015) and 20 Great Skuas (ten each in Foula and Hoy) using the same wing harness design (Wade *et al.* 2014).

As recommended by Phillips *et al.* (2003), the device and harness was <3% body mass (max. 2.9% Lesser Black-backed Gulls and 1.8% Great Skuas). Upon catching, all birds were fitted with uniquely identifiable colour rings to enable subsequent field identification. Lesser Black-backed Gulls were sexed using head and bill length measurements (Coulson *et* *al*. 1983, Camphuysen 2011) recorded along with body mass on capture. Great Skuas were sexed using DNA from feathers (Griffiths *et al.* 1993), previous copulation behaviour, or within-pair relational size from simultaneous viewing of both pair members. Sample sizes of male and female Lesser Black-backed Gulls were sufficient to allow comparative analyses, but too few Great Skuas were sexed to provide meaningful assessment (Supporting Online Appendix S1). Two ringing teams undertook the work (one for Orford Ness and Foula, and one for Hoy) with procedures standardised across teams. The mean bird handling time was 26±10 SD min (range 15–46 mins) for Lesser Black-backed Gull and 25±4 SD min (range 19–32 mins) for Great Skua.

Control groups

To evaluate effects of the device and wing harness, a separate group of birds was also monitored during the 2011 breeding season. These control birds had no device or harness and were captured at the nest in the same vicinity of colonies as tagged birds using the techniques described above. Each bird was then fitted with a colour ring to enable them to be individually identified in the field (Lesser Black-backed Gulls, n = 6 and 47 in 2010 and 2011 respectively; Great Skuas, Foula: n = 10, Hoy: n = 10). In addition, the nests of separate groups of unmarked birds (Lesser Black-backed Gulls, 21 nests; Great Skuas at Foula, 37 nests) also located in the same vicinity as those nests of other marked birds were followed (‘other’ nests in Table 1). The choice of control group is an important aspect to consider in any tagging study (Authier *et al*. 2013), and we therefore attempted to minimise any locational bias, through consideration of nesting density and possible behavioural differences. However, the nests of unmarked birds were located across a slightly wider area, with some nests potentially around colony edges or in sub-optimal locations, which may have contributed to a lower observed breeding productivity compared to the colour-ringed controls

(Table 1, Appendix S1). Nevertheless, these nests were subsequently pooled with the colour-ringed controls to give a larger control group sample size (Appendix S1).

Assessment of device and harness effects

Breeding productivity

During 2011 we assessed whether (i) the number of eggs hatched, (ii) the number of chicks present up to mid-July (Lesser Black-backed Gull, 9 July; Great Skua, 15 July), and (iii) the number of fledglings per nest (for Great Skua at Hoy only) differed between tagged and control birds. Monitoring of Lesser Black-backed Gull nests was undertaken weekly (5 May–9 July 2011). Where gaps in the monitoring of nests were greater than a single day, breeding productivity was expressed as mean minimum and mean maximum scenarios of numbers of eggs or chicks present to provide a level of error (Table 1). For Lesser Black-backed Gulls, it was not possible to monitor the number of chicks present later in the season or in turn the number that fledged, as the origins of many chicks could not be determined due to their greater mobility with increasing age. Consequently, 9 July represented the last point in the season when breeding productivity could be assessed for the species. The nests of Great Skuas were monitored on Foula with daily visits (10 June–15 July 2011) and on Hoy with weekly visits (11 June–15 August 2011). For Great Skuas at Foula, nest monitoring allowed a final estimate to be made of the number of chicks present up to 15 July. However, nests at Hoy were followed for the whole chick-rearing period, allowing fledging success to be assessed. Hatching dates and the duration of monitoring were no different between tagged and control groups (Appendix S2).

