RESEARCH ARTICLE

Accelerometry reveals an impact of short-term tagging on seabird activity budgets

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ABSTRACT
Miniaturized data loggers have revolutionized the study of animal movement. However, data obtained from tagging could be compromised by impacts on animal welfare and behavior. We evaluated short-term (activity budgets, foraging trip metrics, overall dynamic body acceleration [ODBA] of flying, wingbeat frequency, adult mass, and nestling mass) and long-term metrics (breeding success and survival) for breeding female Black-legged Kittiwakes (*Rissa tridactyla*) tagged with both GPS and accelerometer tags (5.2% of body mass), birds tagged with only accelerometers (1.0% of body mass), and untagged birds. Breeding success, survival, adult mass, and nestling mass were not affected by tagging, and there were no differences in trip metrics, ODBA, and flapping frequency for birds tagged with GPS and accelerometer packages vs. only accelerometers. However, accelerometry revealed that, when tagged for 3 days with GPS and accelerometer tags, kittiwakes reduced the amount of time spent flying by 30%. Impacts of short-term tag deployments were detected by measuring metrics over the same short timescale, rather than through measurement of long-term metrics. We suggest that tagging birds alters their behavior, but that such effects may not be detected using coarse-scale measures, such as reproductive success, survival, and body mass, due to behavioral accommodation. We recommend that researchers examine, or at least take into consideration, behavioral changes that may be associated with tagging, even if there are no clear effects on fitness or condition measures.

Keywords: accelerometer, Black-legged Kittiwake, *Rissa tridactyla*, activity budget, ODBA, overall dynamic body acceleration

La acelerometría revela un impacto del marcado de corto plazo en los presupuestos de actividad de las aves marinas

RESUMEN
Los registradores de datos en miniatura han revolucionado el estudio del movimiento de los animales. Sin embargo, los datos obtenidos por medio del marcado podrían verse comprometidos por el impacto en el bienestar y en el comportamiento de los animales. Evaluamos métricas de corto plazo (presupuestos de actividad, métricas de viajes de forrajeo, aceleración corporal dinámica global [ACDG] del vuelo, frecuencia de aleteo, masa del adulto y masa del pichón) y de largo plazo (éxito reproductivo y supervivencia) en hembras reproductivas de *Rissa tridactyla* marcadas con GPS y acelerómetros (5.2% de la masa corporal), aves marcadas solo con acelerómetros (1.0% de la masa corporal) y aves no marcadas. El éxito reproductivo, la supervivencia y la masa de adultos y pichones no fueron afectados por el marcado, y no hubo diferencias entre los tipos de marcadores en las métricas de los viajes, la ACDG o la frecuencia de aleteo. Sin embargo, la acelerometría releva que cuando están marcados por tres días con GPS y acelerómetro, los individuos reducen la cantidad de tiempo volando en un 30%. Los impactos de corto plazo de la colocación de los marcadores fueron detectados por medio de mediciones de las métricas llevadas a cabo durante el mismo período de corto plazo, más que a través de las mediciones de las métricas de largo plazo. Sugerimos que el marcado de las aves altera sus comportamientos, pero estos efectos de los marcadores pueden no ser detectados usando medidas a escala gruesa, como el éxito reproductivo, la supervivencia y la masa corporal, debido a una acomodación del comportamiento. Recomendamos que los investigadores examinen, o al menos tengan en consideración, cambios comportamentales que pueden estar asociados con el marcado, incluso si no hay efectos claros en la adecuación biológica o en las medidas de la condición.

Palabras clave: aceleración corporal dinámica global, acelerómetros, presupuestos de actividad, *Rissa tridactyla*

INTRODUCTION

The invention of miniaturized data loggers has revolutionized our ability to study animal movement, particularly that of wide-ranging species, and, accordingly, the number of tagging studies has increased greatly over the past few decades (Barron et al. 2010, Vandenabeele et al. 2011). However, there is a general consensus that too few studies have examined the impacts of tagging on the subject (Wilson et al. 1986, Casper 2009, Barron et al. 2010, Vandenabeele et al. 2012). Furthermore, tagging may alter the very behavior that the tags are designed to record, compromising any benefit from measuring tagged birds (Phillips et al. 2003, Igual et al. 2005, Ludynia et al. 2012, Gómez et al. 2014). Understanding how tagging affects the subject could lead to improvements in the tagging process, especially for animal welfare (Hawkins 2004, Casper 2009, Barron et al. 2010).

