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Article

Effects of back-mounted biologgers on condition, diving and flight performance in a breeding seabird

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Biologging devices are providing detailed insights into the behaviour and movement of animals in their natural environments. It is usually assumed that this method of gathering data does not impact on the behaviour observed. However, potential negative effects on birds have rarely been investigated before field-based studies are initiated. Seabirds which both fly and use pursuit diving may be particularly sensitive to increases in drag and load resulting from carrying biologging devices. We studied chick-rearing adult common guillemots *Uria aalge* equipped with and without back-mounted GPS tags over short deployments of a few days. Concurrently guillemots carried small leg-mounted TDR devices (time-depth recorders) providing activity data throughout. Changes in body mass and breeding success were followed for device equipped and control guillemots. At the colony level guillemots lost body mass throughout the chick-rearing period. When-equipped with the additional GPS tag, the guillemots lost mass at close to twice the rate they did when equipped with only the smaller leg-mounted TDR device. The elevated mass loss suggests an impact on energy expenditure or foraging performance. When equipped with GPS tags diving performance, time-activity budgets and daily patterns of activity were unchanged, yet dive depth distributions differed. We review studies of tag-effects in guillemots *Uria* sp. finding elevated mass loss and reduced chick-provisioning to be the most commonly observed effects. Less information is available for behavioural measures, and results vary between studies. In general, small tags deployed over several days appear to have small or no measurable effect on the behavioural variables commonly observed in most guillemot tagging studies. However, there may still be impacts on fitness via physiological effects and/or reduced chick-provisioning, while more detailed measures of behaviour (e.g. using accelerometry) may reveal effects on diving and flight performance.

Keywords: animal welfare, biologging, device effects, diving, foraging, *Uria aalge*



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Introduction

Biologging devices, including GPS, TDR (time depth-recorders), accelerometers and cameras, are proving powerful means to learn how free-living animals behave and use their environments (Hussey et al. 2015, Kays et al. 2015). However, the behaviour recorded by such devices may be affected by the additional stressors of carrying the device, thus behaviour may not be representative of untagged animals (Ropert-Coudert and Wilson 2004, Wilson and McMahon 2006, Casper 2009, McMahon et al. 2012). These devices have been particularly insightful for studies of seabirds, whose behaviour away from their nesting grounds is hard to follow through traditional field observation. For instance, biologging has revealed impressive trans-oceanic movements (Croxall et al. 2005, Shaffer et al. 2006) and underwater activity (Kooyman and Kooyman 1995, Huin and Prince 1997). Yet, the potential effects of biologging devices on seabirds are still not well understood (Vandenabeele et al. 2011), with effects on behaviour being particularly challenging to study as the means of measurement (a biologging device) may itself affect the behaviour observed (Wilson and McMahon 2006).

Effects of biologging devices on animals may differ according to device size and mass (Wilson et al. 1986), tag placement (Vandenabeele et al. 2014, Bodey et al. 2017), attachment type (e.g. harness, tape, leg-ring) (Thaxter et al. 2014, Bodey et al. 2017), tag buoyancy (Elliott et al. 2007) and tag shape (Todd Jones et al. 2013). How animals respond to tags will be a combination of direct physiological costs and performance effects together with how the animals respond to these by altering their own behaviour (Wilson et al. 1986). In flying and diving animals, the main mechanical energetic costs of carrying tags will be through increased wing-loading and drag (Bowlin et al. 2010, Pennycuick et al. 2012, Vandenabeele et al. 2012, Todd Jones et al. 2013, Vandenabeele et al. 2015), which are in general a function of tag mass and cross-sectional area respectively. The amount of drag is also influenced by the shape of tags, for example, external antennas or stalks potentially increase drag forces dramatically during both swimming and flight (Wilson et al. 2004, Pennycuick et al. 2012, Morganti et al. 2018), while using a teardrop shape for tags can reduce drag for a given cross-sectional area (Todd Jones et al. 2013). Additional energetic costs associated with tagging could arise via disruption of insulation (Thaxter et al. 2015) or alterations in hormone levels (Elliott et al. 2012).

Device effects may be measured at several levels from direct effects through, for example, impairment of locomotion performance (Wilson et al. 1986), to more indirect effects occurring in behavioural responses of instrumented animals, e.g. changes in activity budgets (Passos et al. 2010, Chivers et al. 2015, Heggøy et al. 2015). Ultimately, such changes in performance and any compensatory changes in activity may cascade to affect fitness outcomes through reduced breeding success and survival if birds are unable to buffer tag effects (Saraux et al. 2011, Thaxter et al. 2014, Weiser et al. 2016,

Morganti et al. 2018). Measuring how animals respond to carrying tags at multiple levels, from the more direct movement performance metrics to changes in activity patterns can demonstrate the mechanisms behind any ultimate effects on fitness. A variety of approaches have been used, including field studies on wild animals (Wilson et al. 1986, Chivers et al. 2015, Heggøy et al. 2015, Morganti et al. 2018), studies of tagged captive animals (Pennycuick et al. 2012, Latty et al. 2016), use of physical and mathematical models (Bowlin et al. 2010, Vandenabeele et al. 2012, Kay et al. 2019), and combinations of these approaches (Todd Jones et al. 2013, Vandenabeele et al. 2015). However, tag effects may be obscured when looking at factors more directly related to fitness, such as changes in body mass or breeding success, as animals may buffer effects by compensating behaviourally or physiologically. For example, even if flight costs increase, daily energy expenditure may be unchanged if birds change their activity budgets (Elliott et al. 2014). During breeding, tagged birds may partially or fully buffer tag effects by reducing their own condition, e.g. using fat stores or reducing self-maintenance (Paredes et al. 2005, Navarro et al. 2008, Jacobs et al. 2013) though such mass loss may be adaptive to increase flight efficiency during the energetically demanding chick-rearing period (Norberg 1981, Croll et al. 1991), and this mass loss may be expected to be greater if a bird is also compensating for the additional load from a tag. In birds with biparental care, the partner may compensate for reduced provisioning by its tagged mate (Paredes et al. 2005).

The impacts from the additional load and drag of carrying a biologging device may be particularly acute for pursuit diving seabirds with continuous flapping flight (Vandenabeele et al. 2012). These species typically have high wing-loading, which is adaptive for diving but increases the energetic cost of flight (Pennycuick et al. 2012, Elliott et al. 2013a), with flight costs potentially raised further by the additional load of a tag (Vandenabeele et al. 2012, Elliott et al. 2014). Furthermore, these species are highly streamlined for efficient diving in the high-drag underwater environment (Lovvorn et al. 2001), and thus tags may increase dive costs or reduce dive performance through increased drag (Vandenabeele et al. 2015).

In this study, we tested how carrying a back-mounted GPS device affected common guillemots *Uria aalge* during the chick-rearing period using multiple measures to assess for potential direct (e.g. changes in dive performance) and indirect tagging effects (e.g. changes in activity budgets or body mass). Guillemots, with their extremely high wing-loading, exemplify the aforementioned evolutionary balance between the use of wings to propel both flight and diving (Pennycuick 1987, Elliott et al. 2013a). During chick-rearing, a large proportion of their time and energy budget is spent on these demanding activities (Elliott et al. 2008b, 2013b), and thus they may be expected to be particularly sensitive to carrying biologging devices. Previous studies of common guillemots and the congeneric Brünnich's guillemot (*U. lomvia*, L. 1758) have found a number of tagging effects including: reduced

breeding success (Takahashi et al. 2008), reduced chick-provisioning rates and decreased adult mass (Paredes et al. 2005, Jacobs et al. 2013), increased trip durations (Wanless et al. 1988, Hamel et al. 2004), and changes in diving behaviour (Elliott et al. 2007, Jacobs et al. 2013). However, effects on measures more directly related to fitness (e.g. reduced breeding success or body mass) are likely to result from how tags directly affect performance and behaviour. In this study we use a dual-tagging approach collecting detailed foraging behaviour data together with monitoring body condition and breeding success. We use these measures to investigate whether the recorded foraging activity from GPS-tagged guillemots is representative of non-tagged guillemots. Then if GPS-tagged guillemots are shown to have reduced fitness (using body condition and breeding success as proxies) we set out to examine how these effects emerge through e.g. changes in diving performance or time-activity budgets.

