



# An experimental study measuring the effects of a tarsus-mounted tracking device on the behaviour of a small pursuit-diving seabird

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## Abstract

Miniaturized tracking devices are taking a rapidly increasing role in studies measuring animal movement and other aspects of behaviour, especially for wide-ranging species such as seabirds that are difficult to observe otherwise. A crucial, but questionable criterion of such migration research is assuming that effects of tracking devices on animal behaviour are negligible, to ensure results of tracking studies are biologically relevant. To address this concern, we experimentally quantified effects of a 2 g (ca. 1.1% of body mass) geolocation device on crested auklet (*Aethia cristatella*) behaviour, including return rate, activity on the colony surface, and measures of reproductive performance in a two-year, two-part field study. In experiment 1, we fitted tracking devices (or identical dummy devices) to one mate of a breeding pair in nesting crevices, to quantify effects on reproductive performance and nest fidelity. In experiment 2, we assigned dummy devices to birds captured at the colony site surface, to quantify effects on social activity, return rate and provisioning behaviour. For birds tagged in crevices, we detected no effect on fledging success, or chick growth rate (mass and wing length). However, mass at fledging age of chicks provisioned with one tagged parent was significantly lower than control, and low nest site fidelity (compared to control birds) was observed for tagged birds. Individuals tagged on the colony surface showed significantly reduced colony surface activity, return rates and provisioning behaviour. This study shows strong 'observer effects' of an attached device well below the recommended size limit for wildlife tagging. Future studies should both quantify effects of attached devices and consider the biological relevance of measures of the behaviour of interest.

## Keywords

Observer Effects, crested auklet, *Aethia cristatella*, geolocator, mate compensation, return rate, seabird, tracking device.

## 1. Introduction

Tracking studies have greatly advanced our knowledge and understanding of the fundamental biology of many animals, lending itself to useful applications in wildlife management and conservation biology (Burger & Shaffer, 2008; Casper, 2009; Robinson et al., 2010; Maxwell et al., 2011). Insight into animal behaviour, ecology, and physiology have taken leaps forward with the use of geographical positioning devices, furthering our understanding of foraging and social behaviour, habitat range, and resource selection of many wide-ranging animals (Murray & Fuller, 2000; Wilson & McMahon, 2006; Recio et al., 2011; Le Corre et al., 2012). Tracking studies investigating animal movement across diverse taxa often ignore potential risk of Observer Effect, failing to acknowledge implications of device-attachment on species welfare and merit of research (Mellas & Haynes, 1985; Wilson & McMahon, 2006). An Observer Effect is the change in behaviour of the subject as a consequence of the observer's presence (Sykes, 1978). The 'Biological Uncertainty Principle' refers to the disturbance caused by the investigator attempting to measure or observe normal behaviour of wildlife because, there is no way of knowing the behaviour without observing it (Mayfield, 1975; Mayer-Gross et al., 1997). However, tracking studies rely on the assumption that tracking devices used to measure movement do not significantly alter natural behaviour of tagged individuals in order to effectively extrapolate data to the larger, unmarked population (Murray & Fuller, 2000; Casper, 2009; Constantini & Møller, 2013).

With the development of increasingly light-weight, cost-effective tracking devices, birds have received growing attention in recent migration research (Casper, 2009). This has opened exciting avenues to understanding previously unknown avian foraging, social and breeding behaviour, migration routes, and year-round temporal and spatial distribution (Lisovski et al., 2012; Bouten et al., 2013). While many (ca. 80%) of avian migration studies acknowledge potential for device effect (Barron et al., 2010), few provide comprehensive experimental studies to detect it. Many experiments are poorly designed, with weak sample size, logistical constraints on duration of study, lack of appropriate control and haphazard qualitative observation (Calvo et al., 1992). This critically limits the statistical strength with which to make confident conclusions and recommendations for future device application (White & Garrott, 1990; Murray & Fuller, 2000).

Externally-mounted devices fitted to birds directly increases overall mass, aerodynamic drag, hydrodynamic drag, and in many cases, alters the balance of marked individuals (Adams et al., 2009; Vandenabeele et al., 2011). These direct changes to impacted birds translates to effects on behaviour and ecology of individuals to varying degrees, primarily influencing energy expenditures and likelihood of nesting the year following device deployment (Barron et al., 2010; Vandenabeele et al., 2012). To mitigate tag effect on birds, researchers have adhered to a rule that no tag deployed exceed 5%, and more recently 3% of individual body mass (Phillips et al., 2003), however reasoning behind this rule is unclear and significant effects have been documented even within this set of constraints (Phillips et al., 2003; Adams et al., 2009; Vandenabeele et al., 2012; Bridge et al., 2013). Additionally, this rule does not account for potential impacts of drag induced by cross-sectional area of the tags, found to significantly reduce flight range in a number of tagged individuals (Barron et al., 2010; Bridge et al., 2013). Forming generalized guidelines for tag deployment is clearly problematic as adverse device effects are specific to attachment methods, species, age, sex, environment. Moreover, authors may only focus on particular behavioural activities with varying degrees of biological importance and many less obvious device effects may go unnoticed (Murray & Fuller, 2000; Casper, 2009; Vandenabeele et al., 2012; Bridge et al., 2013). Taken together, studies of varying tag effect cast doubt on the biological relevance of many studies, as tagged individuals were not behaving normally.

Seabirds are a popular subject for tag-enabled migration tracking, as they are highly mobile and tend to inhabit remote areas, far from direct land observation for the majority of the year (Vandenabeele, Wilson & Grogan, 2011). Few tracking devices have been applied to the family of long-lived, highly monogamous seabirds, the auks (*Alcidae*). Auks, while generally small in size, have a high body mass to wing area ratio (Ackerman et al., 2004). This morphology allows them to be efficient underwater pursuit-divers, however they consequently have an energetically expensive mode of continuous flapping flight (Ackerman et al., 2004; Whidden et al., 2007). Most auklets (*Aethiini*), a tribe within the auks, nest in crevices below the surface of talus slopes, producing a single offspring annually and exhibit bi-parental care during a lengthy breeding season (ca. 35 days incubation, 35 days chick rearing) (Fraser et al., 1999). Both parents invest heavily in rearing their young, sharing roles of incubation, brooding and provisioning; although brooding

and defense of the nest site is often dominated by males (Fraser et al., 1999, 2002). Daily aggregations at the surface of the colony and large swarming behaviours play a critical role in breeding and social behaviour of the smaller auks, particularly in crested auklets (*Aethia cristatella*) (Zubakin et al., 2010). This investment of time and energy in conspecific interaction at the surface of the colony site, including complex visual, acoustic and olfactory displays among breeders and non-breeders is associated with courtship activity, establishment of social hierarchies, and habitat familiarization (Klenova et al., 2011). The unique ecology, physiology and social behaviour of auks suggests that they may be particularly vulnerable to adverse effects of additional mass and drag imposed by a tracking device (Ackerman et al., 2004; Paredes et al., 2005; Whidden et al., 2007).

