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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The use of telemetry has become an important means 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 considered. 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 (hereafter ‘tagged’ birds) and control birds without an attachment. We investigated whether tagged birds could have, in the short-term, lower breeding productivity and, in the longer term, lower over-winter return rates (indicative of over-winter survival) than controls. For Great Skua, we also tested whether territory attendance within the breeding season differed between tagged and control birds. 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. In contrast, for Great Skua, there was no evidence for impacts of the device and harness on territory attendance or breeding productivity, but there was strong evidence for reduced over-winter return rates. Results of a previous study on Great Skua using a different (body) harness design were in accordance with these findings. Consequently, a device attached using a wing harness was considered suitable for long-term deployment on Lesser Black-backed Gull, but not for Great Skua.

**Keywords**: Breeding productivity, foraging behaviour, return rate, seabird, telemetry, wing harness
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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 (see reviews by Barron et al. 2010; Vandanaabele 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; Vandanaabele et al. 2011). Individual 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, Vandanaabele et al. 2011, Bridge et al. 2013). Therefore, while some studies have reported effects, many others have found no such deleterious impacts (Vandanaabele et al. 2011; see for example Davis et al. 2008, Lislevand & Hahn 2013). 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). As a result, 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).

Consequently, there is a pressing need to assess the suitability of particular harnesses and devices for different species across different time scales.

In this study, we compare 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 are 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 (short-term) tagged birds exhibited lower breeding success, and between consecutive breeding seasons (long-term) tagged birds may have lower ‘return rates’. 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 recorded for breeding success (Camphuysen 2011), or for 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 previous studies, we predicted no effects
on Lesser Black-backed Gull on these short- or long-term measures. Previous studies on 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 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 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 and 20 Great Skuas (ten each in Foula and Hoy) using the same wing harness design.

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 (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 mins (range 15–46 mins) for Lesser Black-backed Gull and 25±4 SD mins (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 and 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 = six 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 examined 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). However, 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. At this stage, mean chick age across nests was between 6±8 d (range, 7-35 d) and 14±9 d (range 1-26 d) after hatching (lower and upper values reflecting the uncertainty in estimated hatching dates from the above nest monitoring protocol). 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). Where gaps in the monitoring of nests were greater than a single day, breeding productivity was expressed by mean minimum and mean maximum estimates of numbers of eggs or chicks surviving to provide a level of error (see Table 1). For Great Skuas at Foula, nest monitoring allowed a final estimate to be made of the number of chicks present up to 15 July (when mean chick age was 20±9 d, range 1-35 d). However, nests at Hoy were followed for a longer period into chick-rearing (mean chick age lower estimate, 26±22 d range 1-64 d, upper estimate, 32±21 d range 7-64 d), 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 and normally return to their nest site within the colony.
negligible and return rates are likely to reflect true survival rates. Return rates for the four and
14 tagged Lesser Black-backed Gulls were compared with those of six 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. 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). 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. The
respective tracking systems at each of the sites were also used to check for returning tagged
birds.

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
carried out 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 and territory attendance were different between tagged
and control birds, we used general linear models (GLMs), with Poisson and binomial errors,
respectively. Response variables of the number of eggs hatched, the number of chicks present
per nest and presence or absence in the territory were investigated as separate analyses, with
fixed effects for ‘group’ (tagged and control), ‘sex’ and ‘time of day’ also 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. Differences in over-winter return rates between
tagged and control birds (fixed effect of ‘group’) were examined using binomial
(presence/absence response) general linear models (GLMs, Great Skua), or GLMMs (Lesser
Black-backed Gull). GLMMs included bird ID as a random effect to account for repeat
measurements for individuals in different years, controlling for additional fixed effects of
‘sex’ and ‘year’. Significant terms in all GLMs and GLMMs were selected through
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, 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 (dDev = -1.59, df = 1, $P = 0.207$, $d = 0.07$) and number of chicks present per nest up to 9 July (dDev = -0.28, df = 1, $P = 0.598$, $d = 0.68$, see Table 1, Appendix S1). For Great Skua in 2011, there were no differences between Foula and Hoy in either the number of eggs hatched (dDev = -0.13, df = 1, $P = 0.715$) or number of chicks present per nest up to 15 July (dDev = -0.01, df = 1, $P = 0.910$). Across colonies there were no differences between tagged and control groups in the number of eggs hatched (dDev = -0.27, df = 1, $P = 0.601$, $d = 0.22$) or number of chicks present per nest up to 15 July (dDev = -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 (dDev = -0.20, df = 1, $P = 0.654$, $d = 0.22$; Table 1).