We performed a dual-tagging controlled crossover experiment, whereby all experimental guillemots were tagged for two consecutive periods. Two groups of guillemots were selected, with the first group tagged with both a larger back-mounted GPS together with a second much smaller tag, a time-depth recorder (TDR) attached to a leg-ring then during the second period these guillemots only carried the TDR. The second group received the same set of tags but in the opposite order, i.e. with the TDR only in the first period and GPS plus TDR in the second period. In addition, body condition and breeding success were monitored for a control group that carried no tags. Dual-tagging studies provide detailed information on behaviour away from the colony and how this may change when instrumented with a second larger tag (Ropert-Coudert et al. 2000, Passos et al. 2010, Ludynia et al. 2012, Chivers et al. 2015). The crossover design is a statistically powerful approach for comparing between treatment groups when there are large individual differences (Wellek and Blettner 2012), as is often the case with behavioural traits (Bell et al. 2009, Dingemanse et al. 2010). We quantified a range of measures which may vary if there are tag effects, including measures more related to fitness, such as breeding success and body condition (mass), and measures expected to be more directly affected by carrying tags, such as diving performance metrics, and potentially indirectly affected measures reflecting potential behaviour responses by guillemots to carrying tags, these including activity budgets and dive depth distributions. Body mass was measured at each capture event (pre-, post-, and between treatments for experimental guillemots, and once or twice for control guillemots).

We expect GPS-equipped guillemots to show impaired diving performance in common with studies of other diving birds (Wilson et al. 1986, Ropert-Coudert et al. 2000, Ludynia et al. 2012), and as predicted by the increased drag of carrying a GPS logger (Vandenabeele et al. 2015). Flight costs are expected to increase from both the additional mass and increased drag (Bowlin et al. 2010, Pennycuik et al. 2012, Vandenabeele et al. 2012). Thus, we expected to find changes

in measures likely to be more directly affected by carrying tags, such as reduced diving performance (lower dive efficiency, increased post-dive interval times and slower descent rates). Guillemots may then respond behaviourally to such effects with changes in time activity budgets, foraging locations and dive depths. If the guillemots partially compensate for tag effects behaviourally, measures less directly affected by tags such as breeding success are less likely to change, e.g. if guillemots compensate by increasing time spent foraging. We may expect increased mass loss during chick-rearing, as guillemots buffer the chick from their own increased energy expenditure or reduced foraging success with corresponding increases in physiological stress, e.g. by elevated baseline corticosterone (CORT, Romero 2004, Landys et al. 2006). Finally, we discuss our results for the GPS-equipped common guillemots comparing these to other studies looking at tag effects for both common and Brünnich's guillemots.

Methods

Field-site

Fieldwork was conducted on the island of Stora Karlsö, Gotland, Sweden (17.972°E, 57.285°N) during June 2015. The field site has the largest breeding population of common guillemots *Uria aalge* in the Baltic Sea with ca 12 000 pairs (Hentati-Sundberg et al. 2012). The island is 2.5 km², and is located in the western central Baltic Sea, situated 7 km west of the much larger island of Gotland.

Device deployments and monitoring

Using a noose-pole, we caught 36 adult common guillemots rearing chicks on a natural rock ledge below the Karlsö Murre lab (8–25th June 2015) (Hentati-Sundberg et al. 2012, Evans et al. 2013). Individuals were randomly allocated to one of four groups (Fig. 1) following a controlled crossover design (Wellek and Blettner 2012): experimental guillemots (with devices) with two order groups (caught three times); full controls (caught twice); and background controls (caught once). Twelve guillemots were tagged with devices, all of which were followed for 4.3 ± 0.9 days (mean \pm SD) with GPS and TDR and also for 3.5 ± 1.0 days with TDR only, with the order of deployments swapped for half the group. We additionally captured 24 control guillemots throughout the study period, five of which were full controls, caught twice, allowing their individual changes in mass to be followed, and 19 of which were captured once. The 19 background controls, together with the first capture information (i.e. prior to any potential treatment effect) for all guillemots (including the 12 experimental and five full controls), were used to infer whether there were any background colony level trends in mass.

At first capture, guillemots were marked with metal Swedish ringing scheme rings, unless previously marked. At each capture event, we first took a blood sample from the

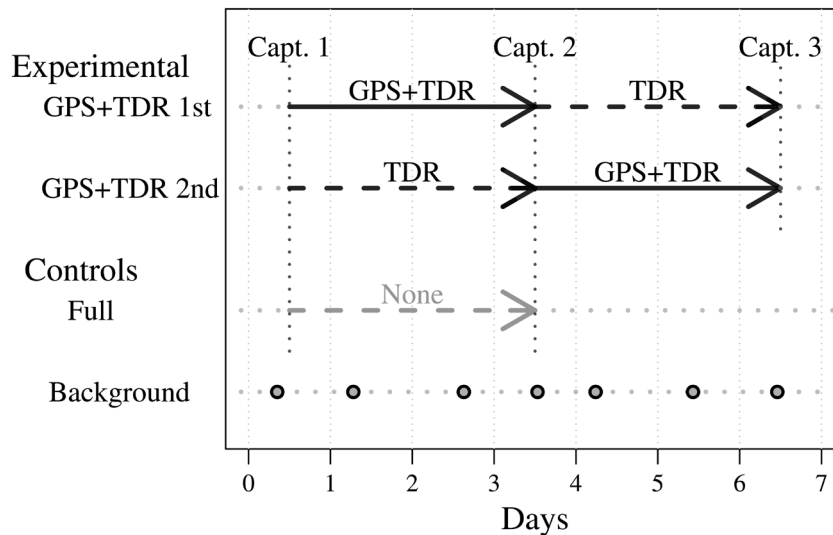


Figure 1. Schematic illustration of the controlled cross-over study design used to look at how common guillemots may be affected by carrying GPS devices during chick-rearing. Twelve adult breeding guillemots were tagged in the experimental group, with half having a GPS and TDR together for ca 3 days, then only a TDR, the other half having the opposite order. Five guillemots (full controls) were caught twice to look at potential within-individual physiological changes, then a further 19 guillemots were caught across the deployment period to assess background colony level trends in mass. On each capture, all guillemots were weighed.

brachial vein, taking < 1 ml (used for sexing and other concurrent studies). Guillemots were then weighed to the nearest 5 g using a Pesola® spring-balance. At first capture, morphological measurements were taken (i.e. tarsus, wing, culmen, head + bill, wing area; these were used for concurrent studies). The control guillemots were thereafter released. For the experimental guillemots at the first and second capture occasions, we deployed either a GPS device (model GT-120 by Mobile Action Technology, Taipei, Taiwan) together with a TDR (LAT 1500 by Lotek Wireless Inc., Newmarket, Ontario, Canada), or a TDR only. The GPS was attached in the centre of the back to feathers using several strips of black tesa™ marine tape (Product 4651, tesa SE, Norderstedt, Germany) and the TDR to a plastic leg ring. On the second and third capture occasions, devices were removed and/or exchanged/added. The TDRs were configured to log continuously at 4 s intervals, recording temperature (resolution 0.1°C), wet-dry state and pressure (resolution 0.1 dBars). The GPS logged at 240 s intervals. The GPS device was housed in heat-shrinkable plastic (diameter 25.4 mm, product FIT-221-1 Clear 4, Alpha Wire, Elizabeth, NJ, USA) formed a rectangular cuboid with tapered ends, thus was somewhat streamlined. The TDR was cylindrical running parallel to the tarsus. Device masses, dimensions and cross-sectional areas were: 18 g, 42 × 25 × 12 mm, 3 cm² for the GPS including housing and 4.3 g, 31 × 8.5 mm, 0.6 cm² for the TDR (mass including plastic leg-ring). These corresponded to percentage increases on the mean guillemot body mass (928 g, this study) and frontal cross-sectional areas (90 cm² from Croll et al. 1992) of 1.9%, 2.7%, for the GPS and 0.5%, 0.5% for the TDR.

