Effects of radiotransmitters on the reproductive performance of Cassin's auklets

Joshua T. Ackerman, Josh Adams, John Y. Takekawa, Harry R. Carter, Darrell L. Whitworth, Scott H. Newman, Richard T. Golightly, and Dennis L. Orthmeyer

Abstract We examined whether radiotransmitters adversely affected the reproductive performance of Cassin's auklets (*Ptychoramphus aleuticus*) breeding on the California Channel Islands during 1999–2001. We attached external radiotransmitters to 1 partner in 108 Cassin's auklet pairs after nest initiation and used 131 unmarked, but handled, pairs as controls. Compared to alpha chicks raised by radiomarked pairs, alpha chicks raised by unmarked pairs had faster mass growth rates (1.95 ± 0.30 g d^{-1} vs. 3.37 ± 0.53 g d^{-1}, respectively), faster wing growth rates (2.46 ± 0.10 mm d^{-1} vs. 2.85 ± 0.05 mm d^{-1}), greater peak fledging masses (118.9 ± 3.5 g vs. 148.3 ± 2.4 g), and higher fledging success (61% vs. 90%). Fledging success was reduced more when we radiomarked the male (50% fledged) rather than the female partner (77% fledged). After fledging an alpha chick, unmarked pairs were more likely to initiate a second clutch (radiomarked: 7%; unmarked: 39%) but did not hatch a second egg (radiomarked: 4%; unmarked: 25%) or fledge a second (beta) chick (radiomarked: 4%; unmarked: 18%) significantly more often than radiomarked pairs. We resighted 12 radiomarked individuals nesting during a subsequent breeding season; each bird had shed its transmitter and healed the site of attachment. We suggest caution in using telemetry to evaluate the reproductive performance of alcids, but marking only females may minimize adverse effects.

Key words alcid, Cassin's auklet, chick growth, double brooding, fledging success, parental care, *Ptychoramphus aleuticus*, radiotelemetry, transmitter effects

Little is known about at-sea movements and foraging ranges of breeding alcids (*Alcidae*), yet this information is critical for their management and conservation. Radiotelemetry is a widely used tool for determining individual movements of free-ranging birds (review by Samuel and Fuller 1996), but it has been used in only a few studies of alcids in the past (Wanless et al. 1985, 1990; Duncan and Gaston

1990). The use of telemetry for studying alcids has been hindered by logistical constraints associated with at-sea tracking, sensitivity of birds to handling, and lack of an effective method for transmitter attachment. With development of smaller transmitters and better attachment methods that increased transmitter retention times (Newman et al. 1999), several recent studies have used radiotelemetry to examine at-sea movements of small alcids (Xantus's murrelets [*Synthliboramphus hypoleucus*], Whitworth et al. 2000*b*; marbled murrelets [*Brachyramphus marmoratus*], Whitworth et al. 2000*a*, Lougheed et al. 2002*a*; Cassin's auklets [*Ptychoramphus aleuticus*], J. Adams, United States Geological Survey, unpublished data). However, few studies have investigated the effects of radio-transmitters on alcids (Wanless et al. 1988, 1989).

Breeding alcids are particularly likely to be adversely affected by externally attached transmitters because they travel long distances from their colonies to feed and forage underwater. Alcids have higher wing loading (i.e., body-mass-to-wing-area ratio) than other seabirds and use energetically expensive flapping flight without intermittent periods of gliding to travel between their colonies and pelagic foraging areas (Pennycuik 1987). Thus, the added mass and increased aerodynamic drag caused by an externally attached transmitter could increase the energy expended while traveling to distant foraging areas (Gessaman and Nagy 1988, Obrecht et al. 1988). Moreover, transmitters can reduce streamlining and increase hydrodynamic drag during underwater foraging, thereby reducing swimming speeds and foraging efficiency during pursuit diving (Wilson et al. 1986). Transmitters also may disrupt birds' waterproofing and thus increase thermoregulatory costs in cold ocean waters (Bakken et al. 1996).

Alcids are relatively long-lived and have many opportunities to breed over their lifetimes; therefore, parents are expected to reduce parental effort when breeding conditions are unfavorable, to maximize their own probability of survival to a time when breeding conditions are more favorable (Stearns 1992). Consequently, alcid parents might transfer any cost associated with an attached transmitter to their offspring so that they do not diminish their own prospects for survival and future reproduction. For example, other long-lived species such as Leach's storm-petrels (*Oceanodroma leucorhoa*; Mauck and Grubb 1995) and Antarctic petrels (*Thalassoica antarcti-*

ca; Sæther et al. 1993) have been shown to respond to a flight handicap (experimentally reduced wing span and increased mass, respectively) by feeding their chicks less frequently. Cassin's auklet chicks require feeding for a 41–50-day fledgling period during which parents feed chicks nightly (Manuwal and Thoresen 1993) following diurnal excursions to foraging areas up to 40 km away from the colony (J. Adams, United States Geological Survey, unpublished data). Therefore, any effects of externally attached transmitters to Cassin's auklet parents may be expressed as reduced chick growth rates and survival to fledging.

We fitted Cassin's auklets (hereafter auklets) breeding on the California Channel Islands with externally attached radiotransmitters after nest initiation and compared their reproductive performance to that of unmarked parents. Specifically, we measured body mass and wing growth rates, peak fledging mass, and fledging success of alpha chicks raised by pairs with and without a partner carrying a transmitter. We also examined the frequency of double brooding by radiomarked pairs compared to unmarked pairs. Additionally, we evaluated whether the sex of the radiomarked partner influenced a pair's reproductive performance.