Over-winter return rates

Comparison of the over-winter return rates of tagged and control birds was based on re-sightings of marked birds. For Lesser Black-backed Gulls, return rates are indicative of over-winter survival (Camphuysen 2011, Klaassen *et al*. 2012). Similarly, Great Skuas are highly faithful to their breeding colonies (Klomp & Furness 1992, Catry *et al*. 1997), hence permanent emigration is considered negligible and return rates are likely to reflect true survival. Return rates for the 4 and 14 tagged Lesser Black-backed Gulls were compared with those of 6 and 47 colour-ringed control birds in 2010 and 2011, respectively. Similarly, return rates for the 20 tagged Great Skuas (10 at each of Foula and Hoy) were compared with those of the equivalent number of colour-ringed controls at each colony. Re-sighting effort was conducted during the breeding season in 2011, 2012 and 2013. In each year, for both species, re-sighting effort included searches of breeding territories, bathing locations and gatherings of birds at the colony, for example at open shingle loafing areas for gulls (Marsh 2013) and non-breeding club-sites for Great Skua. This enabled a return rate to be calculated for 2010-11, 2011-12 and 2012-13 for Lesser Black-backed Gulls and 2011-12 and 2012-13 for Great Skuas. A second estimate of over-winter return rates incorporating information received through the tracking system (Bouten *et al*. 2013) was also made. This combined measure, as it increased re-sighting probabilities, provided a more accurate estimate for comparisons with previous estimates of annual survival (e.g. Wanless *et al.* 1996).

Breeding season territory attendance

For Great Skuas, the presence/absence of tagged and control birds in breeding territories was monitored at Foula in 2011 through spot-checks conducted from vantage points as a measure of foraging effort (Catry & Furness 1999). These data were then used to compare the probability of tagged and control birds being present on their territories. Watches were conducted 2-3 times per day between 3 May and 15 July in a randomised pattern covering morning (05:01–11:00 BST), midday (11:01–17:00 BST) and late afternoon/evening (17:01–23:00 BST) periods. Different vantage points were used to cover the breeding territories (average watch duration, 2.0±0.9 h). If birds could not be identified (e.g. due to obstructed views), then these data were excluded from analysis. Similar monitoring of Lesser Black-backed Gulls was not possible as there were no vantage points that gave clear views due to tall vegetation.

Statistical analysis

To test whether breeding productivity was different between tagged and control birds, we used generalised linear models (GLMs) with Poisson errors. Response variables of the number of eggs hatched and the number of chicks present per nest were tested as separate analyses with fixed effects for 'group' (tagged and control) and 'sex' included. For Great Skua, a pooled analysis for Foula and Hoy was conducted including 'colony' as a fixed effect to control for potential site differences. However, in the case of fledging success, this could only be investigated for birds at Hoy (see above). Tests for breeding productivity were conducted on both minimum and maximum scenarios (see Table 1), but provided equivalent results in all instances, therefore for simplicity, results from the tests of maximum scenarios are presented. To test whether territory attendance differed between tagged and control Great Skuas, a generalised linear mixed-effects model (GLMM) was used, with a binary response for presence/absence and binomial error structure; fixed effects of 'group' and 'time of day' were included and 'bird ID' as a random effect to account for repeat measurements for individuals throughout the day. Differences in over-winter return rates between tagged and control birds (fixed effect of 'group') for Great Skuas were examined using binomial (presence/absence response) GLMs, controlling for additional fixed effects of 'year';

similarly, for Lesser Black-backed Gulls, return rates were examined using GLMMs (Lesser Black-backed Gull) controlling for fixed effects of 'sex' and 'year' and 'bird ID' as a random effect to account for repeat measurements for individuals in different years. Significant terms in all GLMs and GLMMs were selected through analysis of deviance and backwards step-wise deletion. Analyses were conducted using R v 2.5.11 (R Core Team 2013). We conducted a power analysis for all tests for the presence of type I or II errors, presenting the effect size (Cohen's *d*) for each test of 'group'. Appendix S1 includes full discussions of power, effect size and sample size for all measures presented from these analyses, from which we draw conclusions regarding the suitability of initial sample sizes.