Knowledge of avian movement and behavior has been hugely enriched by tagging studies (Burger and Shaffer 2008, Ropert-Coudert et al. 2009). However, as flapping flight is one of the most energetically expensive forms of locomotion (Hendenström 1993, Elliott et al. 2013) and is sensitive to changes in aerodynamics (Pennycuick 2008), the impacts of tagging on flying birds may be particularly pronounced (Obrecht et al. 1988, Vandenabeele et al. 2012). Aerodynamics or hydrodynamics may be changed because the tag increases mass and/or drag (Wilson et al. 1986, 2004, Bannasch et al. 1994, Ropert-Coudert and Wilson 2005, Elliott et al. 2007). In addition, most avian tagging studies occur during the energetically expensive breeding season, when birds are predictably found at the nest and tags can be reliably retrieved (e.g., Drent and Daan 1980, Elliott et al. 2014a, Peterson et al. 2015, Streby et al. 2015). Indeed, a recent meta-analysis demonstrated that tagging devices commonly have a significant negative effect on birds (Barron et al. 2010). However, this meta-analysis did not take into account the duration of tag deployment, which may be a critical factor in determining the manifestation, form, and magnitude of tagging impacts (White et al. 2013). For example, breeding success is often easily measured and is the most frequently used indicator of tag effects on birds (Barron et al. 2010, Vandenabeele et al. 2011, Gómez et al. 2014). Yet, over short-term deployments (days rather than weeks or more), potential impacts on breeding success, such as reductions in foraging ability and nestling provisioning rates, can be compensated for by the partner diverting spare time in its activity budget to foraging (Wanless et al. 1988, Uttley et al. 1994, Paredes et al. 2005, Harding et al. 2007). Furthermore, because of the potential necessity for tagged birds to mediate a tradeoff between self and nestling investment (Elliott et al. 2014a), tagged birds may maintain reproductive success and provisioning rates at a cost to their own condition. Therefore, it may be more appropriate in many cases to use metrics measured over a contemporaneous timescale, rather than long-term outcomes, to monitor tag effects.

Daily energy expenditure is regularly used to identify the effects of tags and seems to be a metric at the appropriate scale for short-term deployments (Barron et al. 2010, Vandenabeele et al. 2011, Elliott et al. 2014a). We know from basic aerodynamic principles that flying with an added, artificial load should increase energy expenditure (Pennycuick 2008, Vandenabeele et al. 2012), and several studies have demonstrated an increase in activity (flight and/or dive) costs when a device is attached (table 1 in Elliott et al. 2014a). In contrast to the strong effect on activity-specific energy expenditure, most studies in the field have been unable to show an effect of tags on daily energy expenditure (cf. Elliott et al. 2014a). An explanation for this anomaly could be that wild birds are already at an 'energy ceiling,' determined by internal constraints on energy processing, which requires them to make behavioral changes consistent with this limit (Drent and Daan 1980, Welcker et al. 2010, Elliott et al. 2014a). Thus, activity budgets and activity-specific energy costs may be more suitable metrics than daily energy expenditure for detecting the impacts of tags over short-term deployments (Elliott et al. 2014a).

At least 2 sets of 'rules' for biologging have been proposed, and these rules are widely applied because of their simplicity of evaluation by both investigators and animal care committees. The use of tags of ∼5% body mass or less (often termed the '5% rule') is widely accepted (Barron et al. 2010, Fair et al. 2010) and has been used by kittiwake researchers in the past (Daunt et al. 2002 [4–6%], Kotzerka et al. 2010, Chivers et al. 2012). However, there is another school of thought whose adherents refer to the '3% rule,' which developed from a study on albatrosses and petrels (Phillips et al. 2003). A meta-analysis of tag effects on birds found little evidence that tag effects increased above 3% body mass (Barron et al. 2010). Neither 'rule' has been thoroughly examined, and recent research and guidelines advise that, as tag impacts depend on many aspects of an animal's biology, there should be no arbitrary 'rule' for all animals, or groups of animals, and that species-specific studies should be carried out (Casper 2009, Vandenabeele et al. 2012). Given that researchers continue to use tags of ∼5% body mass (Daunt et al. 2002, Kotzerka et al. 2010, Chivers et al. 2012, Elliott et al. 2014b), it is important that the effects of tags up to that range continue to be examined.