Methods

Study area

We studied auklets nesting at 2 colonies 90 km apart on Prince Island (34º05′N, 120º15′W) and Scorpion Rock (34º05′N, 119º30′W) in the northern Channel Islands of California during the 1999–2001 breeding seasons (mid-February to mid-July). Prince Island, located 2 km north of San Miguel Island, had the largest colony of auklets in the Southern California Bight. Carter et al. (1992) estimated that 8,900 auklets were breeding on Prince Island and 100 on Scorpion Rock in 1991. The ocean around Prince Island was seasonally influenced by cool, nutrient-enriched water upwelled along the central California coast. In the spring this highly productive water becomes entrained within the Santa Barbara Channel (Harms and Winant 1998, Oey et al. 2001). Scorpion Rock was a small islet <1 km north of Santa Cruz Island. The water around Scorpion Rock typically was warmer and more stratified and had a more variable oceanographic influence from coastal upwelling than water around Prince Island.

Auklets are wing-propelled, pursuit-diving seabirds and the most widely distributed of the true auklets, ranging from the Bering Sea, Alaska, to northern Baja California, Mexico. On Prince Island and Scorpion Rock, auklets nest in shallow burrows excavated in loose, rocky soil and within rock crevices. Auklets incubate their single egg for approximately 39 days (range: 37–57 days; Manuwal 1974, Ainley et al. 1990), with partners exchanging incubation duties every 24 hours (Manuwal and Thoresen 1993, Gaston and Jones 1998). In the southern portion of their breeding range, auklets occasionally produce a second brood during the same nesting season (i.e., double brood) when nearby waters are highly productive (Manuwal and Thoresen 1993). Breeding auklets primarily forage within 40 km of their colony (J. Adams, United States Geological Survey, unpublished data), returning to the colony once per night to feed their chick (Manuwal and Thoresen 1993). At the California Channel Islands, auklet parents fed their chicks primarily with euphausiid crustaceans, particularly *Thysanoëssa spinifera*, *Euphausia pacifica*, and *Nyctiphanes simplex*, but also with pleuronectid fishes, rockfish (*Sebastes* spp.), and cephalopods (*Loligo opalescens* and *Octopus* spp.; J. Adams, United States Geological Survey, unpublished data). Auklets are opportunistic foragers, and diet composition changes as oceanic conditions influence prey availability (Ainley et al. 1996, Hedd et al. 2002).

Treatment and control groups

On Prince Island we captured auklets nesting in natural sites (i.e., burrows and rock crevices), artificial burrows, and artificial nest boxes. Because most natural burrows were extremely fragile and susceptible to investigator damage, we placed 50 artificial nesting boxes at the Prince Island colony in 1986 to facilitate demographic monitoring (Lewis and Gress 1988). In 2000 and 2001, we added 20 and 28 new artificial burrows, respectively, at the Prince Island colony 1 to 2 months before each nesting season to increase the number of accessible nest sites. We constructed artificial burrows from plastic nursery containers fitted with flexible corrugated pipe 10 cm wide and 0.5 m long. We partially covered artificial burrows and made nest contents accessible through a plywood covering. We did not attach transmitters to auklets nesting within artificial nest boxes on Prince Island because they were part of the long-term monitoring program by the Channel Islands National Park.

Therefore, we attached transmitters only to auklets nesting within known natural nest sites and artificial burrows on Prince Island. On Scorpion Rock we placed 20 and 15 artificial burrows within the nesting colony 2 months before the 2000 and 2001 breeding seasons, respectively; no artificial nest boxes were available for study, and we were not able to use natural nest sites at Scorpion Rock. Therefore, we attached transmitters only to auklets nesting within artificial burrows on Scorpion Rock.

We visited Prince Island and Scorpion Rock periodically throughout the 1999–2001 breeding seasons to attach radiotransmitters. Because our goal was to study the effects of transmitters on chick growth and survival, we attached transmitters randomly to one partner of a pair whose egg was either close to hatching or had recently hatched upon our visit. We assigned the remaining artificial burrows and natural nest sites and all of the artificial nest boxes to the control group.

Radiotransmitter attachment

We hand-captured breeding adults at night when the auklets returned to previously marked nest sites on Prince Island (1999, 2000, and 2001 breeding seasons) and Scorpion Rock (2000 and 2001). We also used a nylon mist net to capture adults at Scorpion Rock (4 shelves, 38-mm mesh; Avinet Inc., Dryden, N.Y.). The birds were banded (United States Geological Survey #3 leg bands) and weighed (±1.0 g with a 300-g Pesola® spring scale, Pesola Ag, Baar, Switzerland), and we measured bill depth and length of the flattened wing chord. For radiomarked auklets, we also collected a single drop of blood in a micro-capillary tube by pricking the bird's medial tarsal vein with a sterile needle. Blood was stored in 70% ethanol and thereafter analyzed to determine the auklet's sex using molecular techniques (Zoogen™ sex analysis, Celera AgGen, Davis, Calif.). We determined the sex of auklets from which we did not collect blood ($n = 9$) by comparing bill depths between partners; we classified the bird with the greater measurement as a male (Nelson 1981). Iris coloration on a scale from 1 to 4, with larger integers indicating a younger bird, was used to age auklets (Manuwal 1978).

We attached radiotransmitters (1999 and 2000: Model BD-2G, Holohil Systems Ltd., Carp, Ont., Canada; 2001: Model A4300, Advanced Telemetry Systems Inc., Isanti, Minn.) to the dorsal midline of auklets with a subcutaneous anchor, single rear suture (Ethicon® Prolene 3-0, Ethicon Inc.,

Piscataway, N.J.), and marine epoxy (Marine epoxy #332®, Titan Corporation, Lynnwood, Wash.) following Newman et al. (1999). All auklets marked in 1999 and most auklets marked in 2000 were lightly sedated with an inhalation anesthetic (isoflurane; AErrane, Baxter Pharmaceutical Products Inc., Deerefield, Ill.) prior to attaching transmitters. Birds were masked down using isoflurane at 5% and the oxygen flow meter set at 3 for <2 minutes. We kept birds' heads in the mask until they lost reflexes including a wing withdrawal, response to a toe pinch, and palpebral reflexes. When the birds demonstrated nystagmus followed by eyelid closure, we turned off the isoflurane and oxygen and removed birds from the mask, placed them in position for radio attachment, and then covered them with a drape to limit visual stimulation. We felt that the complications potentially associated with sedation outweighed potential benefit to the birds, so we discontinued sedating auklets in 2001. Transmitters operated at 148–149 MHz in 1999 and 164–165 MHz in 2000 and 2001, weighed 3.0–3.1 g (<2% of auklet body mass), were either 10 mm wide × 10 mm high (Model BD-2G) or 13 mm wide × 7 mm high (Model A4300; both <5% of auklet cross-sectional body area), and had a 15-cm external whip antenna. Immediately after attaching transmitters, we returned birds to their nest sites. The mean ± SD time from capture to release was 29 ± 9 minutes. Thereafter, we monitored radiomarked auklets at sea by fixed-wing aircraft every 1–8 days throughout the breeding season.

