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EFFECTS OF GEOLOCATION TRACKING DEVICES ON BEHAVIOR, REPRODUCTIVE SUCCESS, AND RETURN RATE OF *AETHIA* AUKLETS: AN EVALUATION OF TAG MASS GUIDELINES

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ABSTRACT.—The use of tracking devices (tags) to investigate seabird movements and habitat use has grown rapidly over the last 30 years, but often tracking data are reported without assessment of the effects of tags. The extra mass and bulk may risk altering behavior, and effects likely vary depending on the size, anatomy, and foraging strategy of different species. A guideline that tags should not exceed 3% body mass is widely accepted by seabird researchers, but this guideline was developed for albatrosses and petrels. A review of tracking studies showed that alcids are more likely to be affected by tags than other groups. We found some evidence of a negative effect of tags on Parakeet Auklets' (*Aethia psittacula*; mean mass 266 g, tag 0.8–1.1% of body mass) reproductive success but not return rate or chick growth. Tagged Whiskered Auklets (*A. pygmaea*; mean mass 112 g, tag 1.8% of body mass) showed minor decreases in chick growth, and a 74% lower adult return rate during 2014–2015, despite no significant difference from control returns in 2013–2014. Our study demonstrated negative effects in alcids of tags well below the 3% guideline, confirming that limits for one group should not be uncritically applied to all seabirds. Mass of tags deployed should be kept to a minimum, but other factors (e.g., wing-loading, flight energetics, foraging strategy) may be equally important. To ensure the biological relevance of collected data, we strongly recommend that inclusion of tag effect experiments be considered essential in the design and approval of tracking studies. *Received 31 May 2016. Accepted 20 November 2016.*

Key words: geolocation, Parakeet Auklet, seabird, tag effects, tracking, Whiskered Auklet.

When designing studies to answer biological/ecological questions, scientists must keep in mind that their actions can change the characteristics or behaviors being measured (i.e., observer effects; Sykes 1978, Wilson and Vandenabeele 2012). There are also ethical considerations, and any negative effect (e.g., pain, stress, or mortality) on study subjects should be considered relative to the value of the data obtained (Vandenabeele et al. 2011, Animal Behaviour Society 2012). This issue has become increasingly relevant in seabird research as the use of tracking tags for studies of habitat use and migratory behavior has grown rapidly in the last 30 years (Vandenabeele et al. 2011). In particular, the development of light-weight and inexpensive archival geolocation tags (DeLong et al. 1992, Wakefield et al. 2009, Wilson and Vandenabeele 2012) is allowing deployment on smaller species and at higher sample sizes for more robust analyses. However, extra weight and/or drag of tracking devices (hereafter referred to as 'tags') may make it more difficult for birds to forage and energetically expensive to travel (Barron et al. 2010, Vandenabeele et al. 2012).

Many tracking studies include only a cursory investigation of tag effects, if any (review by Vandenabeele et al. 2011), making it difficult to evaluate the biological relevance of their results. Based on a review of effects on various species of albatrosses and petrels across 20 studies, Phillips et al. (2003) proposed a maximum guideline of ~3% body mass for tags, but it is unclear how well their recommendations apply to other groups of seabirds that rely more on diving for prey (e.g., auks/Alcidae and diving petrels/Pelecanoididae). For diving seabirds (foot-propelled or wing-propelled with feet extended for use as a rudder), any effect may be magnified by increased drag in the much denser sea water (relative to air) in which the birds forage. Streamlined wings adapted for propulsion underwater also lead to greater wing-loading and more energetically expensive flight (Pennycuick 1975, 1987), which could make those species more susceptible to effects from added mass (Elliott et al. 2014). Nevertheless, Phillips et al.'s (2003) review is commonly cited as a justification for tagging a wide range of species, often without any attempt to validate this guideline for the species in question (e.g., McKnight et al. 2013, Hennicke et al. 2015, Weimerskirch et al. 2015). Alternatively, many studies cite a lack of detrimental effects in previous research on their focal species or closely related taxa, but do not take into account temporal or geographic differences in local conditions that can have significant

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impact on the effects of tags, through changes in individual condition or parental investment (Pugesek and Diem 1990, Heggøy et al. 2015). A recent meta-analysis of tag effects in shorebird geolocation studies showed negative effects of devices above 1.5% body mass and high variation among breeding sites within species to suggest that local factors may be important (Weiser et al. 2016).