RESULTS

Breeding productivity

For Lesser Black-backed Gull in 2011, there were no differences between tagged and control groups in the number of eggs hatched (Δdev = -1.59, df = 1, $P = 0.207$, $d = 0.07$) and number of chicks present per nest up to 9 July (Δdev = -0.28, df = 1, $P = 0.598$, $d = 0.68$; Table 1, Appendix S1). For Great Skua in 2011, there were no differences between Foula and Hoy in either the number of eggs hatched (Δdev = -0.13, df = 1, $P = 0.715$) or number of chicks present per nest up to 15 July (Δdev = -0.01, df = 1, $P = 0.910$). Across colonies there were no differences between tagged and control groups in the number of eggs hatched (Δdev = -0.27, df = 1, $P = 0.601$, $d = 0.22$) or number of chicks present per nest up to 15 July (Δdev = -0.40, df = 1, $P = 0.530$, $d = 0.19$). On Hoy, there were no differences in the number of chicks fledged per nest between tagged and control nests (Δdev = -0.20, df = 1, $P = 0.654$, $d = 0.22$; Table 1). There were no effects of sex recorded for productivity analyses ($P > 0.05$).

Breeding season territory attendance

For Great Skuas at Foula in 2011, spot checks of nests showed that there was no difference in territory attendance between tagged and control birds ($\chi^2_1 = 0.22$, $P = 0.636$, $d = 0.06$; probability of presence: control, 74.0 ± 44.0%, tagged, 71.1 ± 45.4%), after controlling for a significant effect of period of day ($\chi^2_2 = 11.01$, $P < 0.001$).

Over-winter return rates

For Lesser Black-backed Gull, there were no differences in over-winter return rates between tagged and control groups ($\chi^2_1 = 2.00$, $P = 0.157$, $d = 0.25$), after controlling for potential differences between years ($\chi^2_1 = 1.70$, $P = 0.427$) and sexes ($\chi^2_1 = 0.09$, $P = 0.754$). The return rates for birds tagged in 2011 were 79% (11/14 birds) for 2011–12 and 71% for 2012–13 (10/14 birds), compared to return rates of 53% (25/47 birds) and 64% (16/25 birds) for control birds over the same periods respectively (Table 2). Including tagged Lesser Black-backed Gulls that were recorded through the GPS system but not re-sighted gave more complete return rates of 14/14 birds (100%) and 13/14 birds (93%) for the 2011 cohort for periods 2011–12 and 2012–13 respectively, and a measure of 94% (17/18 birds) combining the 2010 and 2011 cohorts for the 2011-12 period (Table 2). Two tagged Lesser Black-backed Gulls and five control birds were recovered dead at the colony in 2013 due to fox predation, and another tagged bird was recovered outside the breeding season in Portugal (Appendix S3).

In contrast, there was a highly significant difference in return rates between tagged and control Great Skuas ($\chi^2_1 = 44.69$, $P < 0.001$, $d = 0.70$, Appendix S1). Return rates in 2012 of birds tagged in 2011 were just 10% (1/10 birds) for birds from Foula and 0% (0/10 birds) for those from Hoy, while the one tagged bird that returned in 2012 was not seen in 2013 (Table 2). For control birds, return rates over 2011-2012 and 2012-2013 were 100% (10/10) and

56% (5/9) for Foula, and 80% (8/10) and 75% (6/8) for Hoy respectively (Table 2). Two tagged Great Skuas (one from Foula and Hoy respectively) were recovered dead outside the breeding season in Germany and Portugal and another was seen on migration off the Devon coast (Appendix S3).

Power of the data

Power analyses revealed small effect sizes (and low power) for tests of breeding productivity and survival in both species and territory attendance of Great Skua (see Cohen's *d* values for respective tests and Appendix S1). However there were very small differences between estimates for tagged and control groups (Tables 1 and 2) and very large numbers of birds predicted to detect a significant effect for these tests (Appendix S1). Hence, the presence of type II errors was considered unlikely. In contrast, survival analysis for Great Skua revealed a much larger effect size and power, with the presence of type I errors being highly unlikely (Appendix S1).