To advance tagging protocols and address concerns over animal welfare and data quality, we quantified the potential impacts of using both GPS and accelerometer tags together on Black-legged Kittiwakes (*Rissa tridactyla*; hereafter, kittiwake). We used Global Positioning System

(GPS) data logger tags, which define animal location, speed, and behavior, together with accelerometer tags, which measure movement in 3 axes. When waterproofed, the 2 devices together weighed ∼5% of mean kittiwake body mass. GPS and accelerometer tags have limited battery life and so are suitable only for short-term deployments of a few days. We measured both short-term (activity budgets, foraging trip metrics, overall dynamic body acceleration [ODBA] of flying, wingbeat frequency, and adult mass and nestling mass changes) and long-term (breeding success and survival) metrics to evaluate both short-term and long-term effects of short-term tag deployment. For short-term metrics, we were particularly interested in activity budgets and flying behavior as these were likely to be affected by tagging (Obrecht et al. 1988, Vandenabeele et al. 2012, Elliott et al. 2014a). As previous studies have found that tagging results in less time flying (reviewed by Elliott et al. 2014a), we predicted that flight time and, consequently, trip duration would decrease, while time spent on other activities (i.e. nest attendance, time on the water) would necessarily increase for tagged birds. As Newton's second law states that acceleration should decrease when mass increases for a given force generated by the wing, we predicted that dynamic acceleration would decrease in tagged birds. The acceleration of the body is generated by the movement of the wing through space, and consequently we predicted that the rate of that movement (wingbeat frequency) would decrease in tagged birds.

METHODS

Study Site

On Middleton Island, Alaska, USA (59.4°N, 146.3°W), a derelict U.S. Air Force radar tower has been converted to a kittiwake research station by the construction of wooden shelves around the outside walls, which serve as artificial cliffs. Kittiwake pairs nesting on the shelves are easily monitored from inside the building through small windows constructed of 1-way mirror (Gill and Hatch 2002). Birds are readily captured by snaring a leg with a wire hook through a slot in the wall beneath the window, making the site ideal for multiple deployments of telemetry tags on the same individuals. All birds in this study were sexed and color-banded. Average fledging age for kittiwake nestlings at our study site is ∼45 days (S. Hatch personal observation).

Tagging

Previous studies have found that kittiwake activity budgets can differ between the sexes and may be influenced by the number and age of nestlings (Wanless and Harris 1992, Leclaire et al. 2010, Coulson 2011). To minimize these

FIGURE 1. A Black-legged Kittiwake (*Rissa tridactyla*) with a GPS and accelerometer package weighing ∼5% of body mass.

confounding factors, we studied only female kittiwakes with 2 nestlings between 7 and 14 days old.

We compared birds tagged with a GPS tracking device and an accelerometer combined (5.2% of kittiwake body mass; Figure 1) with birds tagged with an accelerometer alone (1.0% of body mass). Device size is one of the main factors influencing many bird performance parameters (Phillips et al. 2003, Wilson et al. 2004, Elliott et al. 2007, Vandenabeele et al. 2014; but see Barron et al. 2010), and using a smaller tag was as close as reasonably possible to using untagged birds (we used the smallest accelerometers that we were aware of that could record for at least 1 day). Using tagged birds allowed us to examine effects on parameters that could not be observed at the colony (e.g., time spent flying, ODBA, wingbeat frequency). In addition, we compared metrics for birds carrying both kinds of tags with metrics for untagged, control birds for those parameters that did not require tagging. Specifically, comparisons of nest attendance were made between untagged birds and accelerometer-tagged birds to detect any effect of the accelerometer tag alone. To reduce the effect of interindividual variation, we tagged the same birds both ways and compared the behavior of the same individuals with and without the larger tag.