Reproductive performance

Chick growth rate. We used 2 indices of chick growth rate: 1) mass growth rate, and 2) wing growth rate. We visited nest sites several times throughout each nesting season and measured chicks' body masses (±1.0 g with 100-g or 300-g Pesola spring scales) and maximum flattened wing chords (±1.0 mm). We calculated mass growth rates (g d^{-1}) for individual chicks during the developmental period when body mass increased linearly (5–25 days of age; Manuwal 1974, Vermeer 1981, Hedd et al. 2002) using the formula: ($mass_{t2}$ – $mass_{t1}$)/(age_{t2} – age_{t1}), where t_1 was the first measurement and t_2 was the last measurement recorded during the linear growth phase. Similarly, we calculated linear wing growth rates (mm d^{-1}) for individual chicks between 5 and 35 days of age using the formula: (wing chord$_{t2}$ – wing chord$_{t1}$)/(age_{t2} – age_{t1}). We determined the chick's age at each nest visit by 1) subtracting the date we measured the chick from its observed hatching date (±2 d), or 2) if we did not observe the hatching date, we estimated chick age using the linear relationship between wing chord and age calculated from a subset of our data that included chicks with known hatching dates {chick age = [wing chord (mm) – 14.68]/2.25; $n = 64$, $R^2 = 0.93$}. We also used this equation to estimate hatching date by subtracting the chick's estimated age from the date on which the wing chord was measured. We used only the first wing chord measurement, prior to outfitting parents with transmitters, when developing and applying the equation so that any transmitter effects on wing growth would not bias our estimates of chick age and hatching date. In the transmitter treatment group, we calculated growth rates only for chicks with parents that had carried transmitters for ≥3 days between chick measurements (during the linear growth phase) to allow sufficient time for potential transmitter effects.

Fledging success and peak fledging mass. Because travel to Prince Island and Scorpion Rock was logistically difficult and dependent on weather, we visited nest sites sporadically throughout the breeding season and therefore did not measure exact fledging success and fledging mass. Instead, we used indices of these reproductive parameters based on expected fledging age and mass. In the southern portion of their range, Cassin's auklet chicks typically reach peak mass at 37 days (approximate range: 35–45 days) and fledge at 41–42 days (Manuwal 1974, Ainley et al. 1990) at 147–158 g (range of annual means from 1970–1983 at the Farallon Islands; Ainley et al. 1990), depending on environmental conditions. We considered a chick to have fledged if it was still alive at ≥30 days of age, mostly feathered (i.e., fully feathered except for a trace amount of down remaining on the head and neck), and weighed ≥100 g on our last visit before the chick left the nest site (following Martin and Sydeman 1998). Conversely, chicks found dead at the nest site, those that disappeared from the nest site before they were 30 days of age, or those that weighed <100 g after 30 days of age were considered not to have fledged (following Martin and Sydeman 1998). We excluded chicks that did not meet these criteria from analyses of fledging success. As an index of fledging mass, we used peak mass measured between 35 and 45 days of age. Although chicks usually reach asymptotic growth between 35 and 45 days of age, we note

that peak mass is only an approximation of fledging mass because chicks can lose weight just prior to fledging (Manuwal 1974, Vermeer 1981, Ainley et al. 1990, Hedd et al. 2002). We excluded chicks that were not measured between 35 and 45 days of age from analyses of peak mass. We used only the first nesting attempt (first egg laid and chick raised) by a pair during the breeding season (hereafter alpha chicks) for all analyses except when we specifically considered double brooding.

Double brooding. We also measured the frequency with which pairs initiated, hatched, and fledged second clutches after presumably successfully fledging their alpha chick based on criteria established to determine fledging. In the treatment group, we measured the frequency of double brooding only for auklet pairs that were radiomarked during their first breeding attempt for that season (i.e., parents were marked while raising the alpha chick). We examined whether second clutches 1) occurred less frequently among radiomarked pairs than unmarked pairs, 2) had lower hatching success among radiomarked pairs than unmarked pairs, and 3) had lower fledging success among radiomarked pairs than unmarked pairs.

Statistical analyses

We did not randomly assign auklet pairs to treatment groups because we could not radio-mark auklets nesting in artificial nest boxes on Prince Island; hence, we included pairs nesting in the artificial nest boxes in the control group. As a consequence, it is possible that pair quality (e.g., age, experience, pair-bond duration; Emslie et al. 1992, Morbey and Ydenberg 2000, Pyle et al. 2001) differed among treatment groups. Therefore, we statistically controlled for any potential differences due to nest type (natural nest site, artificial burrow, or artificial nest box) by including this variable in each analysis. We also included Julian hatching date as a covariate in each analysis because fledging success and chick growth rates often decline as the nesting season progresses (Ainley et al. 1990, Morbey and Ydenberg 1997). We controlled for yearly variation in nesting phenology by using z-scores. Z-scores were calculated each year by taking the difference between a pair's Julian hatching date and the mean Julian hatching date, and dividing that quantity by the standard deviation for that year. Additionally, we included year and a year × treatment interaction in each analysis. Because the radiomarked group

included pairs nesting in natural sites (i.e., burrows and rock crevices) and artificial nesting burrows, whereas the control group included pairs nesting in these sites and artificial nest boxes, we repeated each analysis after excluding the control pairs nesting in artificial nest boxes to ensure that our results were not an artifact of nest type. Finally, we used unpaired *t*-tests to compare mean age and body mass of pairs in the radiomarked and unmarked groups to evaluate whether parents differed between treatment groups. For these analyses we used either the mean value of a pair when both parents were measured or the value for a single parent when only one parent was measured.