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 (dDev = -1.32, df = 1, $P = 0.250$, $d = 0.06$; probability of presence: control, 74.0±44.0%, tagged, 71.1±45.4%).

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).

By contrast, there was a highly significant difference between tagged and control group
return rates for Great Skua ($\chi^2 = 44.69, P < 0.001, d = 0.70$, 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 Devonshire coast (see Appendix S3).

**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). From a separate study of Great Skuas in Shetland using devices attached with a body
harness, nest survival rates in the breeding season after marking were no different between
tagged and control nests (Crane 2006; Furness et al. 2006). 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). 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). However, 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). By 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 Devonshire 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 published findings of the specific effects of the wing harness on Great Skuas. However, the study of Great Skuas using devices attached to Great Skuas 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.

In accordance with previous studies on Lesser Black-backed Gull, we thus found no short-term impacts on breeding productivity or long-term impacts on over-winter return rates and the device and wing harness were thus 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. Thus, deployment of the GPS device using a wing harness was not suitable for long-term deployment for Great Skuas.

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 (see 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 no different 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. Quantitative methods to define control groups are therefore preferable to rule out such issues (Authier et al. 2013). 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 completely 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 seasons.

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 m² mean of males and females, Camphuysen 1995; Great Skua, 0.214 m², 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/m² and 4.36 kg/m², respectively). Furness & Tasker (2000) also considered Great Skuas (on a scale of 1 to 4) to have a higher foraging cost per unit of time (score of 3) compared to Lesser Black-backed Gull (score of 2). 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 have also 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. It is also possible that the impacts of a device and harness could also differ within a species between colonies or years with different ecological conditions. For instance, birds exposed to extremes of food shortage or weather may be more susceptible to impacts that may not be evident under benign conditions.
The colony productivity of Great Skuas at both Foula and Hoy was low in comparison to previous years (see Wade et al. 2014). However, Lesser Black-backed Gull productivity was relatively low and variable between years over the period of study (Thaxter et al. 2015), and for Great Skuas, no impacts were recorded during the breeding season.

**Implications for further work**

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 between the harness and the device or the use of harness materials that will break under influence of UV-radiation. The attachment of a device for short-term study during the breeding season is currently possible by attachment to feathers on the back or tail. The device then falls off when the feathers are shed and so is less likely to have long-term impacts. 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. 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
positioning (Thaxter et al. 2014, Vandenabeele et al. 2014) and attachment methods of devices (e.g. this study) are taken. Consideration of any single species-specific aspect in isolation or extrapolation based on particular comparable aspects of other species is therefore discouraged. 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.

This study was funded by the Department of Energy and Climate Change (DECC), and the Marine Renewable Energy and the Environment (MaREE) project (funded by Highlands and Islands Enterprise, the European Regional Development Fund, and the Scottish Funding Council). We thank John Hartley (Hartley Anderson), Emma Cole, Mandy King, Sophie Thomas and James Burt (DECC) and Mark Rehfisch (formerly of BTO) for their support of the work on Foula and at Orford Ness. Thanks to the National Trust, Scottish Natural Heritage, RSPB and Natural England for site permissions and thanks to Aileen Adam (University of Glasgow) for sexing of Great Skuas. We are very grateful to all who have helped with discussions and fieldwork. We thank four anonymous reviewers, the Editor Ruedi Nager and Associate Editors Francis Daunt and Mark Bolton for their suggestions on previous versions of the manuscript.
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.

REFERENCES


Sergio, F., Tavecchia, G., Taferna, A., López Jimenez, L. Blas, J., De Stephanis, R.


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).

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

\(^a\)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.