The objective of our study was to rigorously quantify the behavioural effects of tarsus-mounted devices (well within the 3% body mass recommendation) on a small, pursuit diving auk, the crested auklet, through two distinct experiments. The aim of experiment 1 was to quantify reproductive performance, nest site fidelity and body condition of individuals fitted with a device from nesting crevices (the null hypothesis being no tag effect on these aspects of biology). The aim of experiment 2 was to measure return rates, frequency of activity on the colony site surface and provisioning behaviour of tagged individuals captured at the surface of the colony (again, the null hypothesis being no tag effect). From these experiments, we inferred mitigation measures for deploying tracking devices in order to maintain ethical practice and biological relevance of research.

## 2. Methods

### 2.1. Study area

Our research was conducted at Buldir Island (52°11'N, 175°56'E), situated in the western range of the Aleutian chain of Alaska (Sowls et al., 1978; Byrd & Day, 1986). The study area is located at Main Talus, a breeding site supporting more than 100 000 crested and least auklets (*Aethia pusilla*, Byrd et al., 1983). Over 200 crested auklet crevices are accessible to investigators at Main Talus, most of which have been previously monitored for breeding biology studies. An observation blind, constructed on Main Talus, overlooks our research plot where individual banding and re-sighting has been conducted from 1990 until present.

## 2.2. *Experiment 1: device effects on individuals captured in nesting crevices*

### 2.2.1. *Device attachment*

To assess the behavioural effects of archival light-sensing geolocation devices (herein referred to as tags or devices) on crested auklets, we quantified the breeding performance of tagged (fitted with a geolocator) and untagged (no geolocator) individuals captured from nesting crevices located throughout the study area at Main Talus. During the early brooding period (0–4 days after hatch; Knudtson et al., 1982), one pair member only was removed from crevices for tag deployment. This deployment timing was critical to ensure the presence of either mate and reduce the risk of early nest abandonment due to crevice disturbance (Piatt et al., 1990; Whidden et al., 2007). In 2011, we deployed 31 LAT 2900 geolocator tags ( $8 \times 15 \times 7$  mm, 1.9 g, LOTEK, St. John's, NF, Canada) to breeding individuals (21 males, 10 females). We also deployed LAT 2900 dummy tags (identical in size and mass to LAT 2900 geolocator tags but without internal electronics) to 14 individuals (9 males, 5 females). In 2012, we deployed LAT 2900 dummy tags to 19 previously unmarked individuals (8 males, 11 females). Dummy tags were deployed to increase sample size of tagged bird population, and compared to a control group. Our banding effort was covered by Animal Care protocols 11-01-IJ and 12-01-IJ from the Institutional Animal Care Committee of Memorial University.

Using light green Darvic colour bands with a single cable-tie, we secured the tags onto the right tarsus above a single numbered aluminum USFWS band (combined mass of tag, aluminum band, and cable tie was  $2.93 \pm 0.12$  g,  $N = 31$ ; 1.1% of the mean body mass of all tagged individuals). At capture we determined sex by bill depth and shape (Jones, 1993) and recorded biometric measurements of relative body size (mass, wing, tarsus, and culmen length, and bill depth) and feather ornament size (crest, auricular plume and rectal plate length; Jones et al., 2004). Mass was measured to the nearest 1 g using a 300-g Pesola® spring scale, and linear measurements were recorded to the nearest 0.1 mm using Vernier calipers. Average individual handling time for tag attachment was limited to  $7:11 \pm 0:14$  min,  $N = 45$ , before returning the adult to its chick in the nesting crevice. Untagged pair members were left undisturbed.

### 2.2.2. Fledging success and chick growth

In order to assess the effect of fitting one pair member with a device on reproductive performance of a breeding pair, we measured productivity at the study crevices comparing three levels of disturbance: (i) highly disturbed (one member per pair tagged and chick handled), (ii) partially disturbed (untagged and chick handled), and (iii) undisturbed (untagged and chick unhandled). In 2011, we monitored 45 disturbed crevices (31 geolocator tags + 14 dummy tags), 26 partially disturbed and 73 undisturbed crevices (Table 1). In 2012, we monitored 18 disturbed crevices (all dummy tags), 17 partially disturbed, and 79 undisturbed crevices. After tag deployment, crevices were examined every 4–5 days using a small flash light to determine fledging success. Chick age was determined using the mean date between an observed egg and a chick occurrence in consecutive crevice checks ( $\pm 2$  days) and was known more precisely ( $\pm 1$  day) in cases when the chick was observed hatching or piping. Chicks were excluded from our analysis if hatch date uncertainty was greater than  $\pm 3$  days. Fledging success was calculated as the percentage of known crevices where the chick reached fledging age ( $\geq 26$  days after hatch). Differences in fledging success were compared across disturbance levels, testing for sex-specific effects in all groups using Chi-square and Fisher's Exact tests.

To detect device effect on chick quality, we measured both mass and wing length from chicks removed from crevices in the partially disturbed crevices (chick handled and measured; adult undisturbed) and the highly disturbed

**Table 1.**

Summary of crested auklet (*Aethia cristatella*) crevices sample sizes used to detect tag effect on fledging success and chick condition with varying degrees of disturbance (no values for undisturbed crevices measuring chick condition because all chicks measured were disturbed).

Disturbance level	Fledging success		Chick condition	
	2011	2012	2011	2012
Highly disturbed crevices <sup>a</sup>	45	18	30	19
Partially disturbed crevices <sup>b</sup>	26	17	30	16
Undisturbed crevices <sup>c</sup>	73	79	–	–
Total crevices	144	114	90	35

<sup>a</sup> Chick handled and measured; adult equipped with tag.

<sup>b</sup> Chick handled and measured; adult undisturbed.

<sup>c</sup> Chick undisturbed; adult undisturbed.

group (chick handled and measured; adult equipped with tag) every 3–4 days. In 2011, we recorded a single measurement of mass and wing length for each chick, dispersed across varying ages. Comparisons among age cohorts were conducted using ANOVAs assessing mass and wing chord in control and tagged groups. In 2012, we measured chicks every 3–4 days, during the linear growth phase (6–24 days after hatch; Fraser et al., 1999), taking 5 measurements of mass and wing chord for each chick in control and tagged groups. An ANCOVA was conducted to compare rate of growth (mass and wing length) across disturbance levels. Fledgling mass and fledgling wing length were determined to be the last measurement recorded prior to chick fledging, including only measurements of chicks that reached fledging age (26 days) and were compared between disturbance groups.