Though all guillemots were confirmed to be chick-rearing, not all pairs were within the productivity plot where breeding success was monitored. The majority of the guillemots

fitted with devices (11/12) and over half (15/24) of the control guillemots were monitored at least from hatching to fledging or chick disappearance. Pairs were observed every day, though not all pairs' breeding state was confirmed each day. Pairs were considered successful if the chick was 18 days or older at disappearance. For one guillemot with devices, where the date of hatching was unknown, we imputed an expected hatching date based on a regression of 1st capture date against hatching date for the other 11 experimental guillemots ($1st_cap_day = 0.69(hatch_day) + 7.7$, $R^2 = 0.76$). Since guillemots cannot be sexed on plumage or biometrics, sex was determined retrospectively from red blood cells. DNA was extracted using a kit (NucleoSpin® Blood from Machery-Nagel GmbH and Co. KG, Düren, Germany) following the manufacturer's protocol, then sexed by PCR (Griffiths et al. 1998).

Analysis

Colony level trends in mass were analysed for first captures only by a linear regression. This was then used to calculate residual variation in mass not explained by date to assess the effect on mass for guillemots carrying devices, with the rate of change (Δ residual mass/day) used to standardize for different periods between captures.

The remaining analyses were based on the TDR extracted data. TDR data were analysed by first extracting dive and dive bout level summary statistics using MultiTrace-Dive (MTDive, Jensen Software Systems, Laboe, Germany). Dives and dive bouts were categorised following Evans et al. (2013). Dives were recognised as any period when the depth measured was >3 m, with dive start and end times defined as the time that 5% of the maximum depth reached during the

dive (depth_{\max}) was crossed. The descent time was the time to go from the surface to 75% of depth_{\max} , and the bottom phase defined as the period spent $>75\%$ depth_{\max} . Dive bouts were recognised as any sequence of dives where the inter-dive period (PDI) following a dive was <250 s, this followed a previously derived dive bout-ending criterion for the study site showing a rapid decline in the frequency of dives with PDI >250 s (Evans et al. 2013) which was consistent for this study year (not shown). In addition to the extracted dive variables, we derived descent rate and dive efficiency for each dive using MTDive. Descent rate was calculated as Δdepth divided by Δtime for the descent phase of each dive (between 5 and 75% of depth_{\max}). Dive efficiency is the bottom time divided by the total dive cycle time (dive time plus PDI, thus was not calculated for single dives and the final dives of dive-bouts) (Eq. 1 in Zimmer et al. 2010 after Ydenberg and Clark 1989).

We calculated daily activity budgets for active foraging time for full deployment days (i.e. those not including a capture event), with active foraging time defined as total time diving plus PDI time, though with PDI time excluded for single dives (i.e. not in dive bouts) and for the final dives of dive bouts. As guillemots are known to show crepuscular patterns in foraging activity (Regular et al. 2010), we then calculated the proportion of activity occurring during the day as opposed to at night/crepuscularly, with the crepuscular period including the 90 min before sunset and after sunrise (sunset and sunrise times extracted using function *sunrise* in R (www.r-project.org) package *maptools* (Bivand et al. 2016), which calculates when the solar disk is just visible/just drops above/below the horizon for sunrise/sunset accounting for atmospheric refraction).

As the time of the day is known to affect guillemot diving and foraging behaviour (Regular et al. 2010, 2011), we extracted the sun elevation (h , angle in degrees of solar disc centre above horizon) at the start of each dive and dive bout. h was calculated by extracting the solar *zenith* (z) for the dive/dive bout start time at the colony location using function *zenith* in R package *GeoLight* (Lisovski and Hahn 2012), with $h = -(z - 90^\circ)$. This was then used as a categorical variable with three periods, day ($h > 0^\circ$), twilight ($-6^\circ < h < 0^\circ$) and night ($h < -6^\circ$).

The temperature recorded prior to the dive start time (t) was used to estimate sea-surface temperature (SST) for each dive bout. We extracted the median of temperature recorded from $t-40$ s to $t-12$ s (i.e. eight records), excluding the final two records prior to the first dive of the bout ($t-8$ s and $t-4$ s) as these could be affected by movement at the start of the dive. SST was only extracted for a dive bout when the TDR was constantly wet for the 60 s prior to and within this period, this giving time for the TDR temperature to stabilise if the guillemot had been in flight or had leg-tucked. Finally, SST was excluded if the variance within the 28 s window was greater than 0.25°C , suggesting that temperature was not stable, so unlikely to represent SST. Finally, a small number of extreme values were excluded, where SST was greater than

20°C . This led to a dataset of 1150 bouts, with 251 excluded not meeting these analytical criteria.

For our analysis we were interested in the relative SST; that is whether guillemots were foraging in warmer or cooler areas for that time of day/season. As SST varies through the season, we first calculated the mean daily SST for the study area. We extracted daily SST temperatures for the area from the 'NOAA OI SST V2 High Resolution Dataset' (Reynolds et al. 2007), which provides point values on a 0.25° latitude/longitude grid, then for each day we took the mean value for the area from 17.1 to 18.0°E and 57.1 to 57.5°N (8 grid points). We then subtracted the daily mean SST from the dive bout level SST giving the deviation of bout level recorded SST from the mean value on that day for the study area. SST also follows a daily cycle fluctuating by ca 1°C in the Baltic Sea during June, though the strength of this will also depend on weather conditions (Karagali and Høyer 2013). SST should be higher midday and lower at night, though with a short lag such that daily minima and maxima are a few hours after midnight and midday respectively (Karagali and Høyer 2013). Therefore we calculated a variable for time of day, giving high values early afternoon and low values soon after midnight. This calculated as follows:

$$\text{tod} = -\cos\left(\left\{\frac{((h+3)\text{mod } 24)}{24}\right\} \times 2\pi\right)$$

where *tod* is the time-of-day variable calculated, and h the hour of the day (h with time zone UTC). *tod* scales between -1 at 3:00 UTC to $+1$ at 15:00 UTC.

Statistical analysis

We developed generalized linear mixed effects models (GLMM) to look at whether the guillemots were affected differently by carrying a TDR device alone, or both a GPS and TDR together. Models were analysed using the R package *lme4* (Bates et al. 2014b), with model selection by AICc (Burnham and Anderson 2002), with the terms in the selected model considered statistically significant if the 95% wald confidence intervals (Bates et al. 2014a) did not include zero. Model fit was assessed by using marginal R^2 values (R_m^2), which assesses the proportion of total variance explained by fixed effects, then the combined fixed and random effects were assessed with conditional R^2 values (R_c^2) (Nakagawa and Schielzeth 2013) extracted with the R package *MuMIn* (Bartoń 2016). All models were fitted with a normal error structure, except for dive depth which was analysed as a binomial variable (levels with deep 1, and medium depth 0, explanation below) in a GLMM with family binomial and a logit link function.

Our principal focus was to ascertain how devices affect the guillemots, either physiologically, behaviourally, or in terms of performance when attached during the breeding period. Therefore, a candidate set of models was built for each tested

response variable that included a base-model including variables not of direct interest, but that were a priori expected to explain a large proportion of the variance. These included, depending on the response variable: date (day of June) as a continuous variable, chick-age (days since hatching) as a continuous variable, period of day as a factor (day, twilight, night), sex as a factor, time-of day as a continuous variable (SST analysis only, defined above) and dive depth.

All models included individual guillemot identity as a random effect. The SST models, analysed at the dive bout level, also included day (as a factor) both nested within bird and day alone (random effects structure: +1|bird/day+1|day), in effect using day as a replicate within each bird, as individual foraging trip start and end times were not extracted from the TDR data, so foraging trip could not be used as a replicate. Then the day random effect acted to account for overall variation amongst days. The dive level analyses (dive depth and three dive performance measures) included random effects of dive bout nested within day (as a factor) nested within bird. The dive performance models excluded dives of < 10 m, as behaviour may be quite different at shallow depths (Lovvorn et al. 2004).