To examine whether chicks raised by unmarked pairs had faster growth rates and larger peak fledging masses than chicks raised by pairs containing a radiomarked parent, we used analysis of covariance (ANCOVA) in which factors were the treatment group (radiomarked or unmarked pairs), year (1999–2001), and nest type (natural nest site, artificial burrow, or artificial nest box), with Julian hatching date (z-score) as the covariate. To test whether pairs containing a partner with an attached transmitter had lower fledging success than unmarked pairs, we used multiple logistic regression in which the nominal dependent variable was fledge or fail and the explanatory variables were treatment group, year, nest type, and Julian hatching date (z-score). We also used multiple logistic regression to analyze the probability that a pair would initiate a second clutch, hatch a second egg, and fledge a second (beta) chick after successfully fledging their alpha chick. We included treatment group, year, nest type, and Julian hatching date (z-score) as explanatory variables in each model.

We also tested whether the sex of the radiomarked parent influenced reproductive performance. For these analyses, we statistically controlled for the effect of year, but not for hatching date or nest type (as in the other analyses) because transmitters were assigned randomly to a partner within a nest site. We tested the effect of the radiomarked partner's sex on chick growth rates and peak fledging masses using ANCOVA in which the factors were the sex of the radiomarked parent, year, and a sex × year interaction. We tested the effect of the radiomarked partner's sex on fledging success using multiple logistic regression, in which the nominal dependent variable was fledge or fail and explanatory variables were sex of the radiomarked partner, year, and a sex × year interac-

tion. We also tested whether the radiomarked partner's sex influenced the probability that a pair would initiate a second clutch, hatch a second egg, and fledge a second chick after successfully fledging their alpha chick using multiple logistic regression, in which the explanatory variables were sex of the radiomarked parent, year, and a sex × year interaction. We conducted statistical analyses with JMP® (version 4.0.4; SAS Institute Inc. 1998, Sall et al. 2001) or StatView® (version 5.0.1; SAS Institute Inc. 1998), with alpha=0.05. All tests were 2-tailed. We report means ± SE unless otherwise noted.

Results

We attached radiotransmitters to 1 partner in 108 auklet pairs during the 1999–2001 breeding seasons. We used 131 unmarked pairs, identified with leg bands, as controls. There was no difference in the mean iris (age) score (unmarked: 1.37 ± 0.07, radiomarked: 1.44 ± 0.07; $t_{138}=-0.64$, $P=0.52$) or mean body mass (unmarked: 165.2 ± 1.5 g, radiomarked: 163.4 ± 1.1 g; $t_{121}=0.96$, $P=0.34$) of pairs in the radiomarked and unmarked groups. We attached 84 transmitters when parents had young chicks and 31 transmitters when parents were in the late stages of incubation. Of the parents that we radiomarked during the egg stage, 13 of 31 eggs hatched (42%). Egg failure was primarily due to nest desertion (15 of 18 egg failures), but 5 of these pairs renested during the same breeding season. Of those parents marked during the chick-rearing stage, none immediately deserted their chick.

Radiotransmitter failure was especially common in 1999, when 12 of 35 transmitters were confirmed to have failed within 2–90 days. These radiomarked auklets were observed at their nest sites with their transmitters still attached, but the transmitters were not functioning. Fourteen other transmitters were suspected to have failed in 1999 on the basis of poor signal quality and strength. In 2000 and

2001, radio failure was less common and we observed only 5 radiomarked auklets at their nesting sites with attached transmitters that were not functioning.

There were differences in nesting phenology among years. The median Julian hatching dates of the first egg laid were 49 (range: 31–156), 84 (range: 64–170), and 110 (range: 90–177) during 1999, 2000, and 2001, respectively. However, we detected no interaction effect between year and treatment on any of the indices of reproductive performance (all $P>0.10$). We also detected no interaction effect between year and sex of the radiomarked parent on any of the indices of reproductive performance (all $P>0.10$). Therefore, we dropped all interaction terms from further analyses.

Chick growth and survival

Mass growth rate. Chicks raised by unmarked pairs had faster mass growth rates than chicks raised by radiomarked pairs (treatment: $F_{1,37}=4.28$, $P=0.05$; year: $F_{2,37}=1.21$, $P=0.31$; nest type: $F_{2,37}=0.60$, $P=0.56$; z-score Julian hatch date: $F_{1,37}=0.49$, $P=0.49$; Figure 1a). We obtained similar results after excluding pairs nesting in the artificial nest boxes (some of the controls) from the analysis (treatment: $F_{1,24}=4.67$, $P=0.04$; year: $F_{2,24}=3.13$, $P=0.06$; nest type: $F_{1,24}=0.01$, $P=0.91$; z-score Julian hatch date: $F_{1,24}=0.66$, $P=0.42$). Chicks raised by unmarked parents were consistently heavier
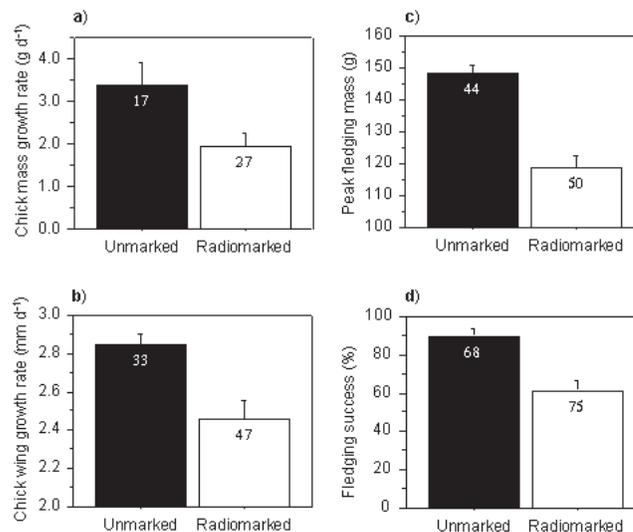