### *2.2.3. Nest site fidelity and body condition*

In order to test for a tag effect on nest site fidelity, we re-checked all 31 crevices in 2012 from which an individual had been tagged in 2011. When an attached tag was observed during a re-check, the individual was re-captured, the tag detached and biometric measurements again taken. Tag recovery rate, representing the degree of nest site fidelity for 2011–2012 was compared to a control group from a long-term data set (1993–2000) of breeding crested auklets captured from crevices, banded and re-captured in the following year. We tested for sex-specific, year effect and tag year effect within the control data and tested for significant differences in nest site fidelity between the control group (1993–2000) and our tagged group (2011–2012), using Chi-square and Fisher's Exact tests. We also compared parameters of body condition between returning birds against that of non-returning birds in 2011–2012, using the biometric measurements taken at time of tag deployment. To detect any device effect on body condition, biometric measurements of body and ornament size were compared between 2011 (prior to tag attachment) and 2012 (taken at recovery), using paired Student *t*-tests. Recaptured individuals were also examined for direct physical injuries attributable to the tag on their right tarsus.

## *2.3. Experiment 2: device effects on crested auklets captured on the colony surface*

### *2.3.1. Device attachment*

To evaluate device effects on social behaviour of crested auklets on the colony site surface and further quantify return rates of tagged individuals,

we simultaneously conducted second tag effect experiment in both years. This experiment was conducted at a single study plot, occupied by an estimated 1000 crested auklet breeding pairs (Jones et al., 2004), where ca. 1200 crested auklets have been colour banded for capture-mark-resight studies since 1990. From 6 June–30 July 2011, 167 crested auklets were trapped on the surface of the 100-m<sup>2</sup> marked plot using noose carpets. Breeding individuals ( $N = 94$ ), identified by the presence of a full brood patch (Jones et al., 2000), were selected for the experiment and alternately (by order of capture, to control for date effect) assigned to a control or dummy tagged group. The group of 48 experimental birds had the same LAT 2900 dummy tags cable-tied to a Darvic plastic colour band and the USFWS aluminum band as described in experiment 1 (except dummy tag was attached on left tarsus and a unique 2-colour Darvic band combination attached on the right tarsus; contributing an additional 0.2 g), for individual identification. The control group (46 individuals) received a stainless steel band, as well as a unique 3-colour Darvic band identifier as previously used at the study plot (Jones et al., 2004). In this experiment, we were able to control for any effects of handling caused by device attachment by treating both control and experimental groups with equal handling time. All banded birds were sexed and measured (Jones et al., 2000), and released back to the colony site.

### 2.3.2. *Surface activity*

Daily re-sighting of banded birds was conducted throughout the 2011 breeding season (31 May–2 August), and repeated in 2012 (26 May–3 August) from the observation blind for 4–6 h every day during the morning surface activity period (10:00–14:00 h) and a brief period of activity at night (22:30–00:30 h). To assess behavioural effects of tags on daily surface activity at the colony, we calculated individual resight frequency in control and tagged groups, from tallied observations of experimental individuals each day. Daily resight frequency was calculated for each group (control and tagged) as: number of individuals observed in a day/total number of individuals in the banded group (control and tagged). In 2011 the total number of birds in the group changed throughout the season as we banded more birds, increasing the number of birds in each group within the marked population. To graphically illustrate this data, we calculated daily resight ratios as: resight frequency of control group/resight frequency of tagged group. To account for temporal differences in surface activity caused by breeding activity, we compared observation frequency in tagged and control groups before



and after the mean hatch date, using Wilcoxon Signed Rank test for paired observations.

### 2.3.3. *Return rate and provisioning behaviour*

We examined the return rates of tagged (disturbed) and control (undisturbed) birds in 2011 and 2012, accounting for sex-specific differences using Chi-square and Fisher's Exact test. For historical context, we compiled a control dataset for return rate from banded resights in 1992–2011. Including only adult, breeding crested auklets (with full brood patches), we measured the proportion of birds captured at the plot and seen the following year, testing for tag effect, year effect and sex-specific effects using Chi-square and Fisher's Exact tests. Provisioning behaviour was compared across tagged and untagged individuals in 2012, recorded as the number of individuals observed carrying food to their young, identified by an enlarged sublingual pouch. We also tested for the effect of individual mass on colony behaviour, as quantified by resight frequency of individuals that returned in 2012, to detect any variability in tag effect with increasing relative tag to body mass. In both 2011 and 2012, daily observations were made at the study plot to assess any direct physical effects of the dummy tags and potential indirect impacts on behaviour of birds interacting at the surface of the colony. We looked for abnormalities in social behaviour, or evidence of impeded walking or flight in dummy-tagged crested auklets. All analyses were computed using R software (R Development Core Team, 2012), and all values are presented as means + SE.