Aethia auklets are a group of small (80–300 g), planktivorous seabirds that breed in large numbers in the Bering Sea and Sea of Okhotsk. Their high breeding site fidelity (Zubakin and Zubakina 1994, Pyle et al. 2001) makes these species excellent candidates for the use of archival tags, although they may be less tolerant of extra weight and/or drag than other species because their wings are adapted for underwater pursuit-diving, and so flight is energetically expensive (Pennycuick 1987, Obrecht et al. 1988, Vandenabeele et al. 2012). Studies of small alcids have shown negative effects of tags $\leq$3% body mass (Ackerman et al. 2004, Whidden et al. 2007, Elliott et al. 2010), and previous work on Crested Auklets (*A. cristatella*, one of the most highly migratory members of the genus) showed strong effects of a tag weighing 1% of body mass on several aspects of reproduction and behavior (Robinson and Jones 2014). In this study, we investigated the effect of similar tags on the smaller, relatively sedentary Whiskered Auklet (*A. pygmaea*), and the larger, moderately migratory Parakeet Auklet (*A. psittacula*). The objectives of this study were (1) to measure the effects of tags on adult return rate and condition, reproductive success and chick growth rates, and (2) to evaluate the commonly accepted 3% guideline for tag mass in alcids in light of our data and a review of the literature. If there was a significant impact of tag attachment on auklets, we predicted reduced return rates of adults, reduced adult mass, reduced fledging success, and/or slower chick growth.

METHODS

Literature review.—We reviewed 82 seabird tagging publications (including 65 tracking studies, and 17 that focused specifically on tag effects; see Supplemental Material for list of publications) for information about the size of device used relative to the size of the study species, how tag effects were measured/acknowledged, and, if measured, whether negative effects were found. This review included a broad range of device types and attachment techniques, and was intended to be a representative (but not comprehensive) sample of this kind of research.

Study site.—This study was conducted 2012–2015, primarily at Buldir (52° 11′ N, 175° 56′ E), in the Aleutian Islands (part of the Alaska Maritime National Wildlife Refuge), where both species are relatively accessible because of the lack of native or introduced mammalian predators. Breeding crevices and burrows used were concentrated within and adjacent to U.S. Fish and Wildlife Service's long-term monitoring plots (see Knudtson and Byrd 1982, Byrd and Day 1986, Hipfner and Byrd 1993). We also tagged Parakeet Auklets at Gareloi Island (51° 47′ N, 178° 47′ W). These breeding sites were not monitored in detail, and so the data are included for adult condition and return rate only.

Treatments.—All breeding sites found were haphazardly assigned to treatments (see below), depending on visibility/accessibility of the bird within the crevice and estimated likelihood of recapture (e.g., crevices with good visibility but possible escape routes were used for visual monitoring only).

Adult tagged group.—We tagged one or both members of the pair, returning every 4–5 days (when chicks were unattended) to measure chick growth and monitor nest fate (see below for details). This treatment was further differentiated for some analyses based on the type of tag (1 g or 2 g) and whether one or both members of the pair were tagged.

High-disturbance control group.—We removed and measured the adult, attached an identification band only and recorded chick growth and nest fate, as in the Adult tagged treatment.

Medium-disturbance control group.—An additional control for chick growth analysis in Parakeet Auklets only. We waited until the chicks were unattended and removed them for growth measurements; the adult was never handled.

Low-disturbance control group.—Visual monitoring of breeding site only; no capture of adults or chicks.

