Tags below three percent of body mass increase nest abandonment by rhinoceros auklets, but handling impacts decline as breeding progresses

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ABSTRACT: Biologging has revealed many of the mysteries surrounding seabird behavior far from land. However, tagging seabirds with biologgers may influence the very traits they are designed to observe. Such 'tag effects' are often argued to be minimal below a threshold of 3 % of body mass. Nonetheless, few studies carefully separate handling from tagging effects, so the effect of tag size is often confounded with the effect of handling. Puffins, including rhinoceros auklets *Cerorhinca monocerata*, are notoriously difficult to work with due to high nest abandonment rates. To examine tagging and handling effects in rhinoceros auklets, we compared abandonment rates of individuals equipped with a GPS weighing ~2.3 % of body mass with abandonment rates of birds handled but not equipped, and of birds not handled at all (controls). We used the egg flotation technique to estimate egg development and predict hatching date, thus allowing treatments to be applied at the appropriate time. Handling more than doubled abandonment rates compared to control birds, and tagging more than doubled abandonment rates compared to birds that were handled but not tagged. Abandonment rates decreased as incubation progressed and were lowest during chick-rearing. We conclude that both handling and tagging of auklets increase abandonment, and that effects are lowest during chick-rearing.

KEY WORDS: Biologging devices · Experiment · Tracking · Desertion · Egg flotation · Reproduction · Rhinoceros puffin

1. INTRODUCTION

Biologging provides an opportunity to observe behavior that is 'unobservable' for remotely foraging species such as seabirds. A better understanding of marine ecosystem health through the use of predators foraging at higher trophic levels (e.g. seabirds) is one example of the benefits of biologging, and seabirds mostly nest in dense colonies on islands, making them easy to observe, capture and manipulate (Sydeman et al. 2001, Piatt et al. 2007, Wakefield et al. 2009, Hatch 2013). With tracking devices becom-

ing smaller and more advanced, data on seabird movement can be more easily obtained and can accelerate our understanding of marine ecosystems (e.g. Wilson et al. 2002, Wakefield et al. 2009). By combining knowledge of ocean conditions, breeding biology, and foraging behavior, we can discern overall ecosystem health (Lescroël et al. 2016, Brisson-Curadeau et al. 2017), monitor the human ecological footprint (Bodey et al. 2014), and make management decisions (Gaston et al. 2013).

Although seabirds are good indicators of marine ecosystems and can be exploited for biologging, the

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effects of attaching a device on a bird can negatively impact survival and reproductive output (Fraser et al. 1999, Vandenabeele et al. 2012, Bodey et al. 2018, Portugal & White 2018). In extreme cases, seabirds may die if carrying the device is too energetically costly or the attachment procedure causes too much stress (e.g. *Uria aalge*, *U. lomvia*, and *Fratercula cirrhata*, Hatch et al. 2000; *Stercorarius skua*, Thaxter et al. 2016). More commonly, deploying a transmitter will cause adults to abandon their breeding attempt or to return to the colony less frequently (*Pygoscelis antarctica*, Croll et al. 1996; *Puffinus griseus*, Söhle et al. 2000); reduced nest attendance can slow chick growth rates (*Ptychoramphus aleuticus*, Ackerman et al. 2004; *Calonectris borealis*, Villard et al. 2011). Even biologging devices that follow the 3% guideline (where the logger needs to be <3% of the bird's body weight; Wilson et al. 2002, Burger & Shaffer 2008) can still cause nest abandonment, lower feeding rates, and decreased reproductive success (Croll et al. 1996, Söhle et al. 2000). Although such 'tag effects' are widely reported, few studies carefully separate device effects from handling effects, so parameters influencing responses to handling and tagging often remain unknown (Elliott 2016).