## 3. Results

### 3.1. *Experiment 1: device effects on crested auklets captured in nesting crevices*

#### 3.1.1. *Fledging success and chick growth*

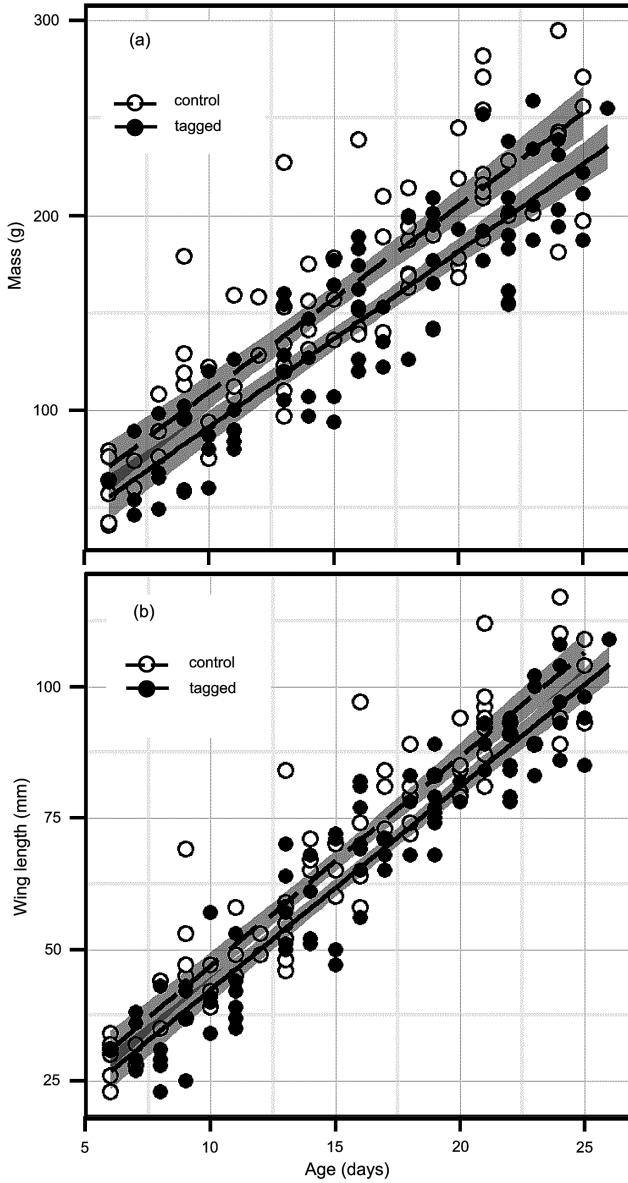
Fledging success in both years was not significantly different across levels of disturbance. In 2011, fledging success was 79% from tagged crevices ( $N = 42$ ; 3 crevices were excluded due to poor hatch date accuracy), 81% from partially disturbed crevices ( $N = 26$ ) and 81% in undisturbed crevices ( $N = 73$ ; Chi-square test:  $\chi_2^2 = 0.093$ ,  $p = 0.95$ ). In 2012, fledging success was 94% in tagged crevices ( $N = 18$ , 1 crevice excluded due to hatch date accuracy), 88% from partially disturbed crevices ( $N = 17$ ) and 90% in

undisturbed crevices ( $N = 79$ ) (Fisher's Exact,  $p = 0.89$ ). Fledging success did not differ significantly according to the sex of the tagged pair member (2011:  $\chi_2^2 = 2.24$ ,  $p = 0.130$ ; 2012:  $\chi_2^2 = 0.05$ ,  $p = 0.810$ ). Fledging success in crevices where tagged individuals were recaptured and geolocators removed one year after deployment was also not significantly different from other groups ( $\chi_2^2 = 0.04$ ,  $p = 0.98$ ).

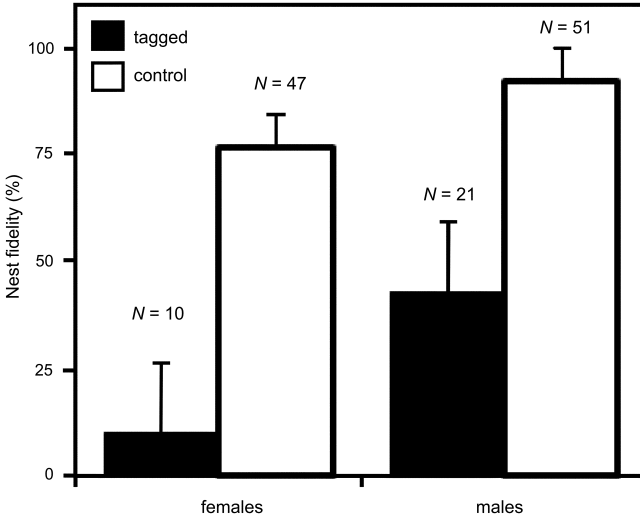
In evaluating chick quality, we found that in 2011 there was no significant difference between mean mass (ANOVA:  $F_{2,71} = 1.39$ ,  $p = 0.243$ ), or wing length (ANOVA:  $F_{2,71} = 1.19$ ,  $p = 327$ ) of each age cohort of chicks, comparing control and tagged groups. In 2012 rates of growth for mass and wing chord were also not significantly different between control and tagged groups (ANCOVA (mass):  $F_{2,158} = 0.50$ ,  $p = 0.480$ , (wing):  $F_{2,161} = 0.208$ ,  $p = 0.650$ ). However, we did determine that slope intercepts were significantly different for mass and wing length between tagged and control groups in 2012 (mass:  $F_{1,159} = 23.04$ ,  $p < 0.0001$ , wing:  $F_{1,162} = 16.84$ ,  $p < 0.0001$ , Figure 1). Additionally, significant difference in fledgling mass (Welches  $t$ -test:  $t = -2.27$ ,  $df = 28.9$ ,  $p = 0.031$ ), but not wing length, (Welches  $t$ -test:  $t = -0.62$ ,  $df = 30$ ,  $p = 0.538$ ) was detected. Mass of chicks in the tagged group ( $213.8 + 7.6$  g,  $N = 17$ ), was lower than chicks in the control group ( $242.2 + 7.8$  g,  $N = 16$ ).

### 3.1.2. Nest site fidelity and body condition

Of the 31 geocator tags deployed in crevices in 2011, 10 were recovered in 2012 (32% recovery). All tags were recovered from their original crevice, with the exception of one individual recaptured near a neighbouring crevice, and all tags detected visually were recovered. Control data of nest fidelity in untagged birds, compiled from 1993–2000, revealed no effect of year ( $\chi_5^2 = 5.31$ ,  $p = 0.379$ ), allowing us to make between-year comparisons. We did detect a significant effect of sex on probability of untagged individuals returning between years ( $\chi_5^2 = 4.57$ ,  $p = 0.033$ ) with males showing 16% greater nest site fidelity compared to females. Treating sexes independently, return rate in tagged males (43%,  $N = 21$ ) was significantly lower than in untagged males (92%,  $N = 51$ ; Fisher's Exact,  $p < 0.0001$ ). Return rate in females was significantly reduced from 76% ( $N = 47$ ) in the untagged group, to 10% ( $N = 10$ ) in the tagged group (Fisher's Exact,  $p < 0.0001$ ; Figure 2). Additionally, there was no significant difference in nest fidelity between tagged males and females (Fisher's Exact,  $p = 0.106$ ).



**Figure 1.** Reduced mass (a) and wing length (b) in chicks measured from tagged group (provisioned by one parent carrying geolocator tag) compared to control group (provisioned by parents, neither carrying geolocator tag). While the rate of growth between tagged and control groups are not significantly different, the intercept is significantly different. The grey area delimits the 95% confidence intervals.



**Figure 2.** Reduced nest fidelity in tagged group (2011–2012), observed both in males and females, as compared to control group (long-term dataset, 1993–2000).