Device attachment.—We attached 19 2-g geolocation tags (LAT2900, 16 × 9 × 7 mm, Lotek Wireless) on Parakeet Auklets (total attachment 3 g, 1.1% body mass, mean 266 g) in 2012. In 2013, we attached 23 1-g tags (Intigeo C65, 14 × 8 × 6 mm, Migrate Technology) to Whiskered Auklets

TABLE 1. Sample sizes for Parakeet and Whiskered Auklets for each experimental treatment per year.[a]

	2012	2013	2014
Parakeet Auklet			
2-g tags	13/19	15/19	n/a
1-g tags	n/a	12/16 (3/4)[b]	36/47 (15/22)[b]
High-disturbance control[c]	2/3	5/7	n/a
Medium-disturbance control[d]	10	3	n/a
Low-disturbance control[e]	19	37	29
Whiskered Auklet			
2-g tags	n/a	n/a	n/a
1-g tags	n/a	12/23	6/25
High-disturbance control[c]	n/a	10/15	6/6
Medium-disturbance control[d]	n/a	n/a	n/a
Low-disturbance control[e]	n/a	61	56

[a] For treatments involving recovery of adults the following year, numbers given as returned/deployed.
[b] Sample sizes for Buldir Island, followed by sample sizes for Gareloi Island in parentheses.
[c] Adults removed and measured, but not tagged. Chicks measured, and reproductive success monitored.
[d] For Parakeet Auklets only: chicks measured and reproductive success monitored. No handling of adults.
[e] Visual monitoring of reproductive success only.

(total attachment 2 g, 1.8% body mass, mean body mass 112 g), 20 1-g tags to Parakeet Auklets (0.8% body mass), and an additional 19 2-g tags to Parakeet Auklets. The 2-g tags were unreliable (7/11 initially recovered provided no usable data), so in 2014 we used 1-g tags exclusively, deploying 69 on Parakeet Auklets and 25 on Whiskered Auklets (see Table 1 for detailed summary of sample sizes). We tagged adults as soon as possible after chicks hatched, because auklets are more prone to nest abandonment during the egg stage (Piatt et al. 1990, Ackerman et al. 2004), and breeding failure can increase the rate of divorce and/or crevice-switching the following year (Pyle et al. 2001), reducing the likelihood of recapture. One adult is usually present in the crevice at all times for a few days after hatch, allowing more reliable capture for tagging. Where we missed that window, we returned to the crevice at night, when one or more adults are often still present throughout the breeding season (C. R. Schacter, pers. obs.).

Birds were removed from the crevice and each given a numbered aluminum band crimped laterally to prevent slippage over the foot. Tagged adults were then given a custom-made Darvic color-band above the aluminum band upon which we attached LAT2900 tags by threading the band and a cable tie through metal loops on the tag. Intigeo C65 tags were attached to a Darvic band with a two part marine epoxy, further secured with a cable tie. For Parakeet Auklets, after a pilot study in 2012 showed that they were resilient to disturbance and able to tolerate the larger 2-g tags, we began tagging both members of the breeding pair when possible to increase the sample size. Because of Whiskered Auklets' smaller size, and a lack of prior studies demonstrating tag tolerance, we tagged only one member of each pair to reduce the likelihood of significant effects on the chicks.

To evaluate the effects of the tags on adult condition, both tagged and control adults were weighed at the time of capture, and again at retrieval the following year. We also collected breast feathers for genetic sex determination (Fridolfsson and Ellegren 1999). If a tag was not retrieved 1 year after deployment, we continued checking that crevice in future years until the tag was recovered or the study ended. All crevices where birds had been previously captured were checked and individuals classified as either returned (the banded/tagged individual was recaptured or observed), or not returned (the crevice was vacant, or confirmed to be occupied by new individuals). The fate of some birds was unclear because the status of one or more members of the pair could not be confirmed, and we classified these individuals as not returned for the purposes of this analysis (the inclusion of unclear returns as a separate category did not change the results). Our 'return rate' refers only to the rate of return to the same breeding crevice. Individuals that did not 'return' may have simply switched breeding sites and/or mates—a possible effect of the stress caused by carrying a geolocation tag (Jones and Montgomerie 1991, Fraser et al. 2004). However, every effort was made to search nearby crevices, and since most accessible crevices within our study areas are monitored, we believe we have maximized our chances of tag recovery.