Indeed, even handling alone has well-documented effects of research disturbance. Intensive handling can reduce foraging efficiency, decrease fledging success, and depress the mass of adult birds (e.g. rhinoceros auklets *Cerorhinca monocerata*, Kato et al. 2003). Parents often desert their eggs when frequent researcher visits are made, especially early in incubation (Götmark 1992, Rodway et al. 1996, Carey 2009). For example, around 88% of studies on alcids and larids have shown that research activities have a visible impact (Götmark 1992). A study by Blackmer et al. (2004) found nearly 91% of breeding failures in Leach's storm petrels *Oceanodroma leucorhoa* were attributable to nest desertion due to handling-related disturbance. Investigators can also cause reduced chick growth; undisturbed chicks have been found to be heavier and to have longer wings (*Aethia pusilla* and *A. cristatella*, Piatt et al. 1990). In some cases, chick survival may also be impacted. Research handling can decrease nest attendance, leaving the chick vulnerable to predation and harsh weather (*Rissa tridactyla*, Sandvik & Barrett 2001). In some studies, however, hatching success and chick growth were unaffected by different intensities of disturbance (*A. cristatella*, Fraser et al. 1999). Nonetheless, studying investigator disturbance can prove useful, as it can help develop techniques to minimize impact and reduce bias in results.

Rhinoceros auklets are generalist predators that dive up to 30 m to capture fish (Burger et al. 1993) and adjust their diet in response to prey availability (Davoren 2000, Carle et al. 2015). Prey availability can also be reflected in their reproductive success, where lack of prey reduces breeding success and can influence phenology (Watanuki et al. 2009), and therefore these birds are considered an indicator of fish stocks (Cunningham et al. 2018). To date, only a few studies have applied biologging techniques to study rhinoceros auklet behavior (Kato et al. 2003, Cunningham et al. 2018, Wilkinson et al. 2018). Auklets hold high potential to be used as an indicator species, but may be sensitive to biologging because pronounced tagging effects have been observed in other puffins (e.g. *F. cirrhata*, Whidden et al. 2007).

The objectives for this study were to (1) quantify and distinguish effects of handling and tagging on the breeding success of rhinoceros auklets, and (2) test whether handling and tagging effects differ across breeding stages. We used an experimental approach to quantify and distinguish the effects of adult manipulation (none, handling, tagging) and breeding stage (early incubation, late incubation, early chick-rearing). We expected that less intensive procedures would cause less abandonment, and that abandonment would decrease as the breeding season progressed.

2. MATERIALS AND METHODS

2.1. Study system

We studied rhinoceros auklets breeding on Middleton Island, Alaska (59.42° N, 146.32° W), sampling birds from 4 sub-colonies: Tower, Rhino Trail, Ship Trail, and Washwater (Fig. 1). During the breeding season, the auklets nest in burrows and have 2 distinct breeding stages: incubation and chick-rearing. Both parents incubate a single egg for 39–52 d (average: 46 d), where they alternate daytime burrow attendance with their mate. During chick-rearing, adults are almost never in the burrow, as the chicks are semi-precocial and can thermoregulate within 2 d of hatching. Instead, adults spend the day resting or foraging and only return to the colony at night to incubate or feed their chick with a 'bill load' (Davoren & Burger 1999).

To find active auklet burrows, we searched for signs of activity at the entrance (e.g. feathers, guano) during mid- to late May. We used a series of access holes to find the nest chamber. Once an egg was dis-

Fig. 1. Study area indicating rhinoceros auklet sub-colonies sampled. Coordinates are decimal degrees

covered, usually attended by a bird, we estimated egg development by measuring the angle or height of the egg when placed in a container of water (see Section 2.2). We then closed access holes and labeled the access hole nearest to the nest chamber with an orange rock so that the burrow could be monitored for the rest of the breeding season.