Upon recapture of tagged individuals, no physical evidence of tag damage was observed and no significant difference in body condition of tagged individual biometric measurements between 2011 and 2012 was detected ( $p > 0.05$ ). In testing for differences in body condition between returning and non-returning tagged individuals from 2011–2012, we found returning individuals had slightly greater body size (mass, tarsus, wing, bill depth, culmen, rectal plate) and ornament size (crest length, average auricular plume length), however for all biometric parameters, this difference was not significant ( $p > 0.05$ ).

### 3.2. Experiment 2: device effects on crested auklets captured on the colony surface

#### 3.2.1. Surface activity

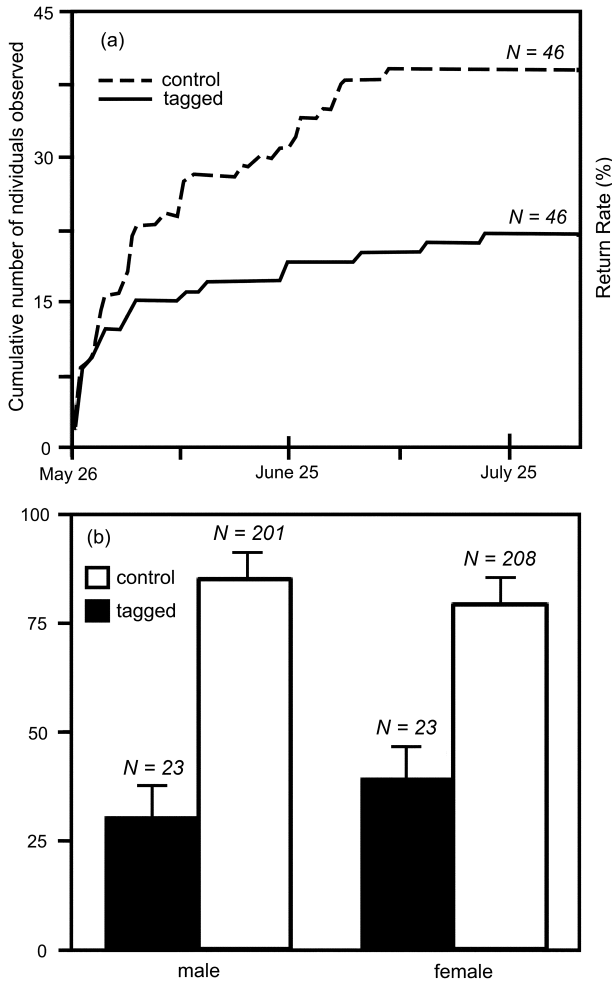
Surface activity throughout the breeding season (based on daily resight frequency) of individuals banded and resighted in 2011 was significantly reduced in tagged individuals ( $0.107 \pm 0.090$  daily resights/individual) compared to control individuals ( $0.188 \pm 0.149$  daily resights/individual; Wilcoxon signed-rank test:  $V = 81$ ,  $N = 35$ ,  $p = 0.0001$ ), particularly after mean hatch (June 28  $\pm$  7.7 days; Wilcoxon signed-rank test:  $V = 51$ ,  $N = 35$ ,  $p = 0.003$ ). Similarly throughout the breeding season in 2012, surface activity of individuals banded in 2011 was also significantly reduced

in the tagged group ( $0.078 + 0.052$  daily resights/individual) compared to control ( $0.173 + 0.133$  daily resights/individual; Wilcoxon signed-rank test:  $V = 319$ ,  $N = 77$ ,  $p < 0.0001$ ). However, prior to mean hatch date (June 29 + 5.5 days), there was no difference in surface activity of returning birds (Wilcoxon signed-rank test:  $V = 232$ ,  $N = 33$ ,  $p = 0.391$ ). Only after mean hatch was a distinct divergence of surface activity detected, with far more daily re-sightings of individuals from the control group ( $0.248 + 0.147$  daily resights/individual) compared to tagged individuals ( $0.081 + 0.060$  daily resights/individual; Wilcoxon signed-rank test:  $V = 9$ ,  $N = 67$ ,  $p = 0.0004$ , Figure 3).

### 3.2.2. Likelihood of return and provisioning behaviour

In 2011, there was a significant difference between tagged and control birds returning to the surface of the colony within the same year of tag deployment: 85% of control individuals ( $N = 46$ ) were seen again, while only 56% of tagged individuals ( $N = 46$ ) were seen again (Fisher's Exact,  $p = 0.010$ ), with no difference between sexes ( $G_1^2 = 3.0$ ,  $p = 0.080$ ). In 2012, the proportion of returning individuals the year after tag deployment was again significantly greater in the control group (87%,  $N = 46$ ), compared to the tagged group (46%,  $N = 46$ , Fisher's Exact = 0.0001). Additionally, the proportion of individuals observed to exhibit chick provisioning behaviour in 2012 was much greater in the control group (82%,  $N = 39$ ) than in the tagged group (36%,  $N = 22$ ;  $\chi_2^2 = 11.1$ ,  $p = 0.001$ ). We also found that there was no linear relationship between return rate in 2012 and relative tag mass (0.99–1.4% body mass) for each individuals ( $F_{1,19} = 0.366$ ,  $p = 0.55$ ).

Incorporating archival data of breeding individuals banded and colour-marked (1993–2011), 81% ( $N = 365$ ) of individuals were seen the year following banding, with no effect of year on return likelihood ( $\chi_5^2 = 5.3$ ,  $p = 0.379$ ). Sex-specific effects were detected however, with males 9% more likely to return between years than females ( $\chi_1^2 = 4.16$ ,  $p = 0.041$ ). Treating sex separately and pooling archival control data with our 2012 control data, the proportion of males tagged with geolocators in 2011 and seen again in 2012 (30%,  $N = 23$ ) was significantly lower than the 85% ( $N = 201$ ) of returning males in our pooled control dataset (1993–2012; Fisher's Exact,  $p < 0.0001$ ). The proportion of tagged females returning between years (39%,  $N = 23$ ) was also significantly lower than the 79% ( $N = 208$ ) of returning females from our long term dataset (1993–2012; Fisher's Exact,  $p = 0.0002$ ).



**Figure 3.** (a) Decreased cumulative number of geolocator-tagged individuals compared to un-tagged, control group, identified from daily plot observation throughout the breeding season, one year following tag deployment. (b) Reduced return rate of tagged individuals one year following deployment in both males and females compared to pooled control group from archival return data (1993–2012).

### 3.2.3. Anecdotal observation

No birds were observed with any leg injuries attributable to LAT 2900 archival geolocator tag or dummy tag attachment. Birds carrying tarsus-mounted geolocator or dummy tags appeared to locomote normally.