To minimize the impacts of the tagging process, we followed the recommendations set out in Casper (2009) as closely as possible. Between June 28 and July 18, 2013, 2 tags were deployed on the same birds in succession, 'Tag A' followed by 'Tag B.' 'Tag A' was a combination of a GPS tracking data logger (CatTrack1; www.mr-lee-catcam.de), with the outer plastic casing removed, and an accelerometer (Axy-1, revision 2; Technosmart Europe, Guidonia, Rome, Italy, Technosmart.eu), sealed together in clear, heat shrink,

waterproof tubing (FiniSHRINK, Swindon, Wiltshire, UK, www.finishrink.com). The mean mass of 'Tag A' was 20.98 ± 0.09 g SE, which was 5.21% ± 0.11% SE of the study female kittiwake body mass. 'Tag B' was an accelerometer alone sealed in tubing. Mean 'Tag B' mass was 3.93 ± 0.24 g SE, which was 1.03% ± 0.08% SE of kittiwake body mass. Tags were weighed before being attached to the central back feathers of kittiwakes using 5 thin strips of marine cloth tape (tesa AG, Hamburg, Germany) following the methods of Wilson and Wilson (1989). Care was taken to attach tags in similar locations on each bird during both deployments. Accelerometers were set to record in the range of ±4.00 g in 3 axes (x [swing], y [sway] and z [heave]) at 25 Hz and to have a sensitivity of 0.03 g. GPS data were not used in this study.

Ten birds were caught at the nest, weighed, had 'Tag A' attached, and were then released. Mean processing time was 6 min 36 s ± 22 s SE. After a minimum of 48 hr, birds were recaptured, 'Tag A' was removed, birds were reweighed, 'Tag B' was attached, and the bird was released. Mean processing time for this was 8 min 23 s ± 59 s SE. After another minimum of 48 hr, birds were recaptured, 'Tag B' was removed, and birds were reweighed. Any regurgitates collected from the tagged birds during handling were weighed and added to bird mass. 'Tag A' was always attached before 'Tag B' because if 'Tag B' had been deployed first and lost, this would have reduced the data available for our main foraging study, which required both GPS and accelerometer data. We assumed that the demands of chicks and environmental conditions would not influence foraging at the timescale of our tagging study and therefore that this design was suitable for our purposes.

Tag Data Processing

We analyzed 24 hr (midnight to midnight) of accelerometer data per bird per tag deployment, as birds were potentially active over the full 24 hr at our sub-Arctic study site. Data were extracted from the middle day of deployment to limit the effects of behavioral changes due to capture and recapture. For 1 bird, we collected 24 hr of data starting at 18:00:00 on the 1st day, because the accelerometer in 'Tag A' failed to collect data in the evening of the middle day. This data collection began 6 hr 14 min 22 s after tag deployment, which we considered was sufficient time for the bird to settle.

Acceleration recorded in 3 axes consists of both a static and a dynamic component. The static component results from body angle with respect to gravity, while the dynamic component results from animal movement (Yoda et al. 2001). As we were only interested in animal movement and dynamic acceleration, the static component (which provides information on posture) was calculated and subtracted from total acceleration (Wilson et al. 2006).

Static acceleration was calculated in IGOR Pro 6 (Wave-Metrics, Lake Oswego, Oregon, USA) using a box smoothing function with 75 points. This is equivalent to using a running mean of 3 s, which is suitable for ODBA calculation (Shepard et al. 2008). The smoothed acceleration data were converted into positive units, and the data from the 3 axes were summed at every point to give ODBA per 0.04 s.

Metrics

ODBA data were graphed in IGOR Pro 6, and times when activity changed were recorded to the nearest second. Three activities were identified: 'nest attendance,' 'other activities,' and 'travel flight' (Figure 2). The length of time spent on each activity was summed and the proportion of 24 hr spent on each activity was calculated. To check consistency in behavioral classification, 5 6-hr sections from 5 different birds were reanalyzed and compared with the initial analyses using t-tests. There was no significant difference, showing that classification of activities was consistent (nest attendance: $t_8 = 0.03$, $P = 0.98$; other activities: $t_8 = -0.05$, $P = 0.96$; travel flight: $t_8 = 0.00$, $P = 1.00$, $n = 5$). The number and duration of whole foraging trips made within 24 hr were determined using the activity budget results. A trip started when a bird left the nest.