Fledging success.—To track the success of each nesting pair, we conducted regular crevice monitoring in the year of tag deployment, following U.S. Fish and Wildlife Service's protocols (Williams et al. 2000). This allowed us to compare our data to their large sample of monitored nests at Buldir as an additional 'low-disturbance' control. Briefly, this consists of visually inspecting crevices with a flashlight every 4–5 days, recording the presence of adult, egg, or chick, and determining the success or failure of each pair based on the age of their chick when last seen (Williams et al. 2000). For tagged and disturbed control sites (i.e., high-disturbance and medium-disturbance controls), we also removed the chick during regular crevice checks and measured mass and flattened wing chord. Chicks were measured at approximately the same time of day, and masses were excluded if the chick had been recently fed (visually indicated by distended throat pouch). We calculated chick growth rates (simple slope) for mass and wing during the linear growth phase (Parakeet Auklets: 4–22 days for wing, 10–31 days for mass; Hipfner and Byrd 1993; Whiskered Auklets: 7–26 days for wing, 2–22 days for mass; Hunter et al. 2002) for comparison among treatments.

Statistical analysis.—All analyses were run in R statistical software (R Core Team 2014). Because of differences in the way the two species were tagged (different years, islands and treatment details), we analyzed each species separately. Some data points were excluded a priori from certain analyses (e.g., two crevices destroyed in an earthquake were excluded from tests of return rates, and late hatching nests were excluded from tests of fledging success if their fate could not be determined). We used a generalized linear model (reporting deviance [D] and P-values from the X^2 distribution; McCullagh and Nelder 1989) for binomial response variables (return rate and fledging success), with treatment, and year as fixed factors, and interactions between treatment and year. We also included island as a fixed factor for return rate of Parakeet Auklets, to account for possible differences between the Buldir and Gareloi colonies. Because sex was known only for manipulated nests, it was included as a factor in all return rate models, but in the case of fledging success, we tested for the effect of sex (specifically the interaction between treatment and sex) separately using only individuals of known-sex, and excluded nests where both adults were tagged. We excluded breeding sites of Parakeet Auklets in 2014 from fledging success analysis, because we left Buldir before the fate of the majority of successful nests could be determined. For adult condition, we fit a general linear model on the difference between mass at deployment and mass at retrieval, with treatment, year, island (Parakeet Auklets only), and sex as fixed factors, and the difference in ordinal date between tagging and retrieval as a covariate to control for seasonal decline in mass (Weiser et al. 2016). For chick growth, we fit a general linear model with treatment (tagged, high-disturbance, and medium-disturbance), year and sex as fixed factors, and the interaction of both year and sex with treatment. For Parakeet Auklets, the tagged adult category encompasses multiple treatments: nesting pairs had either a 1-g tag, a 2-g tag, or both members of the pair were tagged. These three categories were coded separately within the treatment factor for all initial analyses, with additional planned a priori comparisons (Sokal and Rohlf 2012) of (1) all tagged adults versus low-disturbance controls (fledging success only), (2) tagged adults with 1-g versus 2-g tags (fledging success, chick growth), (3) breeding crevices with one versus both adults tagged (fledging success, chick growth), and (4) all disturbed adults (adult tagged and high-disturbance control) versus medium-disturbance controls (chick growth only). We also used a generalized linear model (binomial) to compare return rates of Parakeet Auklets bearing 2-g tags with data from a study Crested Auklets using the same tags (Robinson and Jones 2014). We set an a priori significance level of $P < 0.05$ for all tests, and considered effects where $0.05 < P < 0.1$ to be of marginal significance and worth considering as a potential concern.

RESULTS

Literature review.—Among tracking studies ($n = 65$), 52% made at least minimal measurements of

TABLE 2. Summary of studies included in review of tag effects, broken down by taxonomy, size of species studied, and percent body mass of tag used. Only studies that provided the relevant information were included, so totals may differ.

	Total number of studies reviewed	Number of tracking studies measuring tag effects[a]	Number of studies reporting negative effects[b]
Taxonomic group			
Procellariiformes	32	11 (42%)	2 (12%)
Laridae	8	4 (57%)	1 (20%)
Alcidae	28	14 (74%)	16 (64%)
Adult body mass			
<400 g	19	11 (73%)	5 (33%)
400–1,000 g	38	17 (59%)	11 (41%)
>1,000g	24	6 (30%)	6 (60%)
Percent body mass of tag			
3–5% body mass	12	7 (70%)	4 (40%)
1–3% body mass	43	17 (52%)	12 (44%)
<1% body mass	24	9 (45%)	6 (46%)

[a] Not including studies focused specifically on tag effects.
[b] Includes tracking studies that measured tag effects and studies focused specifically on tag effects.