DISCUSSION

For both Lesser Black-backed Gull and Great Skua, results indicated that the GPS device attached using a wing harness had no deleterious effects on breeding productivity within the season of capture. Similar findings have previously been recorded for Lesser Black-backed Gull in the Netherlands when using the same GPS and harness attachment (Camphuysen 2011). Furthermore, two South Polar Skuas *Stercorarius maccormicki*, a close relative to the Great Skua, have also been studied for up to 45 days during the breeding season using a leg-loop harness with no detrimental impacts on breeding success (Mallory & Gilbert 2008). From a separate study of Great Skuas in Shetland using devices attached with a body harness, nest survival rates in the breeding season when birds were first marked were no different between tagged and control nests (Crane 2006, Furness *et al*. 2006). The GPS device and wing harness used in this study also had no apparent deleterious effects on territory attendance of Great Skuas at Foula. Similarly, at St. Kilda, UK, Votier *et al*. (2006) found that breeding Great Skuas tagged using a GPS device attached to feathers spent on average 69% of their time at the colony, this value being comparable to the probability of tagged (71%) and control birds (74%) being present on their territories in our study. Crane (2006) also found that the territory attendance of Great Skuas tagged using a body harness was no different to control birds.

For Lesser Black-backed Gulls, the GPS device and attachment had no apparent effect on return rates, and thus their over-winter survival. The apparent annual survival rate of Lesser Black-backed Gulls at Orford Ness (as derived from colour-ring sightings) varies between years (from less than 50% to over 90%, Marsh 2013). In this study there were no differences in return rates between tagged and control groups after controlling for annual variation. The more complete return rates of tagged birds to Orford Ness derived by also incorporating information received through the tracking system (Table 2) were similar to previously reported annual survival rates from sites elsewhere (91.3%, Wanless *et al.* 1996; 91%, Camphuysen & Gronert 2012). Similar findings have been reported for Lesser Black-backed Gull at other colonies using the same GPS and harness attachment (Camphuysen 2011). In contrast, the return rate of tagged Great Skuas was much lower than that of controls, which was similar to a previously estimated return rate of 88.8% (Ratcliffe *et al.* 2002). Although individuals may skip breeding attempts, the recovery of two dead tagged Great Skuas and birds' failure to return to the colonies during the two years following the attachment of the device, suggests that mortality was the most likely outcome. The migration routes of the Great Skua found dead in Portugal and the additional bird seen off the Devon coast (Appendix S3) matched the routes recorded previously from other studies using geolocation (Furness *et al.* 2006, Magnusdottir *et al.* 2012). These results suggest that tagged Great Skuas had attempted migration but encountered difficulties during this period. One bird spent the winter in the Bay of Biscay region and made no attempt to migrate back to the colony, before its recovery the following summer (Appendix S3). There have been no other previous published findings of the effects of the wing harness on Great Skuas. However, the study of Great Skuas using devices attached to individuals with a body harness, found that no tagged birds returned and successfully bred the following season (Crane 2006, Furness *et al*. 2006), which also suggests a long-term effect for that attachment method. While technological improvements have allowed a reduction in the weight of devices over time from those used previously with a body harness (30 g) to those used with a wing harness in this study (21 g), this appeared to have had no tangible influence.