2.2. Egg flotation

To estimate egg development, we used the egg flotation method, which is known to be a reliable predictor of hatching date (Liebezeit et al. 2007). As the egg develops, the air pocket inside the egg grows larger, affecting its position inside a container of water (Fig. 2). Near the beginning of development, the egg is heavy, and sits almost horizontally at the bottom of the container. It then slowly tilts up until it reaches 90°. Subsequent development increases the buoyancy of the egg, causing it to float at a 90° angle. At that point, the angle no longer changes but the egg becomes increasingly buoyant, so the height the egg is floating above the water must be measured (thus requiring 2 different measurements). By taking these measurements, we were able to estimate laying date and apply treatment groups appropriately (outlined in Section 2.3).

2.3. Adult manipulations

To test the effects of handling and tagging on rhinoceros auklets, we used 3 levels of manipulation intensity: LOW (no handling control), MODERATE

(minimal handling), and HIGH (GPS deployment).

LOW (no handling control): we monitored the burrow for hatching phenology by checking the contents of the nest chamber every 5 d, starting May 31 and ending when the egg hatched. At each visit, we noted whether an adult was present in the nest chamber as well as the temperature of the egg (warm, cold). If the adult bird was present it was occasionally touched, but never captured or manipulated.

MODERATE (minimal handling): this procedure mirrored the 'no handling control' treatment, except we also pulled an adult bird out of the burrow. Once removed from the burrow, we

weighed, banded, bled the bird by clipping its toenail and collected a small blood sample with a capillary tube (25–50 μ l), and measured horn length, bill depth, culmen, and headbill. All captures took place during daytime.

HIGH (GPS deployment): this procedure mirrored the 'minimal handling' treatment, with the addition of logger attachment and retrieval; procedures were split between the two captures to make the initial handling time similar to the MODERATE treatment (details in Section 2.4). All deployments took place during daytime; early chick-rearing recaptures took place at night (see Section 2.4).

Fig. 2. Angles (for eggs that sank) and heights above water (for eggs that floated) in relation to the number of days incubated by rhinoceros auklets

We assigned 151 burrows to the 3 groups using a random number generator. In total, 60 burrows were assigned for burrow monitoring (LOW), in accordance with existing long-term productivity monitoring protocols at the field site. The remaining burrows were then divided into the other 2 treatments (MODERATE and HIGH). To avoid spatial pseudoreplication, each manipulation intensity treatment included birds from $\frac{3}{4}$ of the sub-colonies. The application of treatments coincided with 3 breeding stages (early incubation: $n = 20$ MODERATE, $n = 0$ HIGH; late incubation: $n = 15$ MODERATE, $n = 30$ HIGH; early chick-rearing: $n = 11$ MODERATE, $n = 15$ HIGH; Table 1); timing was determined by egg flotation (described previously; Fig. 2). We recorded the number of times each burrow was visited before the MODERATE or HIGH treatments, where we counted all visits (including date first accessed) before handling date (date handled was excluded). We measured handling duration for MODERATE and HIGH treatment groups as the time elapsed between capture from the burrow and release after manipulation (at GPS deployment for HIGH).

To maximize chances of finding an adult and a chick in the burrow during early chick-rearing, we checked burrows allocated to MODERATE and HIGH manipulation intensity treatments in early chick-rearing every 2–3 d preceding the anticipated hatch date, because the adult is only in the burrow during the day within the first 2–3 d of hatching. Some birds ($n = 13$) abandoned their nest before a manipulation was applied, and thus were excluded from this investigation.

2.4. GPS deployment and retrieval

We deployed GPS devices (Catlog Gen 2; 12.1 ± 0.3 g) on auklets (body mass: 527.9 ± 6.3 g) during late incubation and early chick-rearing. We deployed a total of 45 devices (incubation: $n = 30$; chick-rearing: $n = 15$). GPS devices were packaged in clear heat-shrink tubing to waterproof, making them $\sim 2.3\%$ of the bird's body mass.