#### **4. Discussion**

The fundamental limitation on behavioural biology is that while attempting to describe or measure any natural behavioural activity, an observer effect is always present (Wilson et al., 1986; Wilson & McMahon, 2006). Animal tracking studies impose added stress on tagged individuals outside of natural conditions, inflicted not only by the device itself, but also by associated handling and attachment procedures (Murray & Fuller, 2000; Casper, 2009). Carefully designed experiments that monitor and control for tag effect are critical in maintaining animal welfare and in improving validity of sound migration research (Wilson & McMahon, 2006). However, with the rapidly increasing number of animal tracking studies conducted in recent years, the number of corresponding device effect studies has not increased similarly (Vandenabeele et al., 2011). Strict standards upheld in all other scientific fields to ensure biological merit through structured experimental design seem to have been dissolved in the thrill of this booming, new technology, at least when applied to marine birds (Ropert-Coudert & Wilson, 2005).

Previous to recent miniaturization of tracking devices, most alcid birds have been too small to be tracked, and documented as being particularly vulnerable to adverse effects due to high metabolic rate necessary to sustain energetically expensive flapping flight and diving behaviour (Ackerman et al., 2004; Burger & Shaffer, 2008). Our study indicates that while some aspects of crested auklet reproductive performance appeared to be unaffected by geolocator tags, fundamental aspects of their behavioural activity at the surface of the colony and their at-sea survival have been critically changed. Our intensive, two year study thoroughly examined these effects using a well-designed experiment, with sufficient sample size and appropriate controls to make effective inferences from our results. An important consideration to make is the potential for handling effects experienced by individuals during the attachment procedure. In experiment 2, handling effects and the effects of carrying the device were clearly differentiated by handling all individuals (including attachment of leg bands) in both the control and experimental groups. In experiment 1, due to limitations in the availability of accessible breeding sites for capturing birds, these effects were not differentiated, making inferences on device effect alone very challenging (the 'control' sample were not handled). While handling was likely to induce stress on individuals during the attachment procedure, we believed this effect would be immediate and would not carry over into the long-term effects of interest in our study.

Furthermore, in all cases, the capture and tag attachment did not result in breeding site abandonment, suggesting that the procedure itself might not inflict significant longer-term disturbance.

#### *4.1. Reproductive performance*

The degree in which chicks are provisioned by their parents has important implications for chick growth, fledgling mass and fledging success, providing valuable predictors of the chick's subsequent survival to recruitment (Williams & Croxall, 1990; Golet et al., 2000; Whidden et al., 2007; Adams et al., 2009). In a monogamous seabird that exhibits shared provisioning of a single offspring (Fraser et al., 2002), the quality of the chick reflects the combined ability of both adults to sufficiently provide for their offspring (Golet et al., 2000). Provisioning is very energetically costly for heavy wing-loaded crested auklet, requiring parents to travel from the breeding site (50–110 km; Hunt et al., 1993), locate at-sea prey aggregations, engage in underwater pursuit foraging, and return back to the nest site carrying a large food load. We would then expect that in a long-lived seabird, with a life-history strategy favouring long-term preservation of the individual over that of a single reproductive season (Navarro & González-Solís, 2007), increased stress induced by carrying a tracking device, would be reflected in reduced fledging success or poor chick quality. However, in experiment 1, fledging success and rate of chick growth (mass and wing) were not significantly affected. We did, however detect a slight, but significant reduction of chick mass at fledging age in the tagged group. As the chick develops and increases in size it requires increased provisioning efforts by the parents to sustain them, posing even greater stress to an already encumbered tagged parent. While the body condition of fledging chicks was marginally reduced in our tagged group, sufficient provisioning allowed for equally successful fledging rates of chicks in both control and tagged birds.

#### *4.2. Mate compensatory behaviour*

The most likely explanation for the observed behavioural effects of tracking devices on crested auklets was mate compensation. This behaviour, observed in other mid-sized alcids, occurs when the untagged individual in the pair compensates for reduced parental quality of their mate (Hamel et al., 2004; Paredes et al., 2005). In a long-lived seabird, maintaining a long-term monogamous relationship is beneficial in synchronizing parental activities,



and minimizing energy allocated for courtship and mating activity (Paredes et al., 2005). It is therefore advantageous to engage in compensatory behaviour in order to benefit from increased lifetime reproductive success. As seen in thick-billed murres, the untagged mate increased parental investment above its normal limits to cover for the mate's deficiency, and successfully reared the single chick to fledging age (18 days; Paredes et al., 2005). Similarly, in a study of common murres equipped with subcutaneous radio transmitters (<1%), reduced provisioning rates were detected in tagged individuals, that made fewer and lengthier foraging trips, but reproductive success was unaffected (Hamel et al., 2004). This indicates a level of flexibility in time-budgeting and foraging roles, allowing individuals to survive in an unpredictable, variable environment (Hamel et al., 2004; Paredes et al., 2005). In a good year for food resources, when prey is more readily available, this behavioural flexibility may accommodate tag effect (Hamel et al., 2004), without having detrimental reproductive consequences. However, negative effects on breeding success may emerge in poor food years, when increased effort by the untagged mate to ensure adequate nestling provisioning can no longer be sustained (Abraham & Sydeman, 2004).

These findings are somewhat inconsistent with other tag effect studies on ecologically similar auks that appear to be unable to engage in compensatory behaviour at the cost of their young. In a study of cassin's auklets (*Ptychoramphus aleuticus*) effects of subcutaneous radio transmitters (<2%) were detected in reduced chick growth, also impacting fledging success, and clutch size of offspring in tagged individuals (Ackerman et al., 2004). Detrimental effects on breeding success were observed in tufted puffins (*Fratercula cirrhata*), equipped with radio transmitters (<1.2% body mass) (Whidden et al., 2007), common (*Uria aalge*) and thick-billed murres (*U. lomvia*) fitted with satellite transmitters (Meyers et al., 1998) and common murres and razorbills (*Alca torda*) fitted with radio transmitters (Wanless et al., 1989).