Figure 1. Alpha chicks raised by unmarked Cassin's auklet pairs (filled bars) had (a) faster body mass growth rates, (b) faster wing growth rates, (c) larger peak fledging masses, and (d) higher fledging success than alpha chicks raised by pairs with one radiomarked partner (unfilled bars) during 1999–2001 at the California Channel Islands, USA (mean ± SE). Numbers within bars indicate sample sizes.

throughout the chick-rearing period and tended to reach peak fledging mass at earlier ages than chicks raised by a radiomarked parent (Figure 2).

Wing growth rate. Chicks raised by unmarked pairs also tended to have faster wing growth rates than chicks raised by radiomarked pairs (Figure 1*b*), but these results were not statistically significant when we controlled for year, nest type, and hatching date (treatment: $F_{1,73}=3.27, P=0.07$; year: $F_{2,73}=0.50, P=0.61$; nest type: $F_{2,73}=0.15, P=0.86$; *z*-score Julian hatch date: $F_{1,73}=8.31, P<0.01$). We obtained similar results after excluding pairs nesting in the artificial nest boxes from the analyses (treatment: $F_{1,47}=2.13, P=0.15$; year: $F_{2,47}=0.46, P=0.64$; nest type: $F_{1,47}=0.01, P=0.92$; *z*-score Julian hatch date: $F_{1,47}=4.77, P=0.03$).

Peak fledging mass. Chicks raised by unmarked pairs had higher peak fledging masses than chicks raised by radiomarked pairs (treatment: $F_{1,87}=13.64, P<0.001$; year: $F_{2,87}=0.31, P=0.73$; nest type: $F_{2,87}=2.08, P=0.13$; *z*-score Julian hatch date: $F_{1,87}=6.60, P=0.01$; Figure 1*c*). We obtained similar results after excluding pairs nesting in the artificial nest boxes from the analysis (treatment: $F_{1,55}=$

10.46, $P<0.01$; year: $F_{2,55}=0.25, P=0.78$; nest type: $F_{1,55}=2.93, P=0.09$; *z*-score Julian hatch date: $F_{1,55}=1.89, P=0.18$).

Fledging success.   Radiomarked pairs fledged fewer chicks than unmarked pairs (multiple logistic regression, $n=143$ pairs; treatment: Wald $\chi_1^2=4.13, P=0.04$; year: Wald $\chi_2^2=0.73, P=0.70$; nest type: Wald $\chi_2^2=0.17, P=0.92$; *z*-score Julian hatch date: Wald $\chi_1^2=9.94, P<0.01$; Figure 1*d*). We obtained similar results after excluding pairs nesting in the artificial nest boxes from the analysis (multiple logistic regression, $n=93$ pairs; treatment: Wald $\chi_1^2=5.22, P=0.02$; year: Wald $\chi_2^2=3.75, P=0.15$; nest type: Wald $\chi_1^2=0.19, P=0.66$; *z*-score Julian hatch date: Wald $\chi_1^2=10.11, P<0.01$).

Double brooding

Altogether, 61 unmarked pairs and 46 radiomarked pairs successfully fledged their alpha
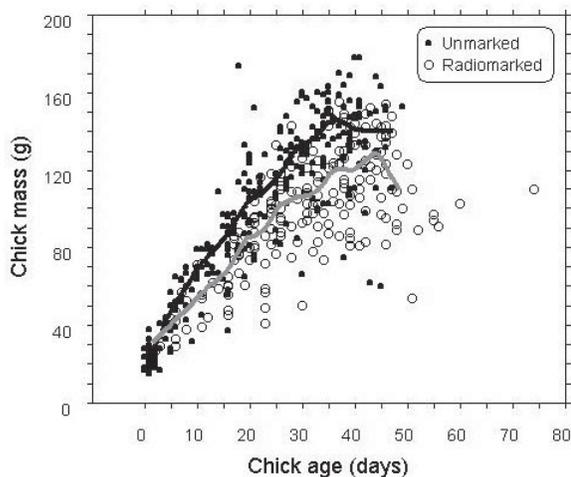

Figure 2. Cassin's auklet chicks raised by unmarked parents (filled circles, dark line, $n = 299$) were heavier than chicks provisioned by a pair with a currently radiomarked parent (unfilled circles, gray line, $n = 199$) throughout the chick-rearing period at the California Channel Islands, USA. Multiple measurements on individual chicks are included, and all years (1999–2001) are pooled. Each data point represents a single alpha chick's measurement and the corresponding status of the parents. Chicks in the radiomarked group that were measured before the parent was actually radiomarked were considered to have unmarked parents until after the transmitter was attached to the parent. Lines were fitted with a LOWESS function through the 50th day of age.
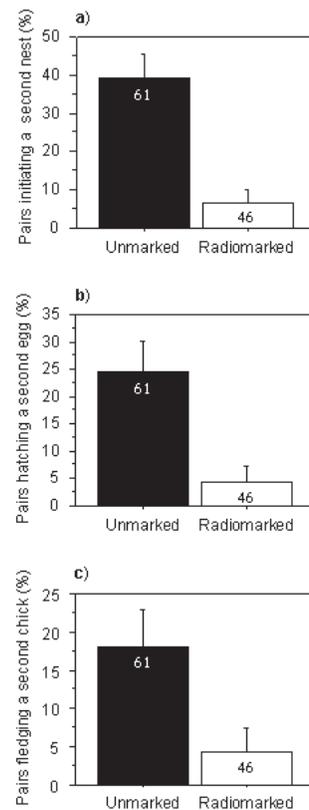