Table 1. Sample sizes for manipulation intensities and breeding stages of rhinoceros auklets on Middleton Island, Alaska. The LOW intensity was a decreasing subset of 60 burrows designated as controls

Manipulation intensity	Early incubation	Late incubation	Early chick-rearing
LOW	60	52	35
MODERATE	20	15	11
HIGH	0	22	15

The handling procedure differed slightly than minimally handled birds, as manipulations were split between deployment and retrieval to minimize initial handling duration. Upon deployment, we weighed the bird, took a small blood sample by clipping the toenail, banded the bird, and attached a GPS device. We attached the device to the back feathers, 1–2 cm above the preen gland, using superglue, tesa marine adhesive tape, and cable ties.

Retrieval attempts began 4 d after deployment, and took place during the day for incubation and at night for chick-rearing (as adults do not attend to chicks during the day). During chick-rearing, we checked the burrow for the targeted bird 3 or 4 times per night, starting 1 h after sunset, until the logger was retrieved. Upon recapture, we removed the device and measured weight and morphometrics (horn length, bill depth, culmen, headbill). Average length of deployment was 4.4 ± 0.3 d.

2.5. Breeding success and abandonment

To evaluate handling effects on breeding success in auklets, we monitored burrows for nest abandonment (yes/no) after each treatment. Due to the nature of the experiment, the definitions for abandonment differed slightly between treatments, but followed a threshold of 15 d because we observed that most burrows were abandoned 7 d after manipulation (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m643p173_supp.pdf; mean: 9.2 ± 1.1 d, excluding 1 outlier that abandoned 31 d after manipulation).

The specific definitions are as follows: LOW (no handling control): since no manipulation took place, abandonment was determined in the following way to ensure a fair comparison with manipulated treatments. All LOW treatment burrows ($n = 60$) were included in early incubation comparisons and considered abandoned if abandonment occurred within 15 d of first access (early May). In late incubation, only burrows active when regular burrow checks began (beginning of June) were included and considered abandoned if abandonment occurred within 15 d of the first burrow check. In early chick-rearing, we only included burrows in which a chick had hatched, and considered it abandoned if abandonment occurred within 15 d of hatching (mid to late June). MODERATE and HIGH treatments: abandonment was defined as desertion within 15 d of treatment application (i.e. an egg not incubated for 15 d [cold] or a dead chick).

2.6. Estimates of lay and hatch dates

We estimated laying date for each burrow using 2 methods. If a chick successfully hatched, we estimated hatch and laying dates using the following equations:

$$\text{Hatch date} = (\text{date first seen as chick} - \text{date last seen as egg})/2 \quad (1)$$

$$\text{Laying date} = (\text{est. hatch date}) - [46 \text{ d} (\text{avg. incubation period})] \quad (2)$$

If an egg did not hatch, we used egg float angle/height to estimate the number of days incubated (DI), because DI was a strong predictor of the angle tilted (Eq. 3: $R^2 = 0.85$, $F_{1,52} = 6.1$, $p < 0.05$) and height floated (Eq. 4: $R^2 = 0.70$, $F_{1,38} = 87.2$, $p < 0.001$) among the sample of eggs for which hatching dates were eventually determined. The equations are as follows (see Table S1): for the egg angle (in °) in response to DI (for eggs that sank):

$$\text{Angle} = \text{DI}^2 \times -0.08 (\pm 0.03 \text{ SE}) + \text{DI} \times 5.31 (\pm 0.80 \text{ SE}) + 10.57 \quad (3)$$

For egg height (in mm) in response to DI (for eggs that floated):

$$\text{Height} = \text{DI} \times 0.34 (\pm 0.04 \text{ SE}) - 5.32 \quad (4)$$

Once the DI for the date that the egg was measured was determined, we could then back-calculate lay date:

$$\text{Estimated laying date} = (\text{date of egg flotation test}) - (\text{est. DI}) \quad (5)$$

2.7. Statistical analyses

All statistical analyses were performed in R v.3.5.1 (R Core Team 2019). All models were binomial generalised linear models (GLMs) using a chi-squared significance test, unless otherwise stated. When interactive effects were non-significant, we removed the interaction term and tested for main effects. We compared body mass at deployment to body mass at retrieval with a paired *t*-test.