One or 2 days before tagging, attendance at the nest of birds due to be tagged was recorded every 10 min in 3 sessions (06:00–09:00, 11:00–14:00, and 16:00–18:00) totaling 8 hr. Nest attendance during the same 3 time periods during both 'Tag A' and 'Tag B' deployments was worked out using the activity budget data. The proportion of the 8 hr spent in nest attendance under the 3 treatments was calculated.

Data and calculations for 1 hr of travel flight were extracted from each 24-hr period. We assumed that 1 hr of flight would provide a good representation of typical flight. The mean ODBA was calculated per bird per deployment. Then, using the smoothed z-axis data (not converted into positive units), the wavelength (λ) of each wingbeat was determined using MS Excel (Microsoft Corporation, Redmond, Washington, USA) formulas that we devised to identify wave peaks and calculate the time difference between them. The mean wingbeat wavelength (λ) per bird per deployment and wingbeat frequency as $1/$mean λ were then calculated.

To determine whether tagging had an effect on nestling growth or overall breeding success, tagged birds were monitored for breeding success, and both nestlings were weighed at day 5 and day 20. Nestling A was the 1st to hatch (on day 0) and nestling B the 2nd, so nestling B was always younger than nestling A. If nestlings survived for 20 days, the difference between nestling mass at day 5 and day 20 was calculated. We made comparisons of nestling growth between the nestlings of tagged birds and nestlings
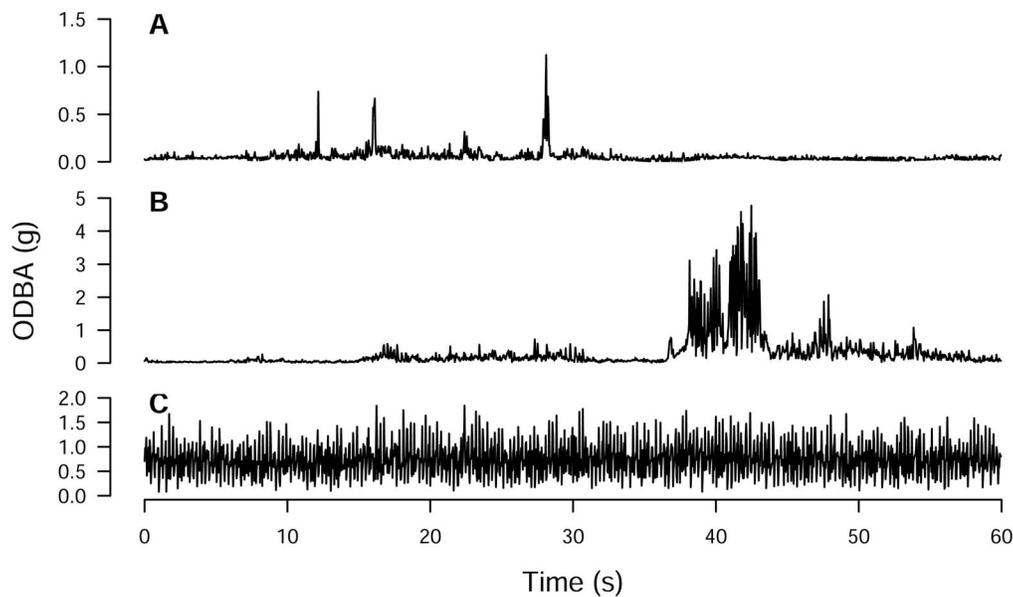
FIGURE 2. Examples of acceleration data showing 3 classifications of Black-legged Kittiwake (*Rissa tridactyla*) behavior. (**A**) Nest attendance: periods of minimal activity bounded by periods of travel flight; (**B**) Other activities: not nest attendance or travel flight, but including feeding and resting on the water; and (**C**) Travel flight: Regular, repetitive, sustained movement, >10 s in duration.

of the same number of control birds that were not tagged and that also had 2 nestlings over 7 days old. To reduce differences in environmental effects on nestling growth, control birds were selected if their nestling A hatched within 1 day of a tagged bird's nestling A. Breeding success was compared between tagged birds and 19 control birds that had 2 nestlings at least 7 days old. To ascertain whether tagging had an impact on survival, resightings of study birds were recorded at the study site in 2014.