effects, 11% made anecdotal statements that birds did not seem affected by tags, 6% cited previous research on their species, 8% cited the 3% guideline (Phillips et al. 2003) as evidence that measuring effects was not necessary, and 23% made no mention of effects. Of studies that measured effects ($n = 51$), 41% reported some negative impact. The likelihood of detecting effects for tags of 3–5% body mass was no higher than tags of 1–3% or <1% body mass (Table 2). We also found no tendency for small (<400 g) species to have more negative effects than large (>1,000 g) species (Table 2). Taxonomy was the best predictor of tag effects in these publications. Fewer than 25% of studies on Procellariiformes or Laridae showed negative effects of tags, compared to 64% for Alcidae (Table 2).

Auklet tracking study.—Overall we retrieved 79% of tags from Parakeet Auklets (deployed in 2012: 68%; 2013: 81%; 2014: 81%; see Table 1 for details), and 42% of tags from Whiskered Auklets (2013: 60%; 2014: 26%; Table 1). Control adult return rates were 70% for Parakeet Auklets (2012: 67%; 2013: 71%; Table 1) and 76% for Whiskered Auklets (2013: 67%; 2014: 100%; Table 1). One Parakeet Auklet had a leg injury of unknown origin that caused the tarsus to swell around the bands and bleed when they were removed. The bird was treated with a clotting agent and released back into the crevice, where it was observed incubating on subsequent visits. Several Whiskered Auklets showed evidence of leg compression (i.e., slight discoloration and indentation of the skin around the leg band) at the upper and lower joints of the tarsus because of the combined length of the aluminum and Darvic bands. This band crowding did not appear to impair leg function.

Parakeet Auklets.—Treatment (Adult tagged 1 g, Adult tagged 2 g, High-disturbance control) had no effect on adult return rate ($D_{2,125} = 1.25$, $n = 136$, $P = 0.90$) or condition ($X^2{}_2 = 3.03$, $n = 90$, $P = 0.22$). In a comparison of Parakeet Auklets bearing 2-g tags (1.1% body mass) with Crested Auklets given the same tags by Robinson and Jones (2014), we found that the two species responded differently despite their similar size (significant interactive effect of Species and Treatment: $D_{1,173} = 7.04$, $P = 0.008$). Tagged Crested Auklets had significantly lower return rates than controls (tagged 32% [10/31] versus control 64% [83/129]; $D_{1,127} = 29.9$, $P < 0.001$), while Parakeet Auklets did not (tagged 74% [28/38] versus control 70% [7/10]; $D_{1,46} = 0.05$, $P = 0.82$). There was a significant effect of year ($D_{1,103} = 15.0$, $n = 105$, $P < 0.001$) but not treatment ($D_{4,99} = 3.52$, $n = 105$, $P = 0.47$) on fledging success when all five categories (Adult tagged 1 g, Adult tagged 2 g, Adult tagged both, High-disturbance control, Low-disturbance control) were considered separately. Fledging success was lower in 2013 than 2012 (Fig. 1B). A priori follow-up tests showed no effect of treatment when comparing all tagged adults to low-distur-

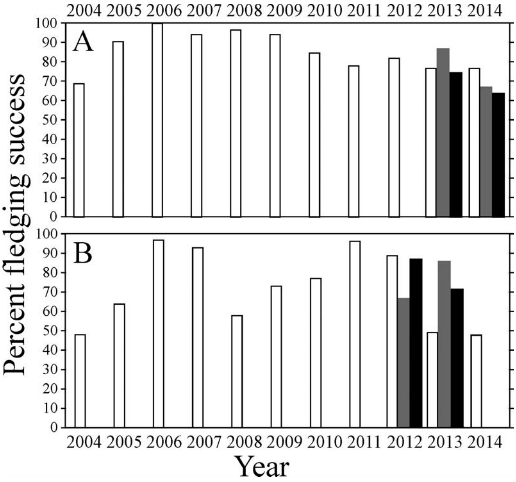

FIG. 1. Fledging success of (A) Whiskered and (B) Parakeet Auklets at Buldir Island, Alaska. Success of breeding crevices where adults were tagged with geolocators (black; all tag types combined) or had only leg bands attached (gray; high-disturbance control treatment). Long-term U.S. Fish and Wildlife Service monitoring data (white; low disturbance; Mudge and Pietrzak 2015) included for context. Chicks from both the tagged and high-disturbance control treatments were captured and measured repeatedly to determine growth rates.