2.7.1. Effects of laying date and date first accessed on breeding success

We modeled hatching success (0/1) and fledging success (0/1), in response to laying date and date first accessed within the control group of burrows ($n = 60$). We did not include the number of visits as a pre-

dicator because we checked the burrow every 5 d for this group, which standardized visits to the burrow.

2.7.2. Effects of breeding stage on abandonment

We tested for effects of breeding stage on abandonment among LOW and MODERATE groups, excluding the HIGH group because no birds received HIGH treatment in early incubation. We modeled abandonment (0/1) in response to breeding stage, manipulation intensity, and a 2-way interaction.

2.7.3. Effects of handling and tagging on abandonment

We extracted 75 birds from the burrow for either MODERATE or HIGH manipulation treatments during late incubation and early chick-rearing. We tested for effects of manipulation intensity (MODERATE/HIGH), breeding stage, handling duration, and an interactive effect between manipulation intensity and breeding stage on abandonment. We did not include number of visits to the burrow prior to handling, because this correlated with breeding stage but not manipulation treatment (Fig. S2). We modeled handling duration in response to breeding stage and manipulation intensity (linear model; Type II ANOVA). We compared abandonment of MODERATE and HIGH twice: (1) using abandonment among HIGH burrows post-deployment, then (2) including total HIGH abandonment (including both post-deployment and post-retrieval abandonment).

3. RESULTS

Abandonment increased with manipulation intensity and decreased as the breeding season progressed (Fig. 3).

3.1. Effects of laying date and date first accessed on breeding success

Among control (LOW burrows, we found no significant effect of laying date (0.01 ± 0.05 , deviance = 0.11, $df = 1$, $p = 0.74$) or date first accessed (-0.06 ± 0.06 , deviance = 0.83, $df = 1$, $p = 0.36$) on hatching success. Only 1 out of 36 chicks that hatched died before fledging, thus we observed no significant effect of laying date (0.03 ± 0.05 , deviance =

Fig. 3. Probability of rhinoceros auklet nest abandonment across breeding stages and manipulation intensities ($n = 151$)

0.38, $df = 1$, $p = 0.54$) or date first accessed (-0.06 ± 0.06 , deviance = 0.84, $df = 1$, $p = 0.36$) on fledging success.

3.2. Effects of breeding stage on abandonment

Among LOW and MODERATE treated burrows, we did not find a significant interaction between manipulation intensity and breeding stage (deviance = 1.0, $df = 2$, $p = 0.61$). We removed the interaction term and found that MODERATE treated burrows had significantly higher abandonment than control burrows (1.2 ± 0.4 , deviance = 7.4, $df = 1$, $p < 0.01$), and breeding stage significantly influenced abandonment (deviance = 6.0, $df = 2$, $p < 0.05$). Differences in abandonment across breeding stages were largely driven by early incubation–early chick rearing (1.7 ± 0.8 , $z = 2.1$, $p = 0.09$), rather than early incubation–late incubation (0.4 ± 0.5 , $z = 0.8$, $p =$

0.70) or late incubation–early chick rearing (1.3 ± 0.8 , $z = 1.6$, $p = 0.26$).

3.3. Effects of handling and tagging on abandonment

We obtained a complete set of measurements for 57 of 75 individuals handled during late incubation or early chick-rearing. Despite efforts to standardize manipulations throughout the experiment, handling duration was 4.5 ± 0.6 min longer for the HIGH treatment ($F_{1,60} = 48.8$, $p < 0.001$) and 2.0 ± 0.6 min shorter during early chick-rearing ($F_{1,60} = 10.3$, $p < 0.01$; Fig. S3).

Breeding stage and manipulation intensity did not interactively affect post-deployment abandonment (deviance = 0.1, $df = 1$, $p = 0.76$) or total abandonment (deviance = 0.2, $df = 1$, $p = 0.63$), so we removed the interaction term from both models and tested for main effects only. Manipulation intensity was the only significant predictor of both post-deployment and total abandonment, where birds that were handled but not tagged were less likely to abandon (Table 2). Breeding stage, handling duration, and laying date did not significantly influence abandonment (Table 2).