We also analysed whether rates of mass loss during GPS deployments are related to time spent diving or in flight using linear regressions, first using t-tests to check for differences between the two deployment order groups.

In results where mean values (\bar{x}) are reported these are given with standard deviation (SD) in the form $\bar{x} \pm \text{SD}$.

Results

We collected body mass data for 35 guillemots, from 62 capture events. One of the birds in the experimental group was excluded after losing its GPS device during the first deployment period, thus we had five from the experimental group (male: 2, female: 3) with GPS + TDR first, and six of the GPS + TDR second (male: 3, female: 3), five for the full-control group (male: 3, female: 2) and 19 back-ground controls (male: 10, female: 6, unknown: 3). The sex distribution across (Supplementary information) the sample was quite well balanced, with close to equal numbers of males and females in nearly all groups. We recorded 85.4 days of TDR data (54% of which was during the GPS + TDR period, irrespective of order of deployment) from the 11 guillemots, with 8691 dives and 1401 dive bouts logged in total. Breeding success was uniformly high across pairs in the colony (70% successful from laying to fledging for 162 monitored pairs, Baltic Seabird Project unpubl.), and all pairs monitored from hatching to fledging or disappearance (26 pairs) raised chicks to a minimum age (the hatching date was uncertain for some pairs by up to three days), of 18 days or greater (median 22 days) at fledging or disappearance, therefore breeding success was not analysed further.

Condition – body mass

All guillemots lost mass (mean body mass 928 ± 38 g; all guillemots at first capture only) across the study period (Fig. 2A).

On average, male guillemots (939.6 ± 27.1 g, $n=18$) were slightly heavier than female guillemots (921.1 ± 43.1 g, $n=14$) on the first capture occasion (which are unaffected by any subsequent treatment effect), however this difference was not statistically significant (t-test, $t=-1.41$, $df=20.7$, $p=0.17$). Analysing only first captures for all guillemots, the mean body mass of guillemots captured reduced by 3.6 g day^{-1} across the study period (95% CI = $\{-6.4, -0.87\}$, $n=35$, $F_{(1,33)}=7.18$, $p=0.01$, $R_{\text{adj}}^2=0.15$). Guillemots carrying GPS and TDR lost mass (confidence intervals do not include zero, Fig. 2A), guillemots carrying TDR only or no devices (controls) on average also lost mass but for each group this was not significant (confidence intervals include zero, Fig. 2A). The daily rate of mass loss for the guillemots carrying GPS and TDR was however not significantly different from the colony level mass trend.

Looking only at guillemots in the experimental group, which were caught three times, we then investigated whether rates of mass loss (standardized by date) differed within guillemots depending on type of device carried, and the order in which these were carried (Table 1). The full model, including an interaction term between device type and order (model 1, Table 1) was the best model following AIC selection, and explained > 23% of variation in mass change. However, this model was not well resolved with wide confidence intervals for all terms; the only term where zero was not included in the CI was for the additive effect of device type, with more mass lost when carrying GPS and TDR (model intercept: -11.9 g day^{-1} , CI = $\{-22.7, -1.0\}$) than when with TDR only (intercept $+6.2$ g day^{-1} , CI = $\{-2.1, 14.4\}$).

Individual rates of mass loss during the GPS deployments were not explained by either the time spent diving per day (individual means: 2.29 ± 0.31 h day^{-1} , $F_{(1,9)}=1.73$, $p > 0.05$), or by the time spent in flight per day (individual means: 1.29 ± 0.57 h day^{-1} , $F_{(1,9)}=1.73$, $p > 0.05$). These tests ran with both deployment order groups pooled, as the time spent diving ($t=1.35$, $df=6.5$, $p > 0.05$) and in flight ($t=-1.75$, $df=8.8$, $p > 0.05$) did not differ significantly between the groups.

Foraging behaviour

Foraging time and time of day active

Common guillemots spent $14.9 \pm 2.6\%$ of each day active foraging (dive time plus inter-dive time), and $64.7 \pm 27.3\%$ of this was during daytime (> 90 min before sunset/after sunrise). Neither the level of foraging activity, nor the timing of activity (proportion of foraging time occurring during daytime) changed with device status nor the order in which the guillemots carried devices (Table 2). Furthermore, activity did not vary between sexes, change through the chick-rearing period, neither according to calendar date nor chick age, with the intercept only model the best for both response variables (Table 2). There was little variation amongst guillemots in their levels of activity (low R_c^2), but individuals varied greatly in the time of day they were active ($R_c^2 > 50\%$).

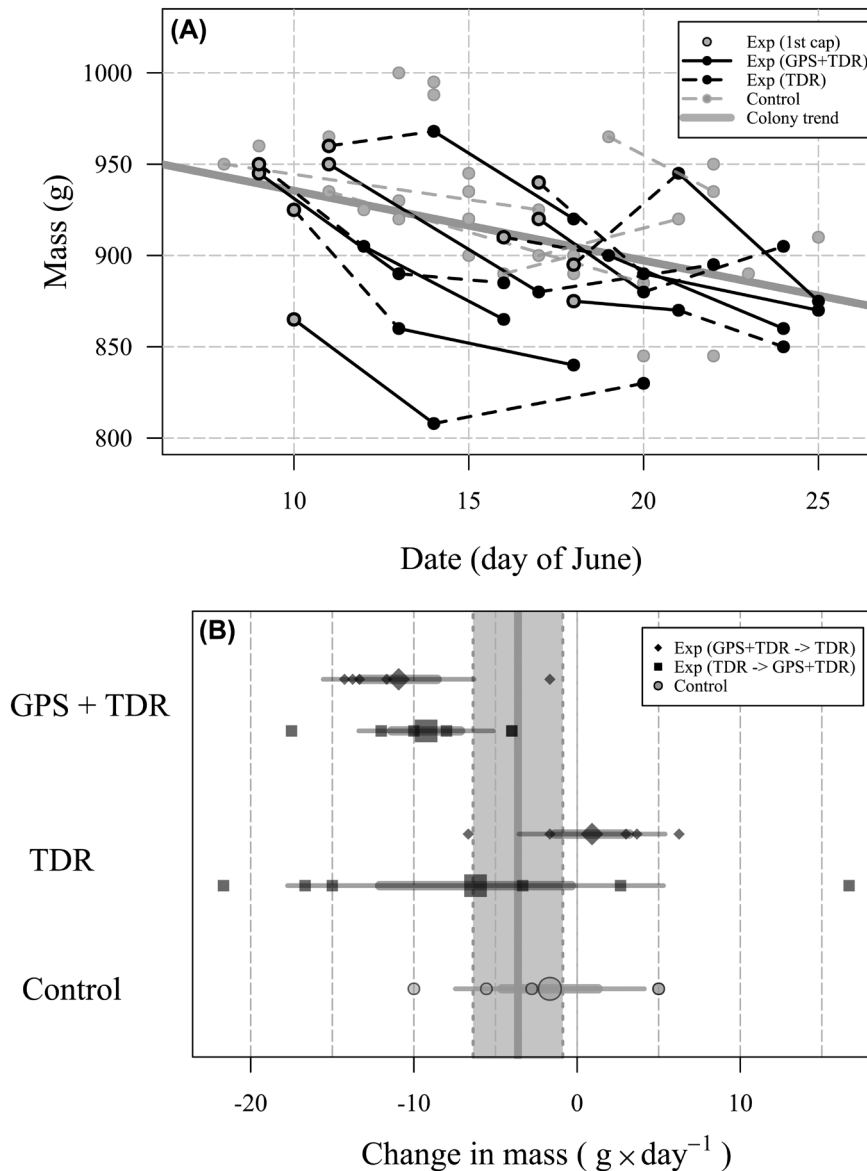


Figure 2. Mass changes for common guillemot across the chick-rearing period (A–B), with individual mass and mass trajectories (A) for experimental guillemots (with GPS and TDR devices), and control guillemots (no device). The first captures of all guillemots were used to derive the seasonal trend in mass, with guillemots caught later in the season having significant lower mass (linear regression line shown, grey thick-line). Daily rates of mass change (B) for the experimental guillemots with either GPS and TDR or TDR only compared to full control and all compared to the colony level trend (vertical thick grey line, with 95% CI illustrated by shaded region), with group means (large symbols), individual means (small symbols) and group mean standard errors (thick horizontal lines) and 95% CI (thin horizontal lines) shown. Non-overlapping 95% CI indicate statistical significance (at $\alpha=0.05$).