Limitations and considerations

Identifying suitable groups of control birds and adequate sample sizes of tagged birds are important aspects to consider when assessing device and attachment effects. The chosen control group may be unsuitable for causal inference, and small sample sizes cannot replicate all characteristics of the total population (Baron *et al*. 2010, Authier *et al*. 2013). In this study, the nests of unmarked control birds had lower productivity compared to colour-ringed controls (Appendix S1). This highlights that caution is needed when defining a meaningful control group. Although our conclusions regarding the impacts of devices and harnesses were the same no matter what combination of the two control groups was used (Appendix S1), the wider group of unmarked nests may have potentially been derived from more sub-optimal locations. Common to other tagging studies, we also had restricted sample sizes of tagged birds and their nests to compare to controls. However, power analyses revealed the observed effect sizes in nearly all statistical tests (with the exception of Great Skua return rate) to be so small as to have little biological meaning. While these analyses do not indicate there were no effects, they demonstrate how a very large sample size (sometimes more than the number of birds available in the population; Appendix S1) would be required to detect the observed effect.

Comparison of species ecology and behaviour

The reasons for the difference in over-winter return rates between Lesser Black-backed Gulls and Great Skuas are unclear, but potentially may be due to species differences in the extent of offshore habitat use during migration and winter, the potential compromise of insulation due to tag impact on plumage, and/or differences in foraging costs, aggressive behaviour and/or piracy. Lesser Black-backed Gulls use a range of terrestrial stopover sites outside the breeding season (Klaassen *et al*. 2012), whereas Great Skuas are thought to remain at sea (Furness 1987). Great Skuas may therefore be in flight for longer periods in maritime areas than Lesser Black-backed Gulls. This may exacerbate any effects that the device and wing harness may have on birds, and may have also increased the feather wear from the attachment, possibly compromising insulation and foraging efficiency. Great Skuas roost at night on the water, and this may be crucial in determining consequences of a reduction in insulation.

For the two gulls predated by foxes, there was no sign of damage to the underlying skin or contour feathers; there was some minor removal of down under the harness straps, but otherwise the feather layer was intact. There was some evidence of feather removal directly under the neoprene pad supporting the device, which created a bare patch (56 x 25, and 47 x 24 mm, for the two birds respectively), but otherwise feather growth was normal. Consequently, the use of this neoprene pad has since been discontinued. It is possible that this may have compromised insulation, either through direct exposure of skin to the air or penetration of water under plumage. However, the neoprene pad itself is likely to have provided some level of insulation.

Although survival estimates do not indicate an impact of the device and harness on Lesser Black-backed Gulls, any compromise of insulation may potentially be more problematic for Great Skuas that use the pelagic environment outside the breeding season. We had no information from the recovered Great Skuas to determine impacts on insulation. However, one Great Skua returned to the colony without its device or harness. This bird was re-trapped and showed no sign of any feather abrasion where the device had been. It is unknown how long the device remained attached to the bird, and it was unclear how the harness and device had been lost; the GPS device and harness remained on the bird at least until 29 August 2011 when the last data transmission from the device was received. It is clear, however, that this bird did not lose its attachment during the breeding season, with its departure from the colony being similar to other tagged birds, including the two birds recovered (Appendix S3). This further suggests that the effects of the device and harness for Great Skua occurred during the non-breeding season.

In addition to the mass of devices and their attachments relative to body mass, wing-loading is also a potentially important consideration in using bird-borne telemetry. Larger birds with higher wing-loadings may not so easily accommodate extra mass within their normal flight power requirements (Vandanebeele *et al*. 2011, 2012). Wing area was not recorded in our study, but using available estimates from other studies (Lesser Black-backed Gull, 0.195 m^2 mean of males and females, Camphuysen 1995; Great Skua, 0.214 m^2, Pennycuick *et al.* 1990), alongside our observed masses of tagged birds (Lesser Black-backed Gull, 0.851±0.085 kg, and Great Skua, 1.346±0.101 kg), we estimated that wing loadings were 44% higher for Great Skua compared to Lesser Black-backed Gull (6.29 kg/m^2 and 4.36 kg/m^2, respectively). Furness and Tasker (2000) also considered Great Skuas (on a sliding scale of 0 to 4) to have a higher foraging cost per unit of time (score of 3) compared to Lesser Black-backed Gull (score of 2); highest scores were given to species with flapping flight with frequent change of direction and lowest scores for economical gliding flight. Therefore, an increase in per unit foraging cost associated with the attachment of a device could have had a greater relative impact on the energetics of Great Skua compared to Lesser Black-backed Gull.