3.4. Additional tagging details

For the HIGH treatment, we retrieved a total of 28 of 45 devices (incubation: $n = 18/30$; chick-rearing: $n = 10/15$), meaning that 17 birds abandoned post-deployment (incubation: $n = 12$; chick-rearing: $n = 5$). However, we also noted that nest abandonment increased upon retrieval, as handling had to occur twice. As a result, a total of 27 birds abandoned from the experiment (incubation: $n = 18$; chick-rearing: $n = 9$). Table 3 shows abandonment rates after deployment and retrievals. On average, birds lost 17.3 g during the deployment ($t_{19} = 3.5$, $p < 0.01$).

Table 2. Parameter estimates for models of post-deployment and total abandonment of rhinoceros auklets among MODERATE and HIGH manipulation intensity groups during late incubation and early chick-rearing

Predictor	— Post-deployment abandonment —				— Total abandonment —			
	Estimate $\pm$ SE	Deviance	df	p-value	Estimate $\pm$ SE	Deviance	df	p-value
Intercept	5.0 ± 7.5	—	—	—	13.5 ± 8.5	—	—	—
Breeding stage: late incubation	0.5 ± 0.7	0.09	1	0.77	0.4 ± 0.7	0.009	1	0.92
Manipulation intensity: MODERATE	-2.2 ± 1.0	5.0	1	0.03	-3.7 ± 1.2	14.5	1	0.0001
Handling duration	-0.2 ± 0.1	1.7	1	0.19	-0.3 ± 0.2	3.5	1	0.06
Laying date	-0.03 ± 0.06	0.2	1	0.64	-0.08 ± 0.07	1.6	1	0.21

Table 3. Nest abandonment (%) of rhinoceros auklets upon GPS retrieval

	Late incubation n = 22	Early chick-rearing n = 15
Abandonment		
After deployment	36.4	33.3
After retrieval	22.7	26.7
Total	59.0	60.0
Retrieval success	63.6	67.7

4. DISCUSSION

We applied an experimental approach to distinguish the effects of handling and tagging on breeding success of rhinoceros auklets relative to unmanipulated controls. Consistent with predictions, nest abandonment increased with manipulation intensity but decreased with breeding stage. Natural abandonment declined as the breeding season progressed, possibly due to selective disappearance of low-quality parents (van de Pol & Verhulst 2006) and/or increased parental investment (Winkler 1987). Handling alone increased abandonment relative to controls, but abandonment declined in both groups as the breeding season progressed. Tagging during late incubation and early chick-rearing had a greater effect on abandonment than handling alone. Thus, both handling and tags that weighed <3% of body mass caused abandonment. Auklets were least likely to abandon in response to handling during early chick-rearing, indicating that manipulations should be delayed until chick-rearing when possible.

This experimental approach produced several data-driven recommendations for future biologging studies on rhinoceros auklets, many of which concur with existing recommendations (see Elliott 2016, Bodey et al. 2018). First, researchers should avoid handling and tagging early in the breeding season, if unnecessary to address the research question. Second, if manipulations must happen during incubation, we recommend late-incubation procedures and use of egg flotation to estimate phenology and reduce investigator disturbance at the nest site. Though the regression equations produced via egg flotation are specific to rhinoceros auklets, they may be applicable to other alcid species. Further, this technique could be broadly applied to other seabird species at coarser scales; for example, a binary response (sink vs. float) alone can be highly informative about embryo development (sink = less devel-

oped; float = more developed). Third, we recommend avoiding multiple handling events, for example by using GPS units that download remotely but detach after several days, obviating the need for recapture. Both the initial tagging and subsequent handling during GPS retrieval caused substantial abandonment. Considering that devices requiring only one handling event can still cause tagging effects, a device that does not detach after several days could therefore cause an equal or greater decrease in fitness. Fourth, we recommend using the smallest and lightest tag available to meet research needs. Devices <3% of body weight negatively impacted breeding success of rhinoceros auklets in this study, and devices may need to be <1% for negative effects to not be detected (Bodey et al. 2018). For example, we observed a decline in abandonment as the breeding season progressed despite using the same manipulation procedure; increased commitment to the breeding attempt, not decreased physiological effects of handling, is the most likely driver of this pattern. Smaller tags are less likely to cause tag effects and more likely to produce data that reflect natural behavior.

