Mate Switching Patterns in Crested Auklets (*Aethia cristatella*): The Role of Breeding Success and Ornamentation

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We evaluated the causes and consequences of mate switching in crested auklets (*Aethia cristatella*). The crested auklet is a small seabird in which both sexes are similarly ornamented and contribute to parental care. We observed 29 pairs and found that 31% changed mates between breeding seasons. In a logistic regression analysis, we used absolute crest length, breeding success, body condition, and the interaction of crest lengths, in year 1, for males and females to predict the likelihood of switching mates in year 2. The best model predicted that female crest length influences the likelihood of mate switching; specifically, short-crested females were more likely to split up between breeding seasons. A benefit associated with mate switching was that individuals that changed mates were more likely to obtain a new mate with a longer crest. One cost identified with switching mates was a delayed hatch date, although chick quality did not appear to be compromised. Distinct differences in behavior and body morphology exist between males and females; therefore, assumptions that the sexes experience similar costs or benefits in switching mates may not be valid.

Seabird   Mate fidelity

In long-lived organisms, such as seabirds, it is assumed that divorce is an adaptive strategy used to maximize reproductive fitness (Choudhury, 1995). This assumption is based on empirical evidence that reproductive success appears higher in pairs that maintain the same partnership over consecutive breeding seasons (reviewed by Choudhury, 1995, but see Ens, Safriel, & Harris, 1993). Therefore, if divorce is an adaptive strategy used to maximize reproductive fitness, the benefits must outweigh the costs of switching mates for some individuals. Benefits identified with mate switching include an increase in parental care, offspring viability, territory quality, territorial defense abilities of mate, and mate attractiveness. Potential costs identified with mate switching include an initial decrease in reproductive rates, increased risk of predation, and increased risk of damage from fights with rivals (Choudhury, 1995; Ens et al., 1993).

Choudhury (1995) proposes that the factors affecting mate-switching rates are related to life history characteristics and are therefore species specific, and possibly even population specific. Most seabirds have a life history strategy of high annual survival and low reproductive rates (Hamer, Schreiber, & Burger, 2002). A coordinated effort

within a pair is required to successfully rear offspring (Lack, 1968), and a mate change is believed to carry a substantial cost (see Bried & Jouventin, 2002). This position is supported by observations of high mate fidelity in most seabirds (ca. 90% or higher; Bried & Jouventin, 2002).

In this study, we investigated some of the causes and consequences of mate switching in crested auklets (*Aethia cristatella*), a seabird in which both sexes are similarly ornamented, invest heavily in a single offspring each year, and achieve high annual survival (Fraser et al. 1999; Jones & Hunter, 1999; Jones, Hunter, Robertson, & Fraser, in press). We focused on whether male and female crest length, breeding success, and/or body condition influenced mate-switching patterns in between-breeding-season pairings. How crest length may influence mate-switching patterns is of particular interest for this species because prior findings suggest a system of mutual mate choice based on crest length (Jones & Hunter, 1993, 1999). In experiments using taxidermic models, longer-crested models were approached and courted more often than shorter-crested models by both males and females (Jones & Hunter, 1993). Further research revealed a positive correlation between crest length and social dominance for both sexes (Jones & Hunter, 1999), but little support for crest length as condition-dependent ornament (Jones, Hunter, & Fraser, 2000). Jones and Hunter (1999) conclude that crest length likely signals a badge of status that should be favored in mate choice due to the related benefits of having a socially dominant mate.

Methods

Subjects

We studied crested auklets on Buldir Island (52° 21′N, 175° 56′E) in the Aleutian Islands, Alaska, for four breeding seasons (1995–1998). The majority of pairs were followed for only two consecutive breeding seasons within the 4-year period. Our study area was located at Main Talus, a colony of an estimated 250,000 crested auklets (Byrd, Day, & Knudtson, 1983). We captured adult auklet pairs at nesting crevices within the first week of chick hatching and measured mass, tarsus length, and crest length. The birds were sexed using bill shape differences (98% accuracy; Jones, 1993a). Each bird was fitted with a U.S. Fish and Wildlife Ser-

vice stainless steel leg band for individual identification.