Foraging location by sea-surface temperature

Satellite-derived SST ($12.5 \pm 0.86^\circ\text{C}$) over the study area changed across the chick-rearing period, initially increasing then decreasing a little (Supplementary information), with the across-period variation greater than that within days across the study area (mean daily range in SST: $0.33 \pm 0.16^\circ\text{C}$). Much of the variation in bout-level SST was explained by the mean daily SST derived from satellite observations ($F_{(1148)}=1158$, $p < 0.001$, $R_{\text{adj}}^2=0.501$, Supplementary information), thus justifying standardizing the bout-level

SST values using the daily satellite derived values. Relating SST to the device status of the tagged guillemots, a model including the device deployment order, but not device status, was the most parsimonious (model 6, Table 3). The guillemots equipped with TDRs first then GPS and TDR selected areas with slightly lower SST than those equipped with the devices in the reverse order (-0.17°C $\{-0.29, -0.06\}$). Guillemots with older chicks selected areas with lower SST ($-0.022^\circ\text{C day}^{-1}$ $\{-0.041, -0.002\}$). Male guillemots selected warmer areas (higher SST) than female guillemots (0.21°C $\{0.08,$

Table 1. LMM models to look at the influence of carrying a GPS logger on daily change in body mass in chick-rearing common guillemots. The most parsimonious models were selected by AICc (selected in bold), with the model fit indicated by R^2 , for the main effects only (R_m^2) and including a random effect for individual bird (R_c^2). Variables; device, either GPS and TDR or TDR only. Order, the order that a bird had the two device categories. All models also include a random effect for individual guillemots. Device \times order indicates inclusion of both additive and interaction terms.

	Model	AICc	Δ AICc	R_m^2	R_c^2
Mass					
Device \times order + sex	1	152.6	0.0	0.232	0.232
Device + order + sex	2	155.5	2.8	0.188	0.188
Device + sex	3	156.5	3.9	0.181	0.181
Order + sex	4	159.4	6.8	0.057	0.057
Sex	5	161.0	8.4	0.043	0.043
Intercept only	6	163.5	10.9	0.000	0.000

0.33}). SST did not vary by calendar date, or period of day (i.e. twilight, night, day) with coefficient confidence intervals including zero. Time of day (i.e. continuous time variable, see Methods) did affect SST, with higher SST at midday than midnight (0.40°C {0.35, 0.44}).

Dive depth

The mean individual dive depth for the instrumented chick-rearing guillemots (n=11) was 33.3 \pm 9.6 m, though dives showed a multi-modal distribution in depth (Fig. 3), with three modes evident, thus we classified dives into shallow, medium and deep dives (<13, 13–50, >50 m, respectively). Medium depth dives were most common (67.4 \pm 18.8%),

followed by deep dives (19.2 \pm 15.2%), then shallow dives (13.4 \pm 19.5%), though 71% of all shallow dives were performed by just two (both of the GPS + TDR second group) out of the 11 guillemots. We therefore analysed dive depth as a binomial variable, either medium or deep dives, with the shallow dives excluded from this analysis. Also as there were no deep dives at night, and few during twilight (32 deep twilight dives), we analysed only the daytime dives (6054 dives, of which 26% were deep dives).

The most parsimonious model for dive depth included the device type, the device deployment order and their interaction (model 3, Table 4). The tendency for deep dives did not change with calendar date nor chick age (CI include zero). Male guillemots were more likely to perform deep dives than female guillemots (3.3 log odds {1.2, 5.3}). How the devices affected the propensity for deep dives differed depending on the order in which the devices were deployed (Fig. 3). For the group having GPS and TDR together for the first period, the guillemots were less likely to perform deep dives in the second period when with TDR only (–2.4 log odds {–4.1, –0.65}) than during the first period with both GPS and TDR. The group having TDR only during the first period were overall less likely to perform deep dives in either period (–6.8 {–9.1, –4.5}), but these guillemots were more likely to perform deep dives during the first period with TDR only (3.8 {0.9, 6.6}).

Dive performance

To assess whether common guillemot diving performance was affected by carrying devices, we analysed three related

Table 2. LMM models to look at the influence of carrying a GPS logger on daily foraging activity in chick-rearing common guillemots for active foraging time (diving time plus inter-dive interval time) and the proportion of activity performed in daytime versus night and crepuscular time. The most parsimonious models were selected by AICc (selected in bold), with the model fit indicated by R^2 , for the main effects only (R_m^2) and including a random effect for individual bird (R_c^2). Variables; device, either GPS and TDR or TDR only. Order, the order that a bird had the two device categories. Date, day of June. Age, age of chick in days. All models also include a random effect for individual guillemots.

	Model	AICc	Δ AICc	R_m^2	R_c^2
Active foraging time					
Order \times device + date + device \times age + sex	1	–113.3	63.7	0.115	0.115
Order + device + date + device \times age + sex	2	–119.4	57.6	0.102	0.102
Order \times device + date + device + age + sex	3	–124.0	53.0	0.110	0.110
Order \times device + date + age + sex	4	–124.0	53.0	0.110	0.110
Order + device + date + age + sex	5	–130.5	46.5	0.102	0.102
Order + date + age + sex	6	–139.6	37.4	0.100	0.100
Device + date + age + sex	7	–138.5	38.5	0.084	0.084
Date + age + sex	8	–147.3	29.7	0.080	0.083
Intercept only	9	–177.0	0.0	0.000	0.038
Time of day active					
Order \times device + date + device \times age + sex	1	25.4	28.2	0.316	0.763
Order + device + date + device \times age + sex	2	27.2	30.0	0.232	0.739
Order \times device + date + device + age + sex	3	19.7	22.6	0.308	0.749
Order \times device + date + age + sex	4	19.7	22.6	0.308	0.749
Order + device + date + age + sex	5	24.9	27.7	0.194	0.716
Order + date + age + sex	6	18.3	21.2	0.194	0.717
Device + date + age + sex	7	21.7	24.5	0.138	0.703
Date + age + sex	8	15.3	18.1	0.137	0.705
Intercept only	9	–2.8	0.0	0.000	0.685

Table 3. LMM models to look at the influence of carrying a GPS on foraging location, as inferred by sea-surface temperature for chick-rearing common guillemots. The response variable was the residual variation in SST after accounting for the mean daily SST (independently derived from satellite observation data). The most parsimonious models were selected by AICc (selected in bold), with the model fit indicated by R_m^2 , for the main effects only (R_m^2) and including random effects for individual bird, day nested within bird, and day as a factor (R_c^2). Variables; device, either GPS and TDR or TDR only. Order, the order that a bird had the two device categories. Date, day of June. Age, age of chick in days. tod, time-of day (see text for calculation). Per, period of day, either night, twilight or daytime.

	Model	AICc	Δ AICc	R_m^2	R_c^2
Order \times device+date+per+tod+age \times device+sex	1	1827.8	2.2	0.173	0.660
Order+device+date+per+tod+age \times device+sex	2	1834.0	8.4	0.162	0.656
Order \times device+date+per+tod+age+sex	3	1831.1	5.6	0.160	0.655
Date+per+tod+age \times device+sex	4	1837.9	12.3	0.143	0.657
Order+device+date+per+tod+age+sex	5	1831.1	5.5	0.157	0.654
Order+date+per+tod+age+sex	6	1825.6	0.0	0.157	0.652
Device+date+per+tod+age+sex	7	1831.6	6.1	0.142	0.653
Date+per+tod+age+sex	8	1826.4	0.8	0.142	0.651
Intercept only	9	2083.0	257.4	0.000	0.520

measures of diving performance: dive efficiency, post-dive interval time (PDI) and descent rate.