Statistical Analyses

Kittiwake mass and nest attendance over 8 hr were compared between control birds that were not tagged, birds tagged with 'Tag A,' and birds tagged with 'Tag B.' Breeding success, nestling growth, and survival were compared between control (untagged) birds and tagged birds. Activity budgets, ODBA, and wingbeat wavelength were compared between birds tagged with 'Tag A' and birds tagged with 'Tag B' only.

Proportions were angular-transformed before statistical analysis. As our sample size was small, Pearson's chi-square tests with simulated *P*-values (999 replicates) were used to compare the number of fledged nestlings per pair (breeding success) and survival between tagged and untagged birds. Comparisons of bird mass and nest attendance over an 8-hr period between control birds (no tag), birds with 'Tag A,' and birds with 'Tag B' were performed using repeated measures ANOVAs. All other analyses were paired *t*-tests between 'Tag A' and 'Tag B' deployments. For all directional *t*-tests, we used 1-tailed

probabilities based on our initial predictions. As our sample size was small, our analyses had low statistical power (paired *t*-test = 0.29), and thus low ability to detect a significant effect if it existed. Therefore, we also calculated effect sizes and their confidence limits. An effect of 0.2–0.5 is low, 0.5–0.8 is medium, and >0.8 is high. All statistics were performed using R 3.0.2 (R Development Core Team 2014).

RESULTS

There was no significant difference in nest attendance between control, 'Tag A,' and 'Tag B' treatments during the 8-hr study period (Table 1). This may have been because the control and 'Tag B' values were very similar. There was also no significant difference between 'Tag A' and 'Tag B' deployments in the proportion of 24 hr spent pursuing 'other activities.' There was a significant difference in the proportion of time that birds spent in travel flight and nest attendance between 'Tag A' and 'Tag B' deployments. When birds were equipped with 'Tag A,' they performed 30% less travel flight and attended the nest 33% more than when equipped with 'Tag B.' There was no significant difference between 'Tag A' and 'Tag B' deployments in the mean duration of trips, and the mean numbers of trips made in 24 hr were similar (Table 1), implying that during 'Tag A' deployment birds made shorter travel flights per trip and that they travelled shorter distances.

Mean ODBA during 1 hr of travel flight and wingbeat wavelength were not significantly different between 'Tag A'

TABLE 1. A summary of the impacts of tag deployment and tag mass on female Black-legged Kittiwake (*Rissa tridactyla*) behavior and condition. Females with 2 nestlings aged between 7 and 14 days were studied at Middleton Island, Alaska, USA, in 2013. Significant results are highlighted in bold type. 'Nest attendance' = bird assumed to be present at the nest; 'Travel flight' = sustained flight, >10 s in duration; 'Other activites' = not travel flight or nest attendance. ODBA = overall dynamic body acceleration.

Variable measured	Mean ± SE (*n* = 10)			Statistical analyses	Effect sizes		
	Control (no tag)	Tag A (GPS and accelerometer)	Tag B (accelerometer)	Repeated measures ANOVA (df = 1, 26)	(η^2 = eta squared, δ = Cohen's *d*)	90% confidence limits	
Bird mass at recapture (g)	404.5 ± 9.6	392.4 ± 6.5	387.1 ± 8.8	F = 2.78, P = 0.11	η^2 = 0.077	0.00, 0.29	
Nest attendance (proportion of 8 hr)	0.36 ± 0.06	0.51 ± 0.06	0.36 ± 0.05	F = 2.39, P = 0.13	η^2 = 0.129	0.00, 0.27	
				Paired *t*-test (df = 9)		95% confidence limits	
Activity budget (proportion of 24 hr)							
Nest attendance		0.48 ± 0.03	0.36 ± 0.05	**t = 1.86, P = 0.048**	δ = 0.915	−0.01, 1.74	
Other activities		0.20 ± 0.02	0.18 ± 0.02	t = 0.62, P = 0.28	δ = 0.286	−0.61, 1.15	
Travel flight		0.32 ± 0.02	0.46 ± 0.03	**t = −3.70, P = 0.003**	δ = 1.705	−2.66, −0.61	
Foraging trips (mean in 24 hr)							
Number of trips [a]		2.00 ± 0.33	2.20 ± 0.21				
Trip duration (hr)		4.59 ± 1.10	6.08 ± 1.38	t = −0.82, P = 0.22	δ = 0.377	−1.24, −0.52	
ODBA at 25 Hz (g) (1 hr of 'travel flight')		0.80 ± 0.02	0.85 ± 0.02	t = −1.74, P = 0.06	δ = 0.651	−1.68, 0.14	
Wingbeat (1 hr of 'travel flight')							
Wavelength λ (s)		0.23 ± 0.01	0.25 ± 0.01	t = −1.69, P = 0.06	δ = 0.714	−1.65, 0.17	
Frequency (1/λ) (Hz) [a]		4.36 ± 0.15	4.06 ± 0.11				