It was not possible to determine whether a nonreturning bird had died or moved away. Therefore, we used the term "split" (Rowley, 1983) to refer to a pair that did not reunite (i.e., at least one member of the pair was known to have mated with a new partner in the following year). Our analysis is limited to splits that occurred between breeding seasons. Within-season splits were logistically impossible to determine. Pairs were followed for two breeding seasons. We used the measurements of ornaments the first year we found the pair and their pairing status (reunited or split) from the subsequent and consecutive year. In our analyses no individuals were used twice (except for a paired analysis of chick quality; see below).

We measured breeding success for both the first year and subsequent year for 26 out of 29 pairs followed. Auks, in general, cannot be handled during incubation due to increased likelihood of abandonment. Therefore, breeding success was limited to pairs that successfully fledged a chick from hatching (i.e., failure during incubation was not incorporated into analyses). Chicks were considered fledged if they lived to 26 days of age (Fraser et al., 1999). Typical of most seabirds, crested auklets cannot rear a chick successfully without the efforts of both parents (see Lack, 1968). Therefore, a pair's breeding success is equivalent to an individual's breeding success (without considering extra-pair fertilizations).

To evaluate if crest length changed in individuals between sample years, we used paired, two-tailed *t*-tests on males and females. We used auklets from the following pairs of study years: 1996–1997 ($N = 7$ females, 10 males) and 1997–1998 ($N = 13$ females, 14 males). The other pair of study years (1995–1996) was not included because of low sample sizes ($N = 2$ females, 3 males).

Causes of Splitting

In a logistic regression (Sokal & Rohlf, 1995), we used absolute crest length, breeding success, body condition (residuals of body mass regressed on tarsus; Fraser, Jones, & Hunter, 2002), and the interaction of crest lengths, in year 1, for males and females to predict the likelihood of switching mates in year 2. Likelihood ratio tests were used for model selection (similar to backwards selection). We did

not consider the difference in crest size between males and females because this would require the assumption that the sexes have the same effect but in opposite directions [i.e., $B_0 + B_1$ (male crest-female crest) = $B_0 + B_1$ male crest − B_1 female crest], and there is no literature to warrant this assumption. Using simple regression models, we examined whether birds that reunited had longer crests than expected for their body size (tarsus length).

Consequences of Splitting

We examined whether breeding success in the second season differed between reunited and new (i.e., one new parent in the pair) pairs using a chi-square analysis. Because breeding success was quite high for both groups (see Results), we also examined chick quality by comparing chicks reared by reunited and new pairs. Chick quality was measured by the following variables: hatch date rank, hatch mass (g), linear growth of mass (g/day; days 3–20), linear growth of wing (mm/day; days 3–20), fledging mass (g), and fledging wing length (mm; both fledging variables were measured within 2 days of fledging; Fraser et al., 1999). We used a nonpaired *t*-test, with sequential Bonferroni correction (Rice, 1989), to compare chick quality for pairs with the same partner versus those with a new partner, and performed a paired test (one-tailed Wilcoxon

matched-pairs signed-ranks test, with Bonferroni correction) for the above chick quality measures on a smaller sample, in which one individual (usually the male) from the old pair remained for a subsequent attempt. This allowed us to investigate whether an individual that had split obtained an offspring of higher quality with the new partner.

We also looked for crest length differences between the old partner and the new partner. For individuals with new partners the following year, we compared the crest length of the new partner with that of the old partner with a one-tailed, Wilcoxon test.