Dive efficiency was not significantly affected by carrying a GPS device, with neither device type (GPS and TDR or TDR only) nor the treatment order affecting dive efficiency (Table 4). Models were not simplified beyond a base model including date, chick age, period of day, sex and dive depth, with these five terms explaining 13.3% of variation in dive efficiency. Dive efficiency was lower for deeper dives (-0.0023 m^{-1} $\{-0.0025, -0.0021\}$), and lower at night (-0.035 $\{-0.051, -0.019\}$) than in daytime, while twilight did not differ from daytime (95% CI included zero, $-0.014, 0.006$). The 95% CI for the coefficients for chick age, sex and date included zero, suggesting that dive efficiency did not change with calendar date, sex, nor chick age.

For post-dive intervals (PDI), the best model (model 3, Table 4) included device status, the device order and the interaction between these, with a decrease in AICc of 6.0 points over the base model. However, the coefficient estimates for the device terms (order and device type and their interaction) included zero in their 95% CI, and the log-Likelihood of this model was not significantly better than the base model (comparing models 3 and 8; $\chi^2=1.042$, $df=3$, $p > 0.05$), and furthermore there was little improvement in the proportion of variance explained ($\Delta R_m^2=0.006$). The base model terms all affected PDI except for chick-age and explained ca 29% of its variance. PDI was greater for male guillemots than for female guillemots (8.7 s $\{0.06, 17.3\}$), PDI increased with dive depth (1.23 s m^{-1} $\{1.17, 1.30\}$), with date (1.53 s day^{-1} $\{0.58, 2.49\}$), and was higher at night (10.0 s $\{5.1, 14.9\}$)

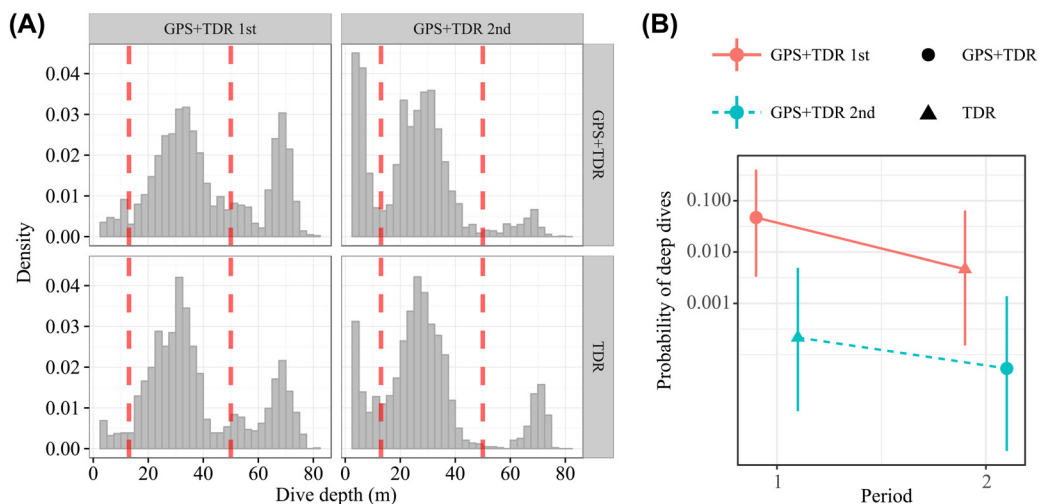


Figure 3. Dive depths by adult common guillemots breeding at Stora Karlsö, Sweden, according to device status. (A) Distribution of dive depths by device status (rows) and the order in which guillemots had the two device combinations (columns). The relative frequency of dive depths is shown in 2.5 m depth interval bins, with a density of 0.01 meaning that 1% of dives depths were in that 2.5 m depth interval (for the given combination of device factors). Dives showed a multimodal distribution so were classified into shallow, medium and deep (<13, 13–50, >50 m, respectively, red dashed-lines). (B) Modelled (see model 3 under dive depth in Table 4) probability of deep dives over medium dives for the two deployment periods, according to the order the devices were deployed. Shown are coefficient estimates together with 95% CI (bootstrapped estimates from 500 runs) for the model fitted for female guillemots.

Table 4. GLMM and LMM models to look at the influence of carrying a GPS on diving behaviour and efficiency in chick-rearing common guillemots for dive depth, dive efficiency, post-dive interval time (PDI) and descent rate. The most parsimonious models were selected by AICc (selected in bold), with the model fit indicated by R^2 , for the main effects only (R_m^2) and including a random effect for individual bird (R_c^2). Dive depth was analysed as a categorical term (medium or deep dives) when used as a response variable using a logistic mixed effects model (in *lme4* with family binomial and logit link), where included as an explanatory variable the continuous variable was used. All models included a nested random effect structure of dive bout within day within guillemot identity. Variables; device, either GPS and TDR or TDR only. Order, the order that a bird had the two device categories. Date, day of June. Age, age of chick in days. Per, period of day, either night, twilight or daytime. Depth, depth of dive.

	Model	AICc	Δ AICc	R_m^2	R_c^2
Dive depth					
Order \times device + date + age \times device + sex	1	3693.5	2.0	0.294	0.986
Order + device + date + age \times device + sex	2	3696.2	4.7	0.288	0.986
Order \times device + date + age + sex	3	3691.5	0.0	0.294	0.986
Date + age \times device + sex	4	3710.9	19.4	0.049	0.986
Order + device + date + age + sex	5	3696.2	4.7	0.288	0.986
Order + date + age + sex	6	3695.7	4.2	0.292	0.985
Device + date + age + sex	7	3709.5	18.0	0.049	0.986
Date + age + sex	8	3708.4	16.9	0.048	0.986
Intercept only	9	3707.2	11.7	0.000	0.985
Dive efficiency					
Order \times device + date + per + age \times device + depth + sex	1	-12109.1	30.6	0.132	0.342
Order + device + date + per + age \times device + depth + sex	2	-12117.0	22.7	0.132	0.342
Order \times device + date + per + age + depth + sex	3	-12121.4	18.3	0.132	0.342
Date + per + age \times device + depth + sex	4	-12123.6	16.1	0.136	0.348
Order + device + date + per + age + depth + sex	5	-12129.6	10.1	0.132	0.342
Order + date + per + age + depth + sex	6	-12133.5	6.2	0.128	0.341
Device + date + per + age + depth + sex	7	-12136.0	3.7	0.137	0.350
Date + per + age + depth + sex	8	-12139.7	0.0	0.133	0.351
Intercept only	9	-11709.3	430.4	0.000	0.313
PDI					
Order \times device + date + per + age \times device + depth + sex	1	61310.2	1.5	0.297	0.399
Order + device + date + per + age \times device + depth + sex	2	61313.2	4.5	0.296	0.398
Order \times device + date + per + age + depth + sex	3	61308.7	0.0	0.297	0.398
Date + per + age \times device + depth + sex	4	61316.0	7.3	0.291	0.392
Order + device + date + per + age + depth + sex	5	61311.5	2.8	0.296	0.398
Order + date + per + age + depth + sex	6	61311.8	3.1	0.297	0.398
Device + date + per + age + depth + sex	7	61314.4	5.7	0.291	0.392
Date + per + age + depth + sex	8	61314.7	6.0	0.291	0.392
Intercept only	9	62459.5	1150.8	0.000	0.394
Descent rate					
Order \times device + date + per + age \times device + depth + sex	1	-1764.6	27.6	0.184	0.423
Order + device + date + per + age \times device + depth + sex	2	-1769.4	22.8	0.184	0.420
Order \times device + date + per + age + depth + sex	3	-1773.6	18.5	0.182	0.423
Date + per + age \times device + depth + sex	4	-1774.9	17.3	0.167	0.408
Order + device + date + per + age + depth + sex	5	-1779.4	12.7	0.183	0.421
Order + date + per + age + depth + sex	6	-1787.1	5.0	0.182	0.421
Device + date + per + age + depth + sex	7	-1784.5	7.6	0.162	0.409
Date + per + age + depth + sex	8	-1792.2	0.0	0.161	0.409
Intercept only	9	-1207.1	585.1	0.000	0.471

than in daytime, though PDI during twilight was not different to during daytime (95% CI included zero).