Great Skuas also have more powerful beaks than Lesser Black-backed Gulls, and may be more likely to try and remove a device they are carrying, and perhaps even injure themselves in the process. However, there was no evidence of any beak marks on the two devices that were recovered. Great Skuas are also known to be mobbed frequently by other birds, and fight between themselves. The GPS device could therefore be seen by other birds as a target, which may then provoke aggressive attacks; the Great Skua recovered in Germany was seen being mobbed by other birds before it died. Great Skuas are also more reliant on piracy (kleptoparasitism) for feeding than most other seabirds (Furness 1987). If a reduction in aerial agility or foraging efficiency affected piracy more than other foraging tactics such as surface feeding or use of discards, then this could have more detrimental impacts on Great Skuas than Lesser Black-backed Gulls.

Implications for further work

In accordance with previous studies on Lesser Black-backed Gull, we found no short-term impacts on breeding productivity or long-term impacts on over-winter return rates and the device and wing harness were considered suitable for deployment across the year. However, for Great Skua, although no deleterious impacts were apparent from the device and wing harness during the breeding season, effects on apparent adult survival over migration and wintering periods were catastrophic. Consequently, deployment of the GPS device using a wing harness is not recommended for long-term deployment for Great Skuas. Advances in remote detachment methods may provide future solutions for studying Great Skuas, allowing devices to fall off safely after one or two months; for example using weak points in the attachment or the use of harness materials that will break under the influence of UV-radiation. Such solutions could also be valuable in other species, where issues identified at the outset may prevent longer term study. Until more suitable deployment methods are developed, the most practical approach for studying the migration and longer-term movements of Great Skuas and many other species is through a geolocator attached to a leg ring (e.g. Magnusdottir *et al.* 2012).

This study demonstrates how species' responses to harness attachments should not be expected to be the same just because they share similar traits such as body size, shape and ecology. For example, some species exhibit marked changes in body shape throughout their annual cycle (e.g. Portugal *et al*. 2007), or have comparatively higher foraging costs (Vandanebeele *et al*. 2012). Behaviour at particular life history stages, e.g. the relative use of different habitats, also needs to be scrutinised closely, but equally, other aspects such as migration strategy or preferred feeding tactics could be highly influential. The ecology, lifestyle, morphology and physiology of the species therefore all need consideration before decisions on the shape and weight (Bowlin *et al*. 2010), positioning (Thaxter *et al*. 2014, Vandenabeele *et al*. 2014) and attachment methods of devices, e.g. this study, are taken. Care must therefore be taken if any single species-specific aspect is considered in isolation or when making extrapolations based on particular comparable aspects of other species. These decisions are not straightforward, but are particularly important within the marine environment as the greater conductivity of water than air means any compromised plumage insulation and heat loss will be magnified, and the higher viscosity of water will increase drag underwater more so than in air (Vandenabeele *et al*. 2011). It is hoped the findings in this study will help inform the planning required for future tracking studies, and also highlight that the absence of breeding season effects does not mean that longer term effects can be discounted.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Sample sizes and consideration of power of data presented.

Appendix S2. Information on duration and timing of breeding periods.

Appendix S3. Additional information on recovered birds.

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Table 1. Mean metrics of breeding productivity (±1 SD) of (a) Lesser Black-backed Gulls at Orford Ness and (b) Great Skuas on Foula and Hoy during 2011 for nests of tagged birds, nests of colour-ringed controls, and other control nests. Uncertainty in measures is expressed as worst case (minimum) and best case (maximum) scenarios (see text for more details).