Results

Causes of Splitting

Thirty-one percent (9 out of 29) of crested auklet breeding pairs on Buldir Island split between breeding seasons (Fig. 1). Three auklet pairs had undetermined breeding success and, of the remaining 26 pairs, 22 successfully fledged a chick (85%). Breeding success in year 1 for pairs that split or reunited was 75% and 89%, respectively (Fig. 1). There were no differences in colony-level breeding success among years (1996 to 1998; Fraser et al., 2002).

In 17 of the 29 auklet pairs (58%), the male crest was equal to or longer than his partner's crest, mean = 6.6, SD = 5.4 mm difference. In the remain-
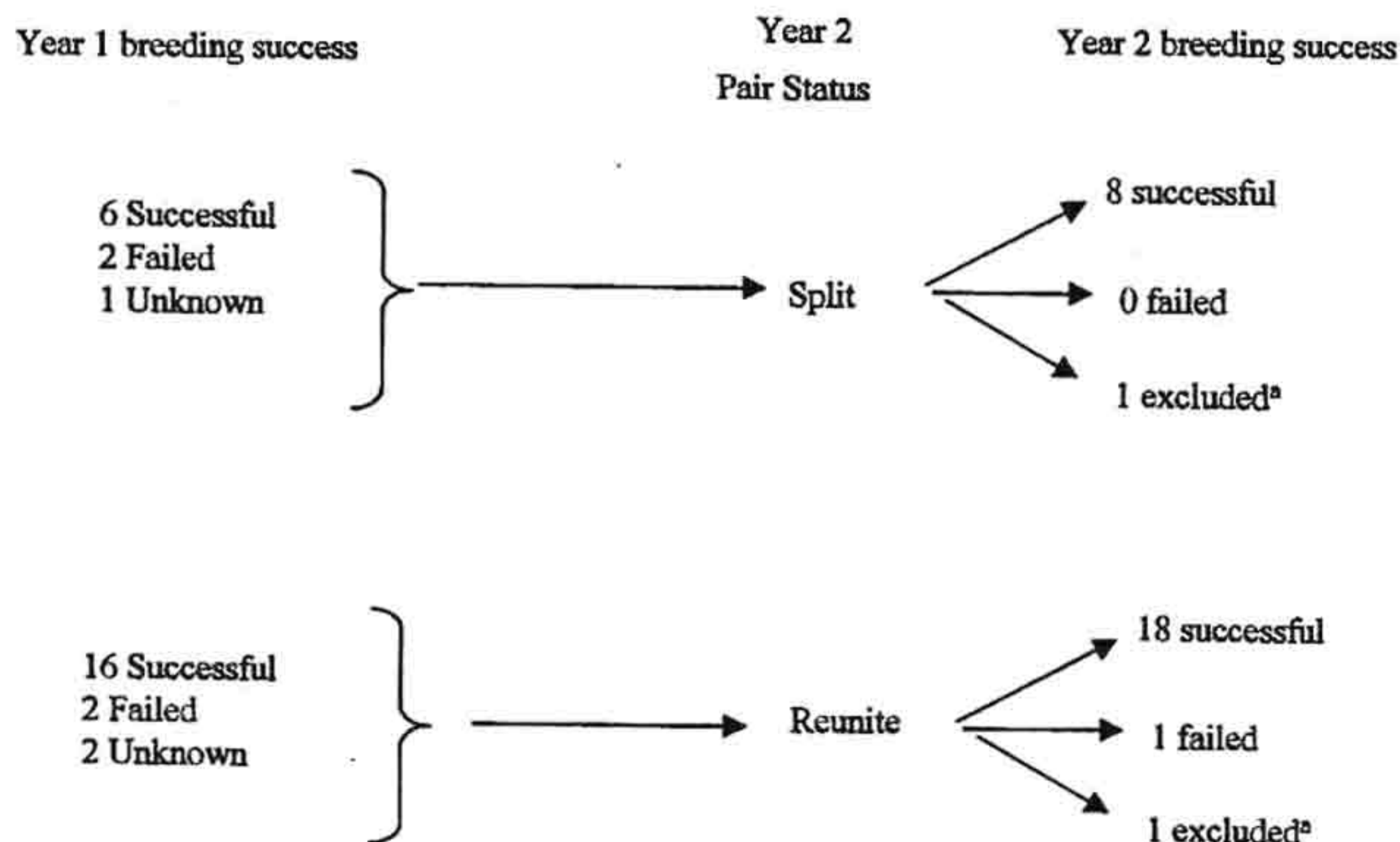