Descent rate was not significantly affected by carrying GPS devices, with the most parsimonious model including neither device type nor deployment order (Table 4). Models were not simplified beyond a base model including sex, date, period of day, chick age and dive depth, with these five terms explaining ca 16.1% of variation in descent rate. Descent rates decreased with dive depth (-0.0048 m s^{-1} $\{-0.0053, -0.0044\}$) and were greater for night (0.18 m s^{-1} $\{0.14, 0.22\}$) than daytime dives, though not different between daytime and twilight

(95% CI included zero). Sex, calendar date and chick age did not affect descent rates (CI included zero).

Discussion

Overall, for the majority of measures, the chick-rearing common guillemots showed few differences when carrying the additional load of the back-mounted GPS device. Breeding success was unaffected, but guillemots did lose significantly more body mass during the GPS deployments, compared

with when only carrying a TDR. Presumably, birds or their breeding partners, compensated behaviourally or physiologically to avoid knock-on effects on breeding success. The measures expected to be more directly affected by carrying tags, foraging behaviour and diving performance, showed few significant differences. The distribution of dive depths changed, though this result was ambiguous because the direction of this effect differed between the two experimental groups of guillemots (either having the GPS for the first or second deployment period).

In general, we should expect negative effects from carrying biologging devices to be more apparent when looking at measures of activity, such as dive performance, which could be directly affected by devices inducing increased drag (Wilson et al. 1986, Todd Jones et al. 2013). Measures related to fitness, such as breeding success, may show few effects if animals compensate for tag effects by adjusting foraging activity or self-maintenance (Ropert-Coudert and Wilson 2004, Navarro et al. 2008). However, in this study, for three measures of dive performance, we found no apparent effect from carrying the additional load of a back-mounted GPS. Though our GPS loggers were relatively streamlined, they did increase the guillemots' frontal cross-sectional area so as predicted should have led to some increase in drag forces. The fact that descent rate did not change could be explained by the guillemots maintaining an optimal vertical swimming speed to stay within an apparently small speed window where the drag coefficient is at a minimum thus minimising the cost of transport (Lovvorn et al. 1999, 2004). Guillemots could maintain swim speeds despite increased drag through increasing their wingbeat frequency or wingbeat strength; captive common guillemots do this to overcome reduced wing-area during moult (Bridge 2004). However, energy expenditure would then be increased, thus the surface recovery time following dives (post-dive interval) should increase when carrying the GPS loggers (Ropert-Coudert et al. 2000). We did not find an increase in post-dive interval time, and moreover dive efficiency was also unaffected, suggesting guillemots did not reduce dive bottom time to compensate for increased energy expenditure during descent or ascent. Dive performance could have been impacted, but in a way that was not apparent when measured with the TDRs, which only measure the vertical component of activity (changes in depth over time). Dive descent rates may have been maintained by birds compensating for reduced absolute swim speed by increasing descent angle which would not be evident from the TDR data. Vandenabeele et al. (2015) suggested that horizontal swimming speeds during dives may be most strongly affected; thus, while GPS-equipped guillemots maintained comparable dive efficiency to those only carrying a TDR, the horizontal distance traversed during dives could be reduced with a likely commensurate reduction in foraging success, similar to findings for diving penguins (Wilson et al. 1986). Recent studies of pursuit-diving predators using approaches to record prey encounter and capture rates suggest that prey may not only be caught in the bottom phase of dives (Viviant et al. 2016,

Chimienti et al. 2017), and as such the measure of dive efficiency used here may be overly simplistic. However, with the TDR data available in our study, more complex measures of dive efficiency were not possible.

Both common and Brünnich's guillemots reduce body mass following incubation at the onset of chick rearing (Birkhead and Nettleship 1987, Harris and Wanless 1988, Croll et al. 1991, Gaston and Perin 1993, Elliott et al. 2008b), which is observed in other seabird species too (Niizuma et al. 2001, Schultner et al. 2013, Kulaszewicz et al. 2016). In guillemots, this reduction in adult body mass post-hatching can be quite rapid, resulting in ca 5–10% body mass loss over just a few days (Gaston and Perin 1993). This mass loss is thought to be an adaptive response to reduce wing-loading when parents are making frequent foraging trips and returning with prey for their chick (provisioning flights) (Croll et al. 1991, Gaston and Perin 1993), though may also confer benefits during diving (Elliott et al. 2008b). Similar to our results, this mass loss has been observed to continue throughout chick rearing (Harris and Wanless 1988, Paredes et al. 2005, Jacobs et al. 2013).

In our study, the GPS-equipped guillemots lost significantly more mass than either controls or when carrying only a TDR. In other studies of guillemots, increased loss in body mass is one of the most commonly observed effects of tagging (5 of 8 studies), while CORT levels have only increased significantly in one study (1 of 4 studies, Table 5). This increased mass loss could be adaptive, as guillemots lose mass to compensate for the additional load of carrying the GPS; alternatively, mass loss may result from higher energy expenditure, reduced foraging success and/or elevated levels of circulating CORT. As diving performance generally appeared to be unaffected, the additional mass loss could have resulted from increased energy expenditure during flight. The morphologically similar Brünnich's guillemot is estimated to use 30 W of energy during diving and 150 W during flight (Elliott 2016), and flight was ca 35 W (+23%) more expensive when carrying a back-mounted tag of comparable size to the GPS in our study (Elliott et al. 2014), though this increase is somewhat more than that predicted from flight mechanical theory (Vandenabeele et al. 2012). As our guillemots spent ca 1.3 h per day in flight, this would equate to an additional energy use of ca 165 kJ day⁻¹, which may correspond to ca 4 g of body fat (assuming 40 kJ g⁻¹ body fat (Pennycuik 2008)). We observed higher mass loss than this, though given the uncertainty in these calculations it is possible that the mass loss could all be due to increased energy expenditure during flight. However, in our study individual mass losses were not correlated with time spent in flight, but as we do not have measures of energy intake rate it could be that those guillemots spending more time in flight also had higher energy intake, e.g. by commuting to more profitable foraging areas.

As outlined in Table 5, a number of device effects have been documented for both common and Brünnich's guillemots; looking across these studies and in light of our new data for the less frequently studied common guillemot we

Table 5. Summary of findings for studies including analyses of various indices of device effects in either common guillemot (CM, *Uria aalge*) or Brünnich's guillemot (TM, *Uria lomvia*). Studies cited are listed below the table, with specific studies included indicated by superscripted letters, in the effects columns: decrease, increase or no change. Brief details of studies are given below the table (type of handicap or device, etc.).

Parameter	Species	Effect			Total
		Increase	Decrease	No change	
Breeding					
Breeding success	CM	0	1 ^d	3 ^{a, b, e}	4
	TM	0	2 ^{f2, h}	3 ^{f1, i, l}	5
	Combined	0	4 ^m	6	10
Chick growth-rate	CM	0	0	0	0
	TM	0	1 ⁱ	0	0
	Combined	0	2 ^m	0	2
Provisioning	CM	0	2 ^{b, d}	0	2
	TM	0	4 ^{g, i*, j*, l}	2 ^{f3, k}	6
	Combined	0	6	2	8
Mate compensation	CM	2 ^{b, d}	0	0	2
	TM	1 ^l	0	1 ⁱ	2
	Combined	3	0	1	4
Condition					
CORT	CM	0	0	1 ^e	1
	TM	1 ^j	0	2 ^{h, i}	3
	Combined	1	0	3	4
Mass	CM	0	1 ^a	1 ^e	2
	TM	0	4 ^{f1, f2, i*, l}	2 ^{g, h}	6
	Combined	0	5	3	8
Activity budget					
Trip duration	CM	2 ^{b*, d}	0	1 ^{ett}	3
	TM	2 ^{j\, l**}	0	0	2
	Combined	4	0	1	5
Diving	CM	0	1 ^{ett}	1 ^a	2
	TM	0	2 ^{g, i}	0	1
	Combined	0	3	1	3
Diving behaviour					
Dive depth	CM	1 ^{*a§}	1 ^{*a§}	1 ^c	3
	TM	0	3 ^{f1, f2*, i}	1 ^j	4
	Combined	1	4	4	7
Dive duration	CM	0	0	1 ^c	1
	TM	0	3 ^{f1, f2, i}	0	3
	Combined	0	3	1	4
Descent rate	CM	0	0	2 ^{a, c}	2
	TM	0	2 ^{f1, f2}	0	2
	Combined	0	2	2	4
Dive efficiency	CM	0	0	1 ^a	1
	TM	0	0	0	0
	Combined	0	0	0	1
Post-dive interval	CM	0	0	1 ^a	1
	TM	2 ^{i, f2}	0	0	0
	Combined	0	0	0	0
Energy expenditure					
Daily	TM	0	0	1 ^g	1
Flight	TM	1 ^g	0	0	1