#### 4.3. Nest site fidelity

Nest site fidelity, measured one year after device deployment in, was greatly reduced in tagged individuals. This failure of tagged individuals to return to previously occupied nest sites between years is likely a result of mate death or divorce, conspecific nest site competition, predation during the breeding season, or over-winter mortality. Divorce in a monogamous seabird engaged

in bi-parental care is much more likely to occur if there is a reproductive failure or if one pair member shows poor quality as a parent (Paredes et al., 2005). Increased stress on tagged individuals may also reduce their ability to defend good quality nest sites, or increase susceptibility to predation (Wilson & McMahon, 2006; Whidden et al., 2007; Rodriguez et al., 2009). In crested auklets, predation at sea is thought to be marginal, however, during the breeding season glaucous-winged gulls (*Larus glaucescens*), bald eagles (*Haliaeetus leucocephalus*) and peregrine falcons (*Falco peregrinus*) can present significant threat to their survival (Knutson & Byrd, 1982) and may take advantage of reduced flight maneuverability or speed of load-carrying individuals (Aldridge & Brigham, 1988). An increased prevalence of divorce, crevice loss or predation during the breeding season in tagged individuals would partially explain the observed decrease in nest site fidelity, caused by reduced parental quality, and decreased ability to avoid predation. However, our results show that not only do fewer tagged individuals return to the same crevice, but the number of individuals returning to the colony surface is also greatly reduced, suggesting that the effects of carrying a tag for a long period of time likely impacts over-winter survival the most. Sex-related differences in nest-site fidelity are evident in untagged crested auklets, as males are more likely to retain crevices in the case of divorce (Fraser et al., 2004), which would explain the low nest-site fidelity observed in tagged females compared to tagged males.

#### 4.4. Return rates

The mechanism responsible for low return rates to the colony in tagged individuals between years is not entirely clear; however, in an alcid, adapted to underwater pursuit-diving and poorly adapted to long distance flight, one would presume that additional mass, aerodynamic and hydrodynamic drag would have compounding effects on migration and foraging ability (Wanless et al., 1989; Hamel et al., 2004). Reduced swimming and foraging efficiency caused by increased drag of tags has been recorded in a variety of marine wildlife, including chinstrap (*Pygoscelis Antarctica*), Adélie (*P. adeliae*), (Croll et al., 1991; Ballard et al., 2001) and African penguins (*Spheniscus demersus*), Atlantic salmon (*Salmo salar*) smolts, rainbow trout (*Salmo gairdneri*) and white perch (*Morone Americana*) (Mellas & Haynes, 1985), green (*Chelonia mydas*) and leatherback (*Dermochelys coriacea*) sea turtles (Watson & Granger, 1998; Fossette et al., 2008) and Antarctic fur seals (*Callorhinus ursinus*) (Walker & Boveng, 1995). In a study assessing the effect

of increased drag and buoyancy on the diving behaviour of thick-billed murres, significant reduction in dive depth and duration was detected (Elliott et al., 2007). Long-term effects of attached devices on nutritional condition of deep-diving alcids was well shown in murres, where corticosterone levels were significantly elevated and body mass was reduced in tagged individuals a year following geolocator deployment (Elliott et al., 2012). Between-year return rate in murres was however not impacted, suggesting that nutritional stress was not pronounced enough to translate to increased mortality, likely due to the very low mass of attached loggers (0.3–0.5% body mass). Increased aerodynamic drag caused by tags has led to reduced flight ranges in a number of long distance migrating birds (Phillips et al., 2003; Bowlin et al., 2010; Vandenamee et al., 2012), which may also translate to dramatic overwinter effects in highly mobile species. Most recently, a study investigating the effects of drag on migration in individuals carrying externally-mounted loggers documented significant reduced bird migration range and decreased energy reserves following migration (Pennycuik et al., 2012).

Locating and accessing available prey items, and avoiding severe weather conditions is paramount to overwinter survival in seabirds (Byrd et al., 2005; Renner et al., 2008). In a species already limited by poor flight efficiency, highly productive wintering areas that tend to be patchily distributed may be too dispersed for individuals carrying additional mass to travel (Jessopp et al., 2013). Impacts of severe winter storms may be much more devastating in individuals already stressed by carrying additional mass and experiencing greater drag as well. This has particular implications in a changing oceanic climate with increasing environmental variability causing yearly fluctuations in prey availability and distribution, and increased prevalence of storm events (Schumacher & Kruse, 2005). Reduced swimming and flight efficiency associated with carrying a tag engenders high energetic costs over time, likely responsible for the steep drop in return rates detected in tagged crested auklets (Figure 3). With such severe device impacts on overwinter survival, it was surprising that chick quality and fledgling success during the breeding season were little affected; however this phenomenon can be explained by mate compensatory behaviour.

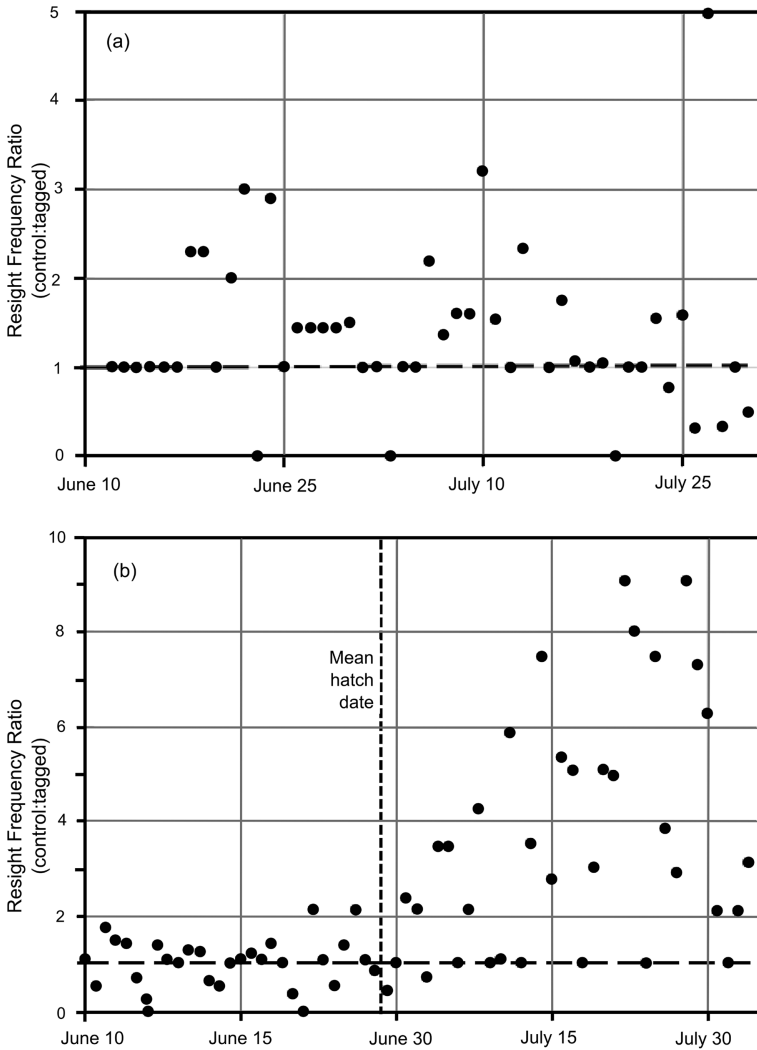
#### 4.5. *Activity at the colony site surface*