Figure 1. Crested auklet breeding success (i.e., fledged chick), and subsequent pair status and breeding success for the following consecutive season. [a]One auklet pair for each category (i.e., split and reunite) was excluded from the chi-square test because failure of breeding was due to investigator disturbance during the incubation period.

ing 12 pairs, the male crest length averaged 6.4 mm, SD = 4.5 shorter than his partner's crest length. We performed a logistic regression on pair status, incorporating all variables (breeding success in year 1, male crest length, female crest length, male body condition, female body condition, and the interaction between male crest length and female crest length), but after applying likelihood ratio tests, only female crest size was incorporated into the model. Thus, mate status in year 2 was influenced by female crest length in year 1 [−log likelihood (1, $N = 29$) = −13.38, $\chi^2 = 5.97$, $p < 0.02$]. Reunited and split females did not have longer crests than expected for their size ($r = 0.20$, $p > 0.39$, $r = 0.24$, $p > 0.54$, respectively). However, reunited males had a significant and positive correlation between crest length and tarsus length ($r = 0.55$, $p < 0.01$), but males that split had no such relationship ($r = 0.36$, $p = 0.35$).

Consequences of Splitting

In the second season, we observed no differences in breeding success between new (100%) and reunited pairs (95%) [Fisher exact test, $\chi^2(1, N = 27) = 0.40$, $p > 0.99$] (Fig. 1). Reunited pairs had chicks of similar quality compared with pairs in which one bird was a new partner (for all quality variables, $p > 0.2$). Although we observed a trend that reunited pairs had an earlier mean hatch date [one-tailed t-test, (1, $N = 26$) = 1.9, $p < 0.03$, mean = 9.0, SD = 1.9 days] compared to pairs with new partnerships (mean = 6.7, SD = 2.9 days), this difference was nonsignificant at the table-wide level with sequential Bonferroni criteria (p must be <0.008; Rice, 1989). Chick quality did not differ before and after a split with one parent remaining the same [Wilcoxon test, ($N = 5$) all $p > 0.2$].

Of the nine pairs that split, 78% of the individuals that returned to the original crevice were male (i.e., seven of nine females were not observed again). Individuals (seven males and two females) were more likely to obtain a new mate with a longer crest in the year following a split [first partner mean = 37.4, SD = 4.6 mm; second partner mean = 43.5, SD = 6.6 mm; one-tailed Wilcoxon test, $z(N = 9) = -2.2$, $p < 0.02$]. If we considered only returning males from this sample they also paired with a new, longer crested female in the following year [first partner, mean = 36.1, SD = 4.1 mm; second partner, mean = 41.6, SD = 6.3 mm; one-tailed Wilcoxon test, $z(N = 7) = -1.7$, $p < 0.05$].

Individual crest length decreased between year 1 and year 2 for both males and females (Table 1).

Discussion

Many long-lived seabirds have high mate fidelity (ca. 90% or higher; Bried & Jouventin, 2002), yet in crested auklets we observed that approximately one third switched mates. We demonstrated that the probability of changing mates between breeding seasons was influenced by crest length, but not by previous breeding success or body condition. Females with shorter crests were in partnerships that were more likely to split than were females with longer crests. Furthermore, in the following breeding season, split individuals returning to the same crevice had a new, longer-crested mate.