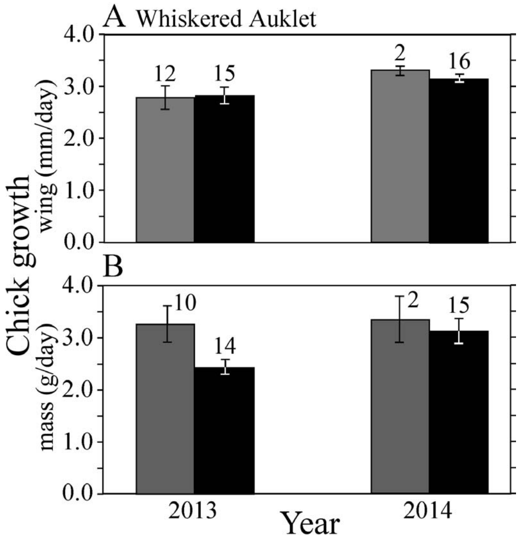

FIG. 2. Growth rates of Whiskered Auklet chicks in wing length (A) and mass (B) during linear growth phase compared across treatments: High-disturbance control (gray), and Adult tagged (black). Sample sizes above bars. Note: we did not include a medium-disturbance control treatment (chick measurements only) for Whiskered Auklets, only Parakeet Auklets.

bance controls ($D_{1,92} = 0.35$, $n = 95$, $P = 0.55$), when comparing adults tagged with 1-g and 2-g tags ($D_{1,30} = 8.41$, $n = 33$, $P = 0.21$), or when comparing nest crevices with one or both adults tagged ($D_{1,36} = 0.23$, $n = 39$, $P = 0.63$). The final a priori test, comparing tagged adults to high-disturbance controls showed a marginal interactive effect of treatment and year on fledging success ($D_{1,45} = 2.98$, $n = 49$, $P = 0.084$), so the 2 years were analyzed separately. There was no difference between tagged and high-disturbance control treatments in 2012 ($D_{1,16} = 0.62$, $n = 18$, $P = 0.43$). However, high-disturbance controls had higher fledging success than tagged adults in 2013 ($D_{1,29} = 4.6$, $n = 31$, $P = 0.032$; Fig. 1B). When only birds of known sex were considered, there was a significant reduction in fledging success in tagged males (high-disturbance control 100%, 1-g tag 67%, 2-g tag 36%; $D_{2,14} = 8.32$, $n = 18$, $P = 0.02$) but not females (high-disturbance control 67%, 1-g tag 50%, 2-g tag 80%; $D_{2,21} = 0.04$, $n = 25$, $P = 0.98$). There was no significant effect of tagging on the rate that chicks increased in mass (average differences 1.23–3.30 g/day, $F_{4,37} = 1.20$, $n = 45$, $P = 0.33$; Fig. 3B) or wing length (average differences 0.01–0.08 mm/day, $F_{2,41} = 0.34$, $P = 0.72$; Fig. 3A). Chick growth rates were significantly lower for both measures in 2013 than 2012 (average differences: mass 4.03 g/day, wing 0.40 mm/day, $P < 0.002$; Figs. 3A–B).

Whiskered Auklets.—There was a significant interactive effect of treatment and year on return rate ($D_{1,59} = 7.50$, $n = 64$, $P = 0.004$), so each year was analyzed separately. There was no difference in return rate for tagged and control adults deployed in 2013 (65% versus 67%; $D_{1,33} = 0.16$, $n = 35$, $P = 0.74$), but tagged adults from 2014 had a dramatically lower return rate the following season (26% versus 100%, $D_{1,27} = 12.9$, $n = 29$, $P < 0.001$). Low recovery rates for tags of Whiskered Auklets deployed 2014–2015 may be partially explained because of a delayed start to fieldwork in 2015. We arrived late in their incubation stage, and many crevices were vacant, but the presence of downy feathers suggested that they had been occupied (and perhaps abandoned) before our first checks. However, this would account for at most half of the missing tags. There was a marginally significant interactive effect of