In a highly social and ornamented bird, daily aggregation at the colony is a fundamental component of crested auklet behaviour, important in

courtship activity, establishment of social hierarchies, and habitat familiarization (Jones & Hunter, 1999; Hagelin et al., 2003). Significant reduction of daily activity in tagged individuals at the colony therefore suggests a biologically significant impact on social and breeding behaviour. Tagged individuals had the greatest reduction of surface activity after mean hatch date during the chick provisioning period (Figure 4). This decrease is likely due to reduced frequency of chick provisioning, extended duration of foraging trips and increased foraging range of tagged individuals, as seen in penguins and shearwaters (Wilson et al., 1986; Ballard et al., 2001; Navarro & González-Solís, 2007; Passos et al., 2010). These effects were not only observed in the same year of device attachment, but also in the following year. This suggests that tagged individuals are not quickly adapting to the presence of the tag as documented with Cory's Shearwaters (Iguar et al., 2004), and even after carrying the device for a year, individuals were clearly experiencing long-term effects, as seen in King Penguins (Le Maho et al., 2011). This is likely explained by differences in foraging guilds, as both penguins and alcids rely on underwater pursuit diving strategies, compared to surface feeding shearwaters that have high flight efficiency.

#### *4.6. Implications for future tracking research*

In a species of pursuit diving seabird that have heavy wing-loading, we believe the effect of the geolocators was likely derived primarily from increased drag, both in air and water, resulting in data that may not reflect normal behaviour. Our results demonstrate that individuals carrying tags had reduced chick mass, reduced activity on the colony surface, reduced nest site fidelity and lower return rates. We suspect that these observed effects were the result of decreased foraging and flight efficiency at sea, subsequently increasing nutritional stress ultimately translating to a failure to breed the following year or more likely, increased at-sea mortality. The very high activity level typical of crested auklets compared to other auklet species (e.g., their lengthy flight displays above the breeding site, their observed travel in fast flying flocks to and from presumably distant foraging locations from the colony during the breeding season) also suggests to us that crested auklets might be more vulnerable to tag effects. The potential for unbalance, due to altered centre of gravity caused by the attachment of the tag to the left leg only, with no mass on the opposite leg, may have also impacted flight maneuverability and efficiency. However, flying crested auklets were apparently able to partly control



**Figure 4.** Daily resight frequency ratio of control group (birds not carrying geolocators) to tagged group (birds carrying geolocator tags) from observation plot on the surface of the colony (a) within banding year (2011), showing most resights occurring in control group (ratio > 1); and (b) year following banding (2012), showing most resights occurring in control group (ratio > 1) after mean hatch date.

for this by shifting the tagged leg to a position close to the centerline of their body, and abnormal locomotion on the colony surface was not observed in tagged individuals.

Based upon these inferences from return rates and behavioural observations at the breeding colony, we can speculate on how tracking devices alter the behaviour of individuals at sea, but we have not measured it directly. To accurately determine the biological relevance of migration data collected from tagged individuals, we need to know the observer effects of tracking devices on the behavioural measures we are trying to obtain (i.e., movement patterns, seasonal distribution) rather than just the effects as far as we can measure it at breeding sites. Additionally, designing experiments to quantify at-sea device effects by controlling for mass and drag could provide useful insights on the flexibility of migration strategies in seabirds. Under a changing climate, evidence has shown that migratory behaviour may be significantly affected, altering routes, destinations and movement phenology (Jenni & Kéry, 2003; Frederiksen et al., 2004; Marra et al., 2004; Dias et al., 2011). Migratory plasticity, illustrating the degree at which species can adapt sufficiently in a changing environment, has only been studied in a few marine vertebrates (sharks, turtles, whales and seabirds), but would have important applications for wildlife management and conservation efforts for seabirds living in a variable environment (Burger & Shaffer, 2008).

Currently, many studies measuring animal movement continue to push limitations of the ethical and meaningful use of tracking devices. Hard and fast rules, maintaining 3–5% tag mass threshold, and 1% tag cross-sectional area threshold for device attachment (Vandenabeele et al., 2012) are highly problematic because they do not recognize species-specific responses to tagging associated with differences in behaviour, ecology, physiology, and sensitivity to disturbance and environmental variability (Adams et al., 2009; Casper, 2009; Bridge et al., 2013). The 3–5% body mass rule, acknowledged and adopted by most seabird studies, focuses exclusively on the effect of additional mass, ignoring potential consequences of decreased camouflage and more notably, increased drag that affects flight speed and maneuverability, underwater mobility, and foraging efficiency (Caccamise & Hedin, 1985; McMahon et al., 2008; Bowlin et al., 2010; Vandenabeele et al., 2012). Although efforts are being made to quantify tag effects impacting seabirds, this necessary component to tracking research is critically lacking in tracking fish (Mellas & Haynes, 1985; Thorstad et al., 2000), sea turtles (Watson & Granger, 1998) and marine mammals (Walker & Boveng, 1995). An additional limitation on our understanding of device effect on animal behaviour is caused by the competitive nature of scientific publication, with lowered

likelihood of studies publishing results that detect no effect (Barron et al., 2010). However, monitoring and controlling for device effects is a necessary component of any wildlife tracking study that imposes a potential handicap to the natural movement and behaviour of individuals to ensure biological relevance and ethical practice in research. Lastly, the pressure to be the first to publish results on the migratory behaviour of an animal, particularly in species that are largely unknown, weighs heavily on researchers. Without rigorous limitations on wildlife tracking, researchers that do not wait for geolocator technology to catch up with tracking demands are awarded with top-tier publications, at the cost of poor data quality that lacks scientific and ethical merit.

Despite obvious challenges associated with gathering accurate tracking data from equipped individuals, this area of research is a rapidly developing field that has certainly made significant leaps in our understanding of migratory ecology and behaviour in a number of taxa. With continuous scrutiny of ethical and scientific practices, tracking studies have incredible potential to link the missing knowledge gaps in migratory biology and significantly improve conservation management strategies. Future wildlife tracking studies should therefore be conducted with caution, with strict consideration for species specific-responses to device attachment and adhering to optimal attachment procedures, timing and device location in order to best accommodate the behaviour and ecology of that species.

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