Figure 3. The frequency of unmarked (filled bars) and radiomarked (unfilled bars) Cassin's auklet pairs that (a) initiated a second clutch, (b) hatched a second egg, and (c) fledged a second chick after successfully fledging their first (alpha) chick during the 1999–2001 breeding seasons at the California Channel Islands, USA (mean ± SE). Numbers within bars indicate sample sizes.

chick. Of these, unmarked pairs were more likely to initiate a second clutch than radiomarked pairs (multiple logistic regression, $n = 107$ pairs; treatment: Wald $\chi^2_1 = 7.05$, $P < 0.01$; year: Wald $\chi^2_2 = 17.80$, $P = 0.0001$; nest type: Wald $\chi^2_2 = 0.78$, $P = 0.68$; z-score Julian hatch date of first clutch: Wald $\chi^2_1 = 7.99$, $P < 0.01$; Figure 3*a*). However, unmarked pairs did not hatch a second egg (multiple logistic regression, $n = 107$ pairs; treatment: Wald $\chi^2_1 = 1.14$, $P = 0.29$; year: Wald $\chi^2_2 = 0.85$, $P = 0.65$; nest type: Wald $\chi^2_2 = 0.13$, $P = 0.94$; z-score Julian hatch date of first clutch: Wald $\chi^2_1 = 3.22$, $P = 0.07$) or fledge a second chick (multiple logistic regression, $n = 107$ pairs; treatment: Wald $\chi^2_1 = 0.01$, $P = 0.97$; year: Wald $\chi^2_2 = 0.16$, $P = 0.92$; nest type: Wald $\chi^2_2 = 0.01$, $P = 0.99$; z-score Julian hatch date of first clutch: Wald $\chi^2_1 = 3.06$, $P = 0.08$) more often then radiomarked pairs (Figures 3*b* and 3*c*).

Sex of radiomarked parent

The probability of fledging an alpha chick depended on the sex of the radiomarked parent (multiple logistic regression, $n = 63$ pairs; sex: Wald $\chi^2_1 = 3.86$, $P = 0.05$; year: Wald $\chi^2_2 = 0.46$, $P = 0.80$). Pairs containing a radiomarked female fledged 77% of their chicks, whereas pairs containing a radiomarked male fledged only 50% of their chicks. However, we detected no difference in mass growth rate (sex: $F_{1,20} = 0.92$, $P = 0.35$; year: $F_{2,20} = 4.11$, $P = 0.03$), wing growth rate (sex: $F_{1,35} = 1.89$, $P = 0.18$; year: $F_{2,35} = 0.10$, $P = 0.90$), or peak fledging mass (sex: $F_{1,38} = 0.01$, $P = 0.97$; year: $F_{2,38} = 0.40$, $P = 0.68$) between chicks raised by pairs containing a radiomarked male or female. Additionally, the sex of the radiomarked partner did not influence the likelihood that a pair would initiate a second clutch (multiple logistic regression, $n = 40$ pairs; sex: Wald $\chi^2_1 = 0.01$, $P = 0.97$; year: Wald $\chi^2_2 = 0.01$, $P = 0.99$), hatch a second egg (multiple logistic regression, $n = 40$ pairs; sex: Wald $\chi^2_1 = 0.01$, $P = 0.98$; year: Wald $\chi^2_2 = 0.01$, $P = 0.99$), or fledge a second chick (multiple logistic regression, $n = 40$ pairs; sex: Wald $\chi^2_1 = 0.01$, $P = 0.98$; year: Wald $\chi^2_2 = 0.01$, $P = 0.99$).

Long-term effects

We resighted 12 of 74 (16%) individuals nesting during a subsequent breeding season after they had been radiomarked in 1999 or 2000. Of these individuals, all had shed their transmitter, healed their attachment sites, and normally molted their feathers around the attachment site. We resighted 37 of 115 (32%) individuals nesting during a subsequent breeding season that were not marked with trans-

mitters in 1999 or 2000. Fifty percent of the 12 resighted individuals in the radiomarked group and 46% of the 37 resighted individuals in the unmarked group nested in the same site they used in the prior year.

Discussion

We found that the reproductive performance of Cassin's auklet parents was reduced by externally attached radiotransmitters. Chicks raised by unmarked pairs had faster body mass and wing growth rates, larger peak fledging masses, and higher fledging success than chicks raised by radiomarked pairs. Overall, radiomarking a partner in a pair reduced chick mass growth rates by 1.42 g d^{-1}, wing growth rates by 0.39 mm d^{-1}, peak fledging mass by 29.4 g, and fledging success by 29% compared to unmarked pairs. Furthermore, of those pairs that successfully fledged their alpha chick, unmarked pairs were more likely to initiate a second clutch but did not hatch a second egg or fledge a second chick more often than radiomarked pairs.

Few studies have examined radiotransmitter effects on alcids, but each has found some adverse effects on breeding behavior and reproductive performance. Using tail-mounted radiotransmitters, Wanless et al. (1989) found that radiomarked common murres (*Uria aalge*) and razorbills (*Alca torda*) tended to make fewer foraging trips per day, were away for longer periods, and returned more often without food for their chicks than unmarked birds. In a similar study using back-mounted radiotransmitters, Wanless et al. (1988) found that common murres fitted with transmitters that had external antennas spent less time attending the breeding colony, were absent for longer periods, and delivered food to chicks less frequently than murres fitted with transmitters that had internal antennas or unmarked murres. However, this change in parental behavior did not reduce fledging success because the mates of radiomarked partners compensated by increasing the amount of food delivered to chicks (Wanless et al. 1988). Similarly, thick-billed murre (*Uria lomnia*) parents that were fitted with time-depth recorders lost weight at a faster rate, attended nests less often, and fed their chicks less frequently than unmarked birds (R. Paredes, Memorial University of Newfoundland, unpublished data). Yet, again, fledging success was not influenced, because the partners of marked birds

increased their feeding rates to compensate for their mates' reduction in parental care (R. Paredes, Memorial University of Newfoundland, unpublished data). Unlike common murres and thick-billed murres, partners of radiomarked Cassin's auklets were either unable or unwilling to compensate for their partners' reduced chick provisioning, and chick growth and survival were negatively affected.