Jones and Montgomerie (1991) report that pairs of least auklets (*A. pusilla*) with longer auricular plumes are more likely to reunite than those with shorter plumes. However, it is male, not female, auricular plume length that influences the probability of divorce; and they conclude mate retention may be controlled by female choice. Thus, ornamentation influences mate-switching patterns in both least and crested auklets, but the sex driving these patterns differ between the species.

Table 1. Changes in Crest Length in Individuals Between Breeding Seasons

Year	Males				Females			
	Mean	SD	N	t-Test (p)[a]	Mean	SD	N	t-Test (p)
1996 to	45.9	6.9	10	4.10 (0.003)	43.0	4.4	7	3.83 (0.009)
1997	42.8	5.4			38.8	5.9		
1997 to	41.6	4.6	14	2.67 (0.019)	42.4	3.8	13	3.26 (0.007)
1998	39.8	4.0			39.6	4.0		

[a]Paired t-test; no individuals were used in more than one analyses.

Crested auklets are one of the few species in which mutual mate choice, based on a sexually selected ornament, has been established experimentally (Jones & Hunter, 1993). Therefore, it is enigmatic that crest length in females, rather than the interactive term for male and female crest length, predicted pair status. Such a pattern could occur if (1) there were sexual differences in survival rates, (2) crest length and survival were correlated for females, and (3) sexual differences in the level of choosiness resulted in male rejection of short-crested females, and/or female intraspecific competition for mates (see Jones & Hunter, 1999). Jones et al. (in press) find no support for the first two explanations. While the latter explanation remains equivocal, Jones and Hunter (1999) offer convincing evidence that longer crested individuals are more dominant and, therefore, may be more likely to remain paired. Furthermore, Fraser et al. (2002) suggest male parental investment may be greater than female parental investment, and sexual selection models predict male-biased mate choice under these circumstances (see Trivers, 1972). To unravel this puzzle further, more data are required to distinguish between male rejection and female–female competition in remating decisions.

The fate of the seven females and two males that split (and were no longer associated with a crevice) was unknown; they could have (1) found a new mate, (2) skipped a breeding season, or (3) died. Adult crested auklets have at least a 90% chance of living from one breeding season to the next (Jones et al., in press). Thus, of the 58 birds followed, approximately six were expected to have died, in which case, the minimum divorce rate (both individuals of pair are alive, but not together) was approximately 10% (3 out of 29 pairs). In another marked population of crested auklets on Talan Island (the Sea of Okhotsk), the minimum divorce rate was 25% (3 of 12 pairs were alive, but not together in the following year) and the maximum rate of splitting (including both missing and divorced birds) was 58% (7 out of 12 pairs split between study years; Zubakin, 1990). There is no significant difference in splitting rates between these studies ($\beta^2 = 2.7$, $p = 0.10$), suggesting these rates are not population specific.

Even if the 31% splitting rate was completely attributed to death, a benefit identified with mate switching was the opportunity to pair with a longer-crested bird. This pattern was not attributable to an-nual changes in individuals' crest length (Jones et al., 2000; this study). A possible cost of mate switching for both sexes was a delayed hatch date. Emslie, Sydeman, and Pyle (1992) and Jones and Montgomerie (1991) observed reproductive costs (e.g., reduced hatching success, delayed hatch dates) associated with mate switching in Cassin's (*Ptychoramphus aleuticus*) and least auklets, respectively. Female crested auklets may bear the additional cost of switching nest sites with a partner change because males were more likely to retain possession of the crevice.

Crested auklets have distinct sexual differences in behavior (see Jones, 1993b), parental care roles (Fraser et al., 2002), levels of aggression (Jones & Hunter, 1999), and body morphology (Jones, 1993a). Thus, we cannot assume that the sexes experience similar costs or benefits in switching mates. Future research should be directed at understanding the relationship between male crest length and crevice acquisition early in the breeding season, measuring costs related to switching nest sites for females, and assessing mate quality for females in new partnerships.

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