* Only with double handicap. † In one or two years studied only. ‡ External antenna group only. § Interaction with deployment order (this study, Results) with opposite effects. ¶ Highest drag group only. ¶¶ Overnight trips longer, daytime trips NS different. ** Males only, females NS difference. †† Trip duration unchanged, but number of trips per day reduced, thus number of dives per day too.

Study codes (study type, attachment type, handicap/tag type, mass of tag, breeding stage): Type of study (main comparison, several include untagged controls too): DT – double tag, where data from smaller tag is used to compare behaviour with and without a second larger tag/handicap. TC – tag-control, where tagged guillemots are compared with untagged guillemots (some studies using self-controls, others untagged other birds). SL – Comparing guillemots carrying large handicaps to those carrying small handicaps. Attachment type: R – leg ring, BT – taped to back feathers, VT – taped to front (ventral) feathers, SA – Sub-cutaneous anchor on back, I – implant. Handicap/ tag type (*device including external antenna): V – VHF radio, G – GPS tag, P – Platform terminal transmitter, T – TDR, A – Accelerometer, HB – buoyancy handicap, HD – drag handicap. Mass (as percentage of body mass): ML < 0.5, MM. 0.5 – 1.5, MH > 1.5%. Breeding stage: E – incubation, C – chick-rearing, B – incubation and chick-rearing.

Studies *Uria aalge*: a. (this study) DT, BT+R, G+T, MH, C; b. (Wanless et al. 1988) TC, BT, V+V*, MM, C.; c. (Camphuysen 2005) SL, BT, T, MH., C; d. (Hamel et al. 2004) TC, SA, V*, MM, C.; e. (Tremblay et al. 2003) DT, VT/R, T/V, MH, C.; *Uria lomvia*: f1–3. multiple comparisons made, used one-tailed tests, so could only detect changes in one direction, e.g. only checked for decreased dive depths, not increased (Elliott et al. 2007) f1: DT, R, HB, MM, B; f2 (further analysed in (Elliott et al. 2008a)): DT, R+BT, HD, MH, C; f3: TC, R, T, ML, B; g. (Elliott et al. 2014) DT, R+BT, T, ML, C; h. (Takahashi et al. 2008) TC, VT, T+A, MH, C; i. One or two ‘floater’ handicaps increasing buoyancy (Jacobs et al. 2013) DT, R, HB+T, ML, C; j. (Paredes et al. 2015) DT, BT+R, G+T, MH, C; k. (Harding et al. 2013) DT, BT, G+T, MH, C; l. (Paredes et al. 2005) TC, BT, T, MH, C. Both *U. aalge* and *U. lomvia*: m. (Meyers et al. 1998) TC, I, P*, MH, E.

can draw some general conclusions. Over a third of the studies reported a reduction in breeding success (4 of 9), though two of these used external antennas on the attached devices (Meyers et al. 1998, Hamel et al. 2004), which likely lead to greatly elevated drag (Wilson et al. 2004, Pennycuik et al. 2012). In three out of four of these studies, reduced breeding success resulted from a higher proportion of tagged birds abandoning breeding rather than reducing parental care, e.g. provisioning rates and brooding. Tagged guillemots lost body mass at a higher rate than non-tagged guillemots in over half of the studies, making this the second most frequently observed tag effect (discussed above). Time activity budgets and trip durations often change for tagged guillemots (Table 5), but these changes are not uniform. In one study, trip durations were only increased for overnight trips (Paredes et al. 2015), and another only for males but not female guillemots (Paredes et al. 2005). If guillemots are impacted by tags, we may expect them to increase diving time in order to increase food intake. This is understudied, as it requires dual-tagging studies, but those that have considered this have found decreased diving time or no change. This may reflect guillemots investing in self-maintenance over chick-provisioning, as reduced chick-provisioning is the most commonly observed effect across studies. Fewer studies have looked at direct impacts of tagging on dive behaviour and performance. Reduced dive depths and dive durations are the most frequently recorded effects, though these are not independent of each other, being highly correlated (Tremblay et al. 2003). Handicapped Brünnich’s guillemots increased post-dive intervals (recovery time) after correcting for dive depth in two studies (Elliott et al. 2008a, Jacobs et al. 2013) and decreased dive descent rates (Elliott et al. 2007). Contrary to these findings, we found no such effects on these dive performance measures for the common guillemots.

Overall, the studies mentioned above (Table 5) suggest that guillemots are affected in some ways by carrying tags, with body mass loss and reduction in chick-provisioning the most commonly observed effects. Though smaller tags will generally show fewer measurable effects over short deployments, even small tags are likely to affect birds over longer time periods, as has been shown for common and Brünnich’s guillemots instrumented with small leg-mounted geolocation devices (Elliott et al. 2012) and king penguins *Aptenodytes patagonicus* with flipper tags (Saraux et al. 2011). These effects are likely indirect and must emerge from direct influences of tags on energy consumption and/or performance and foraging success. Some changes in performance have been observed, such as changes in dive depth distribution or recovery time following dives, but these results are not consistent across all studies. Future studies should try to

determine by what mechanisms carrying tags leads to changes in measures related to fitness and condition (e.g. body mass). How energy expenditure and flight or diving performance are affected by carrying handicaps can be investigated by measuring responses in heart rate, overall-dynamic body acceleration, wingbeat frequency and flow-meters to record swimming speeds (Wilson et al. 1986, Green et al. 2009, Chivers et al. 2015, Noda et al. 2016). Whether foraging success is impeded when carrying tags should also be investigated through direct or indirect approaches (Liebsch et al. 2007, Weimerskirch et al. 2007, Sato et al. 2015, Chimienti et al. 2017). Finally, there has been little investigation or consideration of non-mechanical effects of tags on instrumented birds; these could include disrupting insulation, which was proposed as a potential explanation for negative impacts of harnesses on a pelagic seabird species (Thaxter et al. 2016) or potentially general discomfort which could lead to changes in circulating levels of stress hormones. This area warrants further research and may provide an explanation for why even small devices have shown measurable effects (Schacter and Jones 2017).

Smaller devices deployed appropriately for several days (rather than weeks) will generally not have significant impacts on breeding success, though there may be short-term behavioural changes or reductions in body condition. This study, together with a few similar recent studies (Chivers et al. 2015, Heggøy et al. 2015), supports the need for more detailed analyses of potential device effects beyond metrics such as breeding success and mass changes, looking at measures of behaviour and condition (e.g. CORT, immune function). However, due to the typically high individual variation in such condition parameters (Sorenson et al. 2016), the sample sizes required are likely beyond those practical for most tagging studies. Changes in behavioural traits are increasingly possible to investigate with the rapid development of smaller loggers with larger memory (Elliott 2016) such as TDRs (this study, Ludynia et al. 2012), geolocators (providing light-level geolocation and immersion activity data) (Passos et al. 2010) and accelerometers (Chivers et al. 2015) that can be used to monitor behaviour with and without a second larger device such as a GPS or camera, allowing researchers to get closer to resolving the dilemma outlined by Wilson and McMahon (2006) that the means of measurement (a biologging device) may itself affect the behaviour observed cited at the beginning of this article.

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Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.hqbzkhl1dm>> (Evans et al. 2020).

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