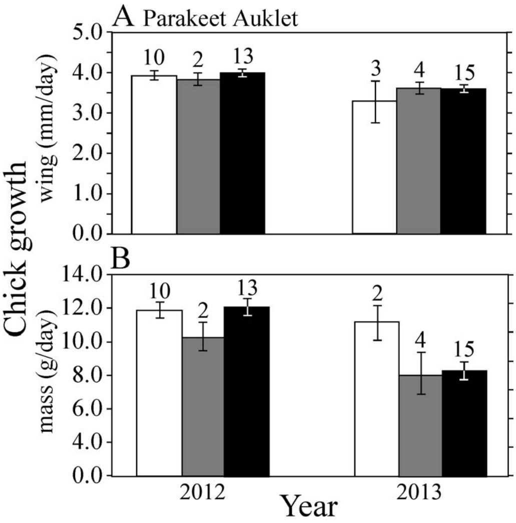

FIG. 3. Growth rates of Parakeet Auklet chicks in wing length (A) and mass (B) during linear growth phase compared across treatments: Medium-disturbance control (white), High-disturbance control (gray), and Adult tagged (black). Sample sizes above bars.

treatment and year on adult condition ($X^2_1 = 3.68$, $n = 64$, $P = 0.055$), so each year was analyzed separately. We found a significant difference in 2013–2014 deployments (tagged adults returned on average 0.75 g lighter than at deployment, control adults on average 5.8 g heavier; $X^2_1 = 11.7$, $n = 22$, $P < 0.001$), but not in 2014–2015 (tagged adults returned on average 10.6 g heavier than at deployment, control adults on average 10.3 g heavier; $n = 12$, $P > 0.9$). Tagging treatment (adult tagged, high-disturbance control, or low-disturbance control) had no effect on Whiskered Auklets' fledging success ($D_{2,175} = 1.38$, $n = 179$, $P = 0.50$; Fig. 1A). There was also no effect of treatment (adult tagged or high-disturbance control; $D_{1,59} = 0.63$, $n = 62$, $P = 0.43$) or interaction between treatment and sex ($D_{1,56} = 0.81$, $n = 62$, $P = 0.37$) when only known-sex individuals were included. Tagging the adult significantly reduced the rate of mass gain in chicks (Fig. 2B; average difference 0.5 g/day, $F_{1,35} = 6.80$, $n = 41$, $P = 0.01$) but had no effect on wing growth ($F_{1,39} = 0.012$, $n = 45$, $P = 0.91$; Fig. 2A). Chick growth was slower (although only marginally significant for wing) in 2013 than 2014, irrespective of tagging status (mass: average difference 0.38 g/day, $F_{1,35} = 3.08$, $n = 41$, $P = 0.02$, Fig. 2B; wing: average difference 0.1 mm/day, $F_{1,39} = 3.53$, $n = 45$, $P = 0.07$, Fig. 2A).

DISCUSSION

Parakeet and Whiskered auklets showed varying tolerance for tags 0.8–1.8% of their body mass. There were minor decreases in chick growth for tagged Whiskered Auklets to suggest that an increased burden reduced their ability to provision offspring, but not enough to affect chick survival. We also found significant negative effects on adult condition and return rates of Whiskered Auklets in some years but not in others. Low recovery rates for tags of Whiskered Auklets deployed in 2014–2015 may be partially because of a delayed start to fieldwork in 2015. However, many of the occupied crevices contained at least one new bird, suggesting high rates of mortality, divorce, or switching of breeding sites (Jones and Montgomerie 1991, Fraser et al. 2004, Paredes et al. 2005). The particularly harsh winter in the Bering Sea 2014–2015 may also have been a factor in the lower return rates. Whiskered Auklets remain resident in the Aleutians year-round (Byrd and Williams 1993), and survival has been shown to vary with local winter conditions, with higher mortality in stormy winters (Jones et al. 2007). The burden of tags may have exacerbated this effect, if birds that could normally compensate were not able to do so when already operating near their metabolic limit (Croll and McLaren 1993, Humphreys et al. 2007). Our data suggest that the tags used (total attachment: 2 g) may have been too large for Whiskered Auklets to bear without experiencing considerable stress, and thus the tracking data produced should be interpreted with caution.