[a] No statistical analysis was performed on this metric.

and 'Tag B' deployments (Table 1). Bird mass was not significantly affected by the presence or type of tag (Table 1). There was no significant difference in change of nestling mass between the ages of 5 and 20 days for nestlings of tagged vs. untagged birds (nestling A: $t_{14} = -1.07$, $P = 0.30$, $\delta = 0.480$ [−1.52, 0.48], $n = 16$; nestling B: $t_{14} = -1.62$, $P = 0.13$, $\delta = 0.646$ [−1.82, 0.23], $n = 16$). The mean difference in nestling B mass between 5 and 20 days old for nestlings of untagged birds was 220.81 ± 15.24 g, and for nestlings of tagged birds was 251.43 ± 8.67 g. There was no difference in breeding success between tagged and untagged birds (Pearson's χ^2 with simulated P-value = 0.004, $P = 1.00$, $n = 29$). All pairs in the study fledged at least 1 nestling (mean number of nestlings fledged per pair: tagged birds = 1.80 ± 0.13, $n = 10$; untagged birds = 1.79 ± 0.10, $n = 19$). Two of the 10 tagged birds and 3 of 10 untagged birds lost 1 nestling aged between 10 and 15 days. All 19 untagged birds were resighted in 2014; 1 out of 10 tagged birds was not (Pearson's χ^2 with simulated P value = 1.97, $P = 0.36$, $n = 29$). The tagged bird that was not resighted maintained body condition over the tagging period (mass before tagging = 400 g, after Tag 'A' deployment = 406 g, and after Tag 'B' deployment = 385 g) and fledged 2 nestlings.

The effect size for time spent flying was the largest of any parameter examined (Table 1), implying that time spent flying was the most sensitive parameter to tag effects. The effect sizes for ODBA, wingbeat wavelength, and nestling B growth rate were all moderate, suggesting that a significant effect may have been revealed with a larger sample size.

DISCUSSION

The impacts of short-term tag deployments were detected by measuring metrics over the same short timescale; had we only measured longer-term metrics, we would have erroneously concluded that the tags did not affect kittiwakes. Kittiwakes tagged for 3 days with devices weighing a mean of 5.2% of body mass reduced their time spent flying. Although we found no statistically significant difference in wingbeat frequency or dynamic body acceleration (P-values of 0.05–0.06), the adjustment in time spent flying implies, to us, that some component of flight costs was increased. We suggest that the extra burden and/or increased drag associated with carrying tags increased flight costs, causing kittiwakes to reduce the amount of time spent flying, perhaps to remain below their energetic ceiling (cf. Elliott et al. 2014a). These findings may have implications for tag data interpretation and utility (Wilson et al. 1986, 2004, Ropert-Coudert and Wilson 2005, Wilson and McMahon 2006). For example, if birds spend less time flying when tagged, the full extent of their range may not be utilized, and this should be taken

into consideration when location data is used to identify potential protected areas (e.g., Chivers et al. 2013). Likewise, interspecific comparisons of behavioral parameters could be compromised if the kinematics and flight times of smaller animals are more affected by tags than those of larger animals (e.g., Sato et al. 2007, Jovani et al. 2015).