In addition to a reduction in chick growth and survival, pairs with a radiomarked partner also initiated fewer second clutches (7%) than unmarked pairs (39%) after successfully fledging their alpha chick. Raising a second chick during the same breeding season is unique to Cassin's auklets breeding in the southern portion of their range (Manuwal and Thoresen 1993). Because the cost of initiating and successfully rearing a second chick is substantial (Ainley et al. 1990), the occurrence of double brooding typically indicates that parents are in good physical condition and environmental conditions are particularly favorable for breeding. Thus, although we did not measure parental condition directly, the 32%, 21%, and 14% reduction in the number of radiomarked pairs initiating, hatching, and successfully fledging a second chick, respectively, suggests that transmitters reduced parents' body condition. In accordance, several studies have documented mass loss after attaching external recording devices to alcids (Croll et al. 1992; Falk et al. 2000; but see Tremblay et al. 2003).

The mechanism by which externally attached transmitters reduced the reproductive performance of Cassin's auklets is unclear. Cassin's auklets have relatively high metabolic rates, probably due to high costs of flapping flight and pursuit diving and must consume about 67% of their body mass equivalent in euphausiids daily to meet their energy expenditure during chick rearing (Hodum et al. 1998). We speculate that radiomarked birds expended more energy and foraged less efficiently than unmarked parents due to an increase in aerodynamic and hydrodynamic drag during long-distance flights to foraging areas (mean distance = 18 km; J. Adams, United States Geological Survey, unpublished data) and underwater pursuit diving for prey (average maximum diving depth = 28 m; Burger and Powell 1990). For instance, although fitting common murres with transmitters that had external antennas reduced parental care, fitting common murres with transmitters that had internal antennas had no adverse effects on parental care despite the heavier mass of the internal transmitter

package (Wanless et al. 1988). Wilson et al. (1986) found that swimming speeds of African penguins (*Spheniscus demersus*) were inversely related to the size of an externally attached data-recording device and concluded that while attachments should have as little mass as possible, it is more important that the stream-lining of marine animals be altered as little as possible. Similarly, the foraging-trip durations of chinstrap penguins (*Pygoscelis antartica*; Croll et al. 1991; but see Croll et al. 1996), adélie penguins (*Pygoscelis adeliae*; Watanuki et al. 1992; but see Ballard et al. 2001), royal penguins (*Eudyptes schlegeli*; Hull 1997), and Humboldt penguins (*Spheniscus humboldti*; Taylor et al. 2001) were lengthened by attaching external recording devices. These results suggest that an increase in hydrodynamic drag caused by externally attached radiotransmitters had an important influence on the energy expenditure and foraging ability of Cassin's auklets.

An increase in mass and aerodynamic drag also might have contributed to reduced reproductive performance of radiomarked auklets. Cassin's auklets commonly carry meal loads to chicks that weigh (22.9 ± 9.1 g, mean ± SD; J. Adams, United States Geological Survey, unpublished data) far more than the radiotransmitters we used (3 g). Therefore, it is unlikely that the mass of the transmitter adversely affected auklets, but aerodynamic drag may have contributed. The increased hydrodynamic and aerodynamic drag associated with an externally attached radiotransmitter probably

An adult Cassin's auklet with an externally attached radiotransmitter. Photo by J. Adams.

increased the energy expenditure and reduced foraging efficiency of radiomarked parents, causing a reduction in the amount of energy available to provision chicks. Because Cassin's auklets are relatively long-lived, it is likely that radiomarked parents transferred the cost of carrying a transmitter to their offspring by reducing their chick provisioning rates (e.g., Sæther et al. 1993, Mauck and Grubb 1995) or deserting the reproductive attempt (J. Adams, United States Geological Survey, unpublished data), such that they did not diminish their own prospects for survival and future reproduction (e.g., Stearns 1992).

Interestingly, we found that fledging success was reduced more when we attached transmitters to the male parent (50% fledged) than when we radiomarked female Cassin's auklets (77% fledged). It is possible that male parental care during chick rearing is more important to fledging success than female care and that radiomarking males disproportionately reduced the amount of parental care received by the chick. Sex differences in parental care are not well known for Cassin's auklets, but Pyle et al. (2001), using long-term data, concluded that the reproductive success of Cassin's auklets may be optimized by the behavior of the male rather than the female. Additionally, several studies on alcids have shown male-biased parental care during chick rearing. For example, male little auks (*Alle alle*) fed chicks more often and spent more time at the colony than females during the late chick-rearing period (A. M. A. Harding, Polish Academy of Sciences, unpublished data). Similarly, male marbled murrelets visited nests and presumably fed chicks more often than females during the latter half of chick rearing (Bradley et al. 2002). In addition, sex differences in types of prey delivered to chicks have been observed in razorbills (*Alca torda*; Wagner 1997) and crested auklets (*Aethia cristatella*; Fraser et al. 2002). Thus, male parental care also may be more important to chick survival than female parental care in Cassin's auklets. However, it is unclear why fledging success was influenced by the sex of the radiomarked parent, but chick growth rates and peak fledging masses were not.