(a)				**Control birds**		
Colony	**Year**	**Measure**	**Tagged birds**	**Colour-ringed**	**Other**	**All**
Orford Ness	2011	No. nests	13[a]	26[b]	21	47
		Eggs hatched/nest (min, max)	1.8±1.1-2.6±1.0	1.2±1.0-2.6±0.5	1.1±1.1-1.4±1.2	1.2±1.0-2.0±1.1
		Chicks present/nest[c] (min, max)	0.8±1.1-1.9±1.0	0.7±1.0-2.1±0.9	0.3±0.5-1.2±1.1	0.5±0.8-1.7±1.1
(b)						
Foula	2011	No. nests	10	10	37	47
		Eggs hatched/nest	1.5±0.7	1.7±0.5	1.3±0.7	1.4±0.7
		Chicks present/nest[d] (min, max)	0.8±0.9-1.0±0.9	0.9±0.7-1.5±0.8	0.8±0.8-0.9±0.8	0.8±0.7-0.9±0.9
Hoy	2011	No. nests	10	10		
		Eggs hatched/nest (min, max)	1.1±0.7-1.6±0.8	1.1±0.7-1.5±0.7		
		Chicks present/nest[d] (min, max)	0.4±0.7-0.6±1.0	0.5±0.5-0.8±0.8		
		Chicks fledged/nest[e]	0.2±0.4	0.3±0.5		

[a]Two tagged birds were from the same nest (14 birds monitored at 13 nests).

[b] Of the total sample of 47 colour-ringed birds, the nests of 19 were not followed, and for two nests, both members of the pair were marked (i.e. 28 birds were monitored at 26 nests);

[c]Up to 9 July 2011;

[d]Up to 15 July;

[e]Up to 14 August;

Table 2. Over-winter return (survival) rates of (a) Lesser Black-backed Gull, and (b) Great Skua between consecutive breeding seasons, based on (i) observations of colour-ringed birds, and (ii) also including additional records obtained through the GPS system. *n* = the number of marked birds at the end of the preceding breeding season.

(a)			2010-11			2011-12			2012-13		
Colony	**Year marked**	**Group**	***n***	**No. re-sighted (%)**	**No. re-sighted / recorded by GPS (%)**	***n***	**No. re-sighted (%)**	**No. re-sighted / recorded by GPS (%)**	***n***	**No. re-sighted (%)**	**No. re-sighted / recorded by GPS (%)**
Orford Ness	2010	Tagged	4	1 (25%)	3 (75%)	3	2 (67%)	3 (100%)	3	1 (33%)	1 (33%)
		Control	6	4 (67%)		4	3 (75%)		3	2 (67%)	
	2011	Tagged				14	11 (79%)	14 (100%)	14	10 (71%)	13 (93%)[a]
		Control				47	25 (53%)		25	16 (64%)[b]	
(b)						2011-12			2012-13		
Colony	**Year marked**	**Group**				***n***	**No. re-sighted (%)**	**No. re-sighted / recorded by GPS (%)**	***n***	**No. re-sighted (%)**	**No. re-sighted / recorded by GPS (%)**
Foula	2011	Tagged				10	1 (10%)	1 (10%)	1[c]	0 (0%)	0 (0%)
		Control				10	10 (100%)	10 (100%)	9[d]	5 (56%)	5 (56%)
Hoy	2011	Tagged				10	0 (0%)	0 (0%)	0[e]	0 (0%)	0 (0%
		Control				10	8 (80%)	8 (80%)	8	6 (75%)	6 (75%)

[a]Two tagged Lesser Black-backed Gulls (459 and 492) subsequently found dead at the breeding colony in 2013; one further tagged Lesser Black-backed Gull (483) found dead in Portugal on 26 November 2013.

[b]Five colour-ringed control Lesser Black-backed Gulls subsequently found dead at the breeding colony in 2013;

[c]One tagged Great Skua (419) found dead in Germany 15 October 2011, one Great Skua (450) returned to breed in 2012 but without its tag and harness;

[d]One colour-ringed control Great Skua found dead at the breeding colony in 2012;

[e]One Great Skua (467) found dead in Portugal 13 August 2012.