We examined the effects of manipulation on a single, sensitive species. The rhinoceros auklet is an auk species and a short-winged, wing-propelled diver; a review of tag effects in auks showed widespread impacts of devices 3% of body size, possibly because the high wing loading of this family means that they are particularly susceptible to increases in loading (Elliott et al. 2010, Vandenabeele et al. 2012). Responses to devices found in this study might be shared by other auk species and other species of different seabird families known to exhibit greater tagging effects (e.g. shearwaters; Söhle et al. 2000, Villard et al. 2011). However, a metaanalysis found little evidence for phylogenetic heritability of tag effects (Bodey et al. 2018), suggesting that tag effects are likely linked to species-specific morphology, behavior, and ecology. We used individuals that had never been captured in the burrow, but it is possible that continued researcher presence could habituate birds to human disturbance (Burger & Gochfeld 1999) or select for tolerant individuals. Although we found a decrease in abandonment as the breeding season progressed, we did not manipulate birds after early chick-rearing. It is possible that abandonment continues to decline throughout chick-rearing, but we did not include this breeding phase. An important factor to note is that, despite best efforts to standardize manipulations, the tagged birds experienced longer handling durations and burrows allocated

to later treatments experienced more researcher visits. Thus, we might be underestimating the effects of handling duration on abandonment and underestimating the decline in abandonment due to breeding stage. Finally, it is important to acknowledge that the small sample size per treatment group in this study may explain statistically non-significant effects (e.g. post hoc tests, handling duration). We emphasize that, despite these limitations, the experimental approach could be applied to improve manipulation and biologging practices in almost any seabird system.

This study raises a difficult question: do the conservation and knowledge benefits of a biologging study exceed the fitness costs to the study individuals? For marine health indicators that are sensitive to researcher disturbance, such as the rhinoceros auklet, what is good for understanding the population, species, seabird community, and regional ocean health is clearly costly to individual breeding success in the study year. However, long-term diet monitoring data from this population of rhinoceros auklet has produced valuable knowledge on greater ecosystem dynamics (e.g. Sydeman et al. 2017, Cunningham et al. 2018, Thompson et al. 2019); individual movement data provide necessary context to interpret these diet data. We suggest that when the conservation and knowledge benefits of a biologging study exceed the fitness costs to the study individuals, failure rates are acceptable, while acknowledging that the currencies involved may not be immediately comparable or easy to measure. In the context of this particular study, we believe that these findings will decrease future research-induced failure rates (reducing negative impacts on individuals and population) and increase data returns in future studies (increasing positive impacts on marine conservation and management).

In conclusion, we advocate a data-driven approach to reduce impacts of biologging on a given study species. We recommend incorporating experimental designs into biologging studies, such as the one used here, that allow for quantification of investigator effects—customized to the study system—that will improve future field methodology.

Acknowledgements. We thank Alyssa Piauwasdy, Luis Ramos, and Hannes Schraft for their assistance in the field. This work was supported by NSERC (A.S., S.W., K.H.E.), a Canada Research Chair in Arctic Ecology (K.H.E.), and the Institute for Seabird Research and Conservation (S.A.H.). Three anonymous reviewers provided feedback that greatly improved the quality of the manuscript.

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Editorial responsibility: Thierry Boulinier,
Montpellier, France

Submitted: October 17, 2019; Accepted: April 20, 2020
Proofs received from author(s): May 26, 2020