Parakeet Auklets, on the other hand, showed very few negative effects of tagging. In 2013 (a bad year for chick growth and survival overall), fledging success was lower for tagged birds than high-disturbance controls, but higher than the large sample of low-disturbance control nests monitored (Fig. 1B), and so the statistical difference may not be biologically meaningful. We also found that tagging of males was more likely to result in a negative effect on fledging success, suggesting that males may take on a greater share of the effort when provisioning the chick. Overall, though, Parakeet Auklets showed a good tolerance for devices in this size range, with significantly higher return rates than Crested Auklets provided with the same 2-g tags (Robinson and Jones 2014). Although closely related and similar in size, they differ in many ways, including the Parakeet Auklets' lower wing-loading, shorter migration, etc. (Jones 1993, Jones et al. 2001), all of which likely contribute to their greater ability to carry the tags.

A review of seabird tagging studies illustrated the lack of consistency in reporting of tag effects in the literature. Among tracking studies, 52% made at least minimal measurements of effects, and of those, 41% reported some negative impact, although the statistical power of many studies was low because of limited comparative sample sizes, and thus they were unlikely to detect anything but severe effects. Nevertheless, even a rudimentary examination of tag effects has value when it comes to interpreting the results of tracking studies, and researchers are urged to evaluate tag effects as a matter of standard practice (Vandenabeele et al. 2012). Taxonomy was the best predictor of tag effects in the publications reviewed (alcids were more than twice as likely to show negative effects of tags than other taxa; Table 2), suggesting that factors such as foraging style, or flight physiology/energetics may play a greater role than relative mass when predicting likely tag effects (Barron et al. 2010, Vandenabeele et al. 2012). Although relative tag mass alone was a poor predictor of tag effects (Table 2), studies testing multiple tag masses on the same species found that negative impact did increase with device size (e.g., Wilson et al. 1986, Elliott et al. 2007, Ropert-Coudert et al. 2007), so percent body mass of tags deployed should be kept to a minimum.

Our study was not designed specifically to measure tag effects but rather reflects the kind of data that can be gathered in the course of a larger tracking project, and we would encourage more researchers to incorporate at least minimal effects monitoring in all tracking studies. High rates of breeding failure (fewer active breeding sites to work with) at the colony in some years limited the size of our control samples (Table 1), and may have reduced our ability to detect more subtle tag effects, but having multiple years of data helps to make stronger conclusions. We have shown that effects can vary significantly among closely related species of similar size, and among years within the same species at the same colony. Given this variation, it is difficult to justify simply citing previous research when evaluating the potential for tag effects in any new study.

This study and others have demonstrated negative effects on reproduction, behavior, and return rates in alcids of tags well below the 3% guideline typically cited (e.g., Ackerman et al. 2004, Paredes et al. 2005, Robinson and Jones 2014). These results suggest that not all species are equally affected by tags, and that guidelines, even those that are well-established for one group, should not be universally applied to all seabirds without validation (Vandenabeele et al. 2012). Temporal and geographic variation in tag effects within species (e.g., this study, Weiser et al. 2016) also highlight the dangers of relying on previous effects studies, even of the same species. Factors other than tag mass may be at least as important. Most seabirds routinely carry food loads well in excess of 5% of their body mass (Ackerman et al. 2004, Ortega-Jimenez et al. 2011), and it has often been suggested that aerodynamic and/or hydrodynamic drag may be responsible for the increased energy costs at the root of many observed effects (Wilson et al. 1986, Obrecht et al. 1988). Despite this, although nearly all tagging studies report gear mass, many fail to include tag dimensions.

Advances in light-weight tracking technology provide researchers with a powerful new source of data on seabird ecology during the non-breeding season. We can test hypotheses about migration behavior, map winter habitat to inform the design of marine protected areas, or answer other conservation questions. This information is valuable, but should, whenever possible, be reported alongside an assessment of tag effects. Depending on the duration of researcher presence and the accessibility of the site, many studies could incorporate a basic assessment of reproductive success and/or adult return rates relative to control birds with minimal additional effort and disturbance. Including effects studies in tracking projects would provide a measure of confidence for their interpretation and allow us to weigh the value of the resulting data.

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