<table>
<thead>
<tr>
<th>Group</th>
<th>Colony</th>
<th>Year marked</th>
<th>2010-11</th>
<th>2011-12</th>
<th>2012-13</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>No. re-sighted (%)</td>
<td>No. re-sighted / recorded by GPS (%)</td>
<td>No. re-sighted (%)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>( n )</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Orford Ness</td>
<td>2010</td>
<td>Tagged</td>
<td>4</td>
<td>1 (25%)</td>
<td>3 (75%)</td>
</tr>
<tr>
<td>Control</td>
<td>6</td>
<td>4 (67%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2011</td>
<td>Tagged</td>
<td></td>
<td>14</td>
<td>11 (79%)</td>
<td>14 (100%)</td>
</tr>
<tr>
<td>Control</td>
<td>47</td>
<td>25 (53%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Foula</td>
<td>2011</td>
<td>Tagged</td>
<td>10</td>
<td>1 (10%)</td>
<td>1 (10%)</td>
</tr>
<tr>
<td>Control</td>
<td>10</td>
<td>10 (100%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2011</td>
<td>Tagged</td>
<td></td>
<td>10</td>
<td>0 (0%)</td>
<td>0 (0%)</td>
</tr>
<tr>
<td>Control</td>
<td>10</td>
<td>8 (80%)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hoy</td>
<td>2011</td>
<td>Tagged</td>
<td>10</td>
<td>8 (80%)</td>
<td>8 (80%)</td>
</tr>
</tbody>
</table>

\(\(^a\)\) 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.
Appendix S1. Sample sizes and consideration of power of data presented

Breeding productivity of control birds

In this study, two types of controls were included for comparing breeding productivity with nests of tagged birds – nests where adult birds were colour-ringed, and additional nests that were also followed. For both Lesser Black-backed Gull and Great Skua, these additional nests were in the same vicinity as the nests of both the colour-ringed controls and the tagged birds. However, for Lesser Black-backed Gulls in 2011, the maximum number of eggs hatched per nest and chicks present per nest up to 9 July 2011 for these additional nests were both significantly lower (dDev = -6.81, df = 1, P = 0.009; dDev = -6.03, df = 1, P = 0.014, respectively) than for the nests of colour-ringed controls; minimum numbers of eggs and chicks were not significantly different (P > 0.05 in both cases). For Great Skuas at Foula, the maximum number of chicks present up to 15 July was lower for these additional nests than for the nests of colour-ringed controls (Table 1 in main paper) but was not significantly different (dDev = -2.33, df = 1, P = 0.127). For both species, the nests of the sample of unmarked birds included nests from the wider area, including the periphery of both colonies, and so were likely to have included some sub-optimal nesting sites, presumably resulting in lower productivity compared to other colour-ringed control birds. Note, however, there was no significant difference between the nests of colour-ringed control birds alone and those of tagged birds for any measures of breeding productivity (P > 0.05 in all cases). To provide as wide as possible a sample of breeding productivity of the nests of control birds to compare to tagged birds, we therefore pooled both groups of control nests together. Tests for breeding productivity in the main paper 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.
Sample sizes of sexed birds

In this study, birds of both species were sexed to allow further investigations into potential differences in device and harness attachment effects. For Lesser Black-backed Gulls at Orford Ness, tagged and control birds were sexed using head and bill length measurements (Coulson et al. 1983; Camphuysen 2011). Out of 18 tagged birds, ten were males and seven were females, with the remaining bird not assigned sex due to uncertainty. Out of the 28 control birds, 17 were males and 11 were females. A sufficient number of males and female Lesser Black-backed Gulls from tagged and control groups were therefore available to investigate device and harness effects on breeding productivity and over-winter return rates.

For Great Skuas, tagged and control birds were sexed using either DNA from feather samples (Griffiths et al. 1993), previous known sex from ringing data or within-pair relational size from simultaneous viewing of both pair members. For tagged birds at Foula and Hoy, out of a total of ten birds at each site, three and five females and two and three males were identified, respectively, with the remaining birds not assigned sex due to uncertainty; for control birds at both sites, five females and zero males were identified. Therefore for Great Skua, given the small sample sizes and particularly the lack of male control birds, sex differences in the effects of device and harness on breeding productivity and over-winter return rates were not investigated.