While time spent flying decreased when 'Tag A' was deployed, nest attendance increased (at least relative to 'Tag B' birds and, with near-significance, relative to controls), and, as at least one partner was present with the young nestlings throughout the study period, this means that the partner of the tagged bird spent more time on foraging trips. We suggest that the untagged partner buffered the effect of tagging on its mate by increasing its foraging effort to maintain nestling provisioning rates, and thus nestling growth rates and breeding success, as has been shown in other charadriiform seabirds (Wanless et al. 1988, Paredes et al. 2005).

No impacts on animal welfare (breeding success, survival, adult mass, and nestling mass) were detected. However, our study was carried out during a year of good food availability; the fledging rate was ~1.8 nestlings per nest, compared with a long-term average of <1.0 nestling per nest (Hatch 2013). During less favorable conditions, the impacts of tags on flying time may be more pronounced (Igual et al. 2005). During poor years, it may be harder for adults to maintain provisioning rates, even with buffering by the untagged partner, which may lead to lower nestling growth rates, lighter adult body mass, and, ultimately, lower adult survival (Igual et al. 2005). Such effects may be particularly pertinent to kittiwakes, which increase foraging range when food availability is low and have a limited ability to increase foraging effort because, during the breeding season, they work close to maximum capacity and have little spare time to redirect to foraging (Hamer et al. 1993, Furness and Tasker 2000, Enstipp et al. 2006, Chivers et al. 2012). In this study, adult body condition was maintained during tagging, which may explain why there was no apparent impact of tags on survival (Jacobsen et al. 1995). Overall, the survival rate for female kittiwakes on Middleton Island is 0.94, with no difference between the sexes (Hatch et al. 1993). Given our small sample size, the survival rate of 0.90 for tagged birds means that there was likely very little impact of tags on survival.

A potential drawback of our study is that we did not randomize the order of device attachment, and therefore we cannot say that factors such as nestling age, carryover effects from 'Tag A' deployment, and handling effects did not influence bird behavior during 'Tag B' deployment. Given that kittiwake nestlings take ~45 days to fledge at our study site and the difference in timing of attachment was only 1–2 days, we believe that it is unlikely that

nestling age played a strong role. We found no difference in nest attendance between control and 'Tag B' groups, which excludes the possibility that birds developed a habit of attending the nest longer or avoided the nest to prevent recapture after 'Tag A' deployment. Although we found no evidence of these potential carryover or handling effects, we may have been unable to detect other, but likely minor, effects. Furthermore, our sample size was limited, although higher per treatment than other similar studies that have detected an effect previously (e.g., Elliott et al. 2007, Vandenabeele et al. 2014). By using a paired design that reduced interindividual variability, we also increased our statistical power.

Conclusion

Tagging studies have made, and will make, valuable contributions to our knowledge and conservation of species, but it is of paramount importance that tags do not compromise animal welfare or influence the data collected. While we found no measurable effects on animal welfare, our findings have implications for tag data efficacy, because birds changed their behavior when tagged. Comparisons among years or study sites in time spent flying, and possibly foraging distance, using tags of different sizes could detect spurious differences (or fail to detect true differences) if devices of different sizes were to be used or if effects were to vary depending on environmental conditions. Ideally, before carrying out any tagging study, a pilot study should be performed to detect any effects of tags that may influence the data, so that: (1) improvements can be made to the process to reduce or eliminate such impacts; (2) further studies can be implemented to assess the representativeness of the data; and (3) the main study data can be interpreted while being mindful of the pilot study results. Our study demonstrates that, for short-term tagging studies, measuring long-term metrics may not reveal more subtle tag impacts that are apparent over the short term, so the metrics measured should match the timescale of tag deployment. The research station on Middleton Island made it possible for a detailed tagging impact study to be performed, but this is unusual as researchers generally encounter poor access to and visibility of birds and/or nestlings that preclude such studies. We have 2 considerations for researchers unable to undertake 'tag effect' studies. First, given our observed effects on foraging behavior, tags may cause distress, hunger, and fatigue for individual birds, even if there is no impact on adult body mass, reproductive success, or survival. Aside from animal welfare considerations, such subtle effects may alter physiological and behavioral parameters if the same individuals are used in other studies. Second, movement patterns observed via tagging may not be representative and may therefore cause bias when planning marine reserves or obtaining values to input into modeling exercises (e.g., Chivers et al. 2013, Gaston et al. 2013).

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