Although we could not directly examine the effects of radiotransmitters on adult survival or at-sea distribution, we found little evidence of adverse effects. Of the 136 Cassin's auklets we radiomarked, only 9 (7%) individuals were not subsequently found. Because radio failure was com-

mon, especially in 1999, these results indicate that (immediate) transmitter-associated mortalities were rare. Furthermore, of the 12 previously radiomarked individuals we resighted nesting during a subsequent breeding season, each individual had shed the transmitter, the attachment site was healed, and the feathers around the attachment site had molted normally. We also found no evidence that radiomarking reduced nest-site fidelity; 50% of the 12 resighted individuals in the radiomarked group and 46% of the 37 resighted individuals in the unmarked group nested in the same site they had used in the prior year. Finally, radiomarked Cassin's auklets foraged in similar areas (J. Adams, United States Geological Survey, unpublished report) compared to unmarked Cassin's auklets that were surveyed concurrently by aircraft (J. W. Mason, United States Geological Survey, unpublished report) and previously by ship (Hunt et al. 1981). Additionally, Whitworth et al. (2000*b*) found that radiomarked Xantus's murrelets foraged at similar or greater distances from their colony during the breeding season than had been previously reported for (unmarked) Xantus's murrelets by Hunt et al. (1981) and Briggs et al. (1987). These results indicate that the at-sea movements and distribution of alcids were relatively unaffected by radiotransmitters.

Management implications

Despite the negative effects of externally attached radiotransmitters on the breeding performance of Cassin's auklets, telemetry remains an essential tool for studying alcids and other seabirds. For example, radiotelemetry currently is the only reliable technique for finding nests and assessing the breeding phenology of marbled murrelets (Lougheed et al. 2002*b*), a species of critical conservation concern. However, biologists should be aware of the potential effects telemetry has on their study animal so that management decisions are not biased by research techniques. The results of our study on Cassin's auklets and those on larger alcids such as common murres, thick-billed murres, and razorbills (Wanless et al. 1988, 1989; R. Paredes, Memorial University of Newfoundland, unpublished data) indicate that externally attached devices negatively affect the breeding performance of several species of alcids. We suggest that telemetry should be used with caution when evaluating the reproductive performance of alcids, but it prob-

ably is still a valuable technique to assess their at-sea movements, foraging ranges, and risks at sea. In addition, our results suggest that radiomarking females rather than males may partially mitigate some of the adverse effects on reproductive performance.

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Joshua T. (Josh) Ackerman is a wildlife biologist with the Biological Resources Discipline of the United States Geological Survey. He received his B.Sc. in wildlife, fish, and conservation biology (1997) and his Ph.D. in ecology (2002) at the University of California, Davis, where he studied factors influencing nest predation and population dynamics of waterfowl. His research interests include linking behavioral, population, and community ecology with the management of waterbirds. ***Josh Adams*** is a biologist with the Biological Resources Discipline of the United States Geological Survey. He received his B.A. in biology at University of California, Santa Cruz (1993) and his M.Sc. in marine science at Moss Landing Marine Laboratories, California State University (2004), where he studied the foraging ecology and breeding biology of Cassin's auklets nesting at the California Channel Islands. His research interests include foraging ecology, oceanography, and seabird conservation. Josh currently is working with Ashy storm-petrels in southern California, and plans to resume additional foraging behavior studies involving Cassin's auklets. ***John Y. Takekawa*** is a research wildlife biologist with the Biological Resources Discipline of the United States Geological Survey. He received his B.Sc. in wildlife science at the University of Washington (1979), his M.Sc. in wildlife resources at the University of Idaho (1982), and his Ph.D. in animal ecology at Iowa State University (1987). His research interests include application of radiotelemetry in studies of migration and wintering ecology of waterbirds and wetland restoration in the San Francisco Bay estuary. ***Harry R. Carter*** has studied alcids and other seabirds in the North Pacific Ocean since 1974. He received his B.Sc. in zoology at the University of British Columbia (1978) and his M.Sc. in zoology at the University of Manitoba (1985). He developed various seabird research projects in California, working as a staff biologist for Point Reyes Bird Observatory (1983-1988) and as a faculty associate in the Department of Wildlife at Humboldt State University (1989-2003). Harry continues to write up past seabird studies and assist government and private groups with seabird conservation, research, monitoring, restoration, and management issues through private contracts. ***Darrell L. Whitworth*** has been studying California seabirds since 1991 as a biologist with Humboldt State University (1991-2003) and currently as a wildlife biologist with the California Institute of Environmental Studies. He received his B.Sc. in wildlife and fisheries biology at the University of California, Davis (1989). He has participated in several radiotelemetry studies investigating the at-sea ecology of alcids and is currently leading the research and conservation efforts for Xantus's murrelets in the California Channel Islands. ***Scott H. Newman*** is the Conservation Medicine Scientist at Wildlife Trust and is currently an adjunct professor in the Ecology, Evolution and Environmental Biology Department at Columbia University. He received a B.Sc. in biology from Union College (1987), a D.V.M. from Tufts University School of Veterinary Medicine (1992), and a Ph.D. in comparative pathology from University of California, Davis (1998). Formerly, he worked at the Wildlife Health Center and Oiled Wildlife Care Network at University of California, Davis. His radiotelemetry research has contributed to understanding at-sea ecology of alcids and survival of oiled rehabilitated seabirds. His current research is focused on evaluating relationships between disease emergence, pollutants, and the health of wildlife, humans, and the environment. ***Richard T. (Rick) Golightly*** is a professor in the Wildlife Department at Humboldt State University. He received his B.Sc. in biology at the University of California, Irvine (1972), his M.Sc. in zoology (1976) and his Ph.D. in zoology (1981) at Arizona State University. His research interests include conservation, energetics, and habitat use by seabirds and terrestrial carnivores. ***Dennis L. Orthmeyer*** is currently the director of waterfowl and wetlands programs for the California Waterfowl Association. Formerly, he worked as a wildlife research biologist for the U.S. Department of Interior for 20 years. He received his B.Sc. in zoology at North Dakota State University (1976) and his M.Sc. in wildlife biology at the Montana Cooperative Wildlife Research Unit at the University of Montana (1987). His research interests include population dynamics of waterfowl and wildlife-habitat relationships.

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