Power of the data presented

The power of all tests presented in this study was assessed for the presence of type I or II errors that may have occurred with limited sample sizes and low statistical power. Effect sizes here are presented as Cohen’s $d$, and sample sizes are presented that would be needed to reach significance at an alpha level of 0.05 and a power of 0.8. It should be noted that the number of birds tagged and monitored as control groups was relatively high for this study.
Tests for differences in the breeding productivity of tagged and control groups of Lesser Black-backed Gulls and Great Skuas were non-significant, and in most cases associated with low effect sizes. For Lesser Black-backed Gull, the effect size for number of eggs hatched was 0.07, with a power of 0.05, and the sample size needed for a significant difference to have been observed between tagged and control birds was 3,651 nests. This compares to a colony size of 540–620 pairs at Orford Ness (Marsh 2013). The mean differences between values for tagged and control birds in all cases were very small and standard deviations and overlaps in the distributions of variables were very high (see Table 1). Therefore, it is very unlikely that Type II errors occurred. For Lesser Black-backed Gull, there was a non-significant tendency for nests of tagged birds to have more chicks present up to mid-July in 2011 than control nests (Table 1), which was opposite to our expectation had tags and the harness been deleterious to foraging behaviour. In this case, the effect size was 0.68, and the power was also quite high at 0.6, and the sample size needed for a significant difference to have been observed between tagged and control birds was just 35 nests. However, given the direction of the effect, it is quite unlikely that a Type II error occurred here.

For Great Skua at Foula and Hoy respectively, the effect size for eggs hatched per nest was 0.17 and 0.26, with a power of 0.07 and 0.08, and the sample size needed for a significant difference to have been observed between tagged and control birds was 576 and 236 nests. Likewise, the effect size for number of chicks present per nest up to 15 July was 0.19, with a power of 0.11, and the sample size needed for a significant difference was 432 nests. For Hoy, the effect size for number of chicks fledged per nest was 0.22, with a power of 0.08, and the sample size needed for a significant difference was 324 birds. This compares to colony sizes of 1 657 AOTs at Foula and 1 346 AOTs at Hoy (JNCC Seabird Monitoring Programme database, last accessed 6 November 2014).
**Over-winter return rates**

For Lesser Black-backed Gull, the effect size for return rates was 0.25, resulting in a low power of 0.15 and thus a high sample size of 251 birds needed for a significant difference to have been observed between tagged and control birds. The difference between mean return rates (across all years) was 0.13 (see Table 2 for return rate estimates). These results suggest the non-significant result for Lesser Black-backed Gulls was very robust, and not subject to type II errors. For Great Skua, the difference in mean return rates (over 2012 and 2013) between tagged and control birds was 0.70. This resulted in a very high effect size of 2.10 and a very high power of 0.99. For this difference, a sample size of just five birds would have been needed for a significant difference to have been observed between tagged and control birds. As such it is conclusive that sample sizes were sufficiently high to detect the effect recorded in differences in over-winter return rates between tagged and control groups of Great Skuas, and unlikely a type I error occurred.

**Breeding season territory attendance**

For Great Skua at Foula, the effect size for territory attendance was 0.06, with a power of 0.05, and the sample size needed for a significant difference to have been observed between tagged and control birds was 3 952 predicted. This value is more than twice the number of AOTs at Foula (see above). The very similar mean estimates and large overlaps in standard deviations (control = 74.0±44.0%, tagged = 71.1±45.4%) show that it is highly unlikely that any effect was missed using the sample sizes obtained.

**REFERENCES**


Appendix S2. Information on duration and timing of breeding periods

To assess the effects of the GPS device and harness on Lesser Black-backed Gull and Great Skua, a comparison of breeding productivity was made between nests of tagged birds (with a GPS device and harness) and control birds (birds without a device and harness). Clutch size was not investigated as nests were discovered at different times during incubation, hence the initial clutch size was not always known. However, the number of eggs hatched, the number of chicks present up to mid-July, and the number of chicks fledged per nest were investigated between control and tagged groups. It is important therefore that the two groups were followed for similar periods (and thus that the risks of failures were the same) to ensure that correct conclusions were reached.

For Lesser Black-backed Gull, the earliest and latest estimates of mean hatch dates in 2011 were 5 and 14 June for tagged nests and 8 and 16 June for control nests. The number of chicks present at nests was recorded in the early stages of chick-rearing. The lengths of time that nests of tagged Lesser Black-backed Gulls were monitored after hatching during the chick-rearing period ranged from a minimum of 7±8 d to a maximum of 15±8 d. For control birds, nests were monitored from 6±8 to 13±9 d. The ranges for minimum and maximum estimates were 1-26 d and 7-35 d for the respective groups. The standard deviations indicate variability across nests monitored, while the lower and upper values represent uncertainty in estimated hatching dates due to the frequency of nest monitoring. For Great Skua, nests were monitored daily at Foula until 15 July 2011. The mean first egg hatching dates were 18 June for tagged nests and 23 June for controls. The length of time that nests were monitored during the chick-rearing period was consequently 22±9 d for tagged birds and 20±10 d for control birds. At Hoy, nests were monitored weekly in 2011. Mean earliest and latest estimates of first egg hatching dates for nests of tagged birds were 17–21 June, and for nests of control birds, 17–25 June. The mean length of time that nests were monitored for during the chick-
rearing period when birds still had eggs or chicks was 20±25 d (range, 1–65 d) for tagged birds and only slightly longer 26±19 d (range, 3–64 d) for control birds. At Hoy, two nests of tagged birds and three nests of control birds successfully fledged chicks. For neither species were there significant differences in the hatching dates of nests or the ages of chicks monitored between the nests of tagged and control birds (GLMs of ‘chick age’ and Julian date ‘laying date’, considering minimum and maximum estimates in separate analyses, testing a fixed effect for ‘group’ (tagged and control): P > 0.05 in all cases for each species). Hence, any differences in the number of chicks present between the nests of tagged and control birds would not have been due to the relative length of time that nests were monitored during the chick-rearing period.
Appendix S3. Additional information on recovered birds

Lesser Black-backed Gull

Two tagged Lesser Black-backed Gulls from 2011 were subsequently found dead due to fox predation within the breeding colony during 2013, and another was recovered dead at Corroios, Seixal, Portugal (38°38’ N, 9°8’ W) on 26 November 2013. Five colour-ringed control birds were also recovered dead due to fox predation in June 2013. Although sample sizes were small, it is therefore unlikely that birds wearing a device and harness were more vulnerable to fox predation.

Great Skua

One control Great Skua on Foula was recovered dead within its breeding territory on 12 May 2012. Another Great Skua was reported off the coast of south Devon on 12 October 20111 with its GPS device and wing harness in place. Two further birds were recovered dead with their device and harness in place outside the breeding season. One from Foula was found near Norddorf, Germany (54°42’ N; 8°20’ E), on 18 October 2011. The GPS data showed that this bird departed the colony on 25 August 2011, remaining in the North Sea, reaching the Lincolnshire coast, UK on 16 September 2011 before venturing back out to sea prior to its subsequent recovery. A tagged Great Skua from Hoy was recovered at Praia do Meco, Setubal, Portugal (38°28’ N; 9°12’ W) on 13 August 2012. The GPS data showed that this bird left the colony on 10 September 2011 migrated along the west coast of Scotland and Ireland, reaching the Bay of Biscay on 17 September 2011, where the bird spent the 2011/12 winter and following months before its recovery. Movements of these birds are shown in Figure S3.1.

Only one Great Skua tagged in 2011 returned in 2012 (Table 2), but without its device and harness. This bird was tagged at Foula and was present at the colony until 29 August 2011 (last recorded GPS fix). This date was similar to other tagged Great Skuas at Foula in 2011 (mean 22 August ±17 days, max 18 September). The two birds recovered with their device and harness intact left the breeding colony on 25 August and 10 September 2011. This strongly suggested that Great Skuas departed with their device and harness intact. In 2012 the previously-tagged bird at Foula laid two eggs (2011, same clutch size), and weighed 1 305 g (5 June 2011 09:10 h BST) upon re-trapping. This was heavier than its weight upon initial trapping in 2011 (1 220 g, 5 June 10:24 BST) and both weights were similar to breeding birds on Foula during 2011 (range 1 180–1 490 g, mean 1 324±100 g, n = 20 birds).
Figure S3.1. Map showing the GPS locations of two Great Skuas after they departed their breeding colonies prior to final recoveries, and a re-sighting of another bird off the Devonshire coast (see text in Appendix S3 for details).