Mating and remating of least auklets (Aethia pusilla) relative to ornamental traits

We investigated mating patterns of the least auklet, a small monogamous seabird, at St. Paul Island, Alaska, during three breeding seasons. Least auklets mated assortatively with respect to both plumage color, a trait important in status signaling, and tarsus length, an index of body size. Least auklets mated disassortatively with respect to the extent of facial plumes, but neither assortatively nor disassortatively for any other ornamental trait (bill color, bill ornament size). Mate fidelity was lower in least auklets than in some long-lived seabird species; when both members survived to a following year, only about two-thirds of pairs reunited. Nearly half of the auklets paired in 1 year obtained a new mate in the following year, either because of mate disappearance or divorce. Interyear fidelity to mates was related only to male ornamentation; males with larger facial plumes were more likely to reunite with their mates the next year than males with smaller plumes. There were no significant differences in the ornaments of females in reunited and divorced pairs. Pairs that reunited also had significantly lighter plumage than pairs that divorced, and the plumage of males reuniting with their mates was significantly paler than that of divorced males. We conclude that the probability of both divorce and remating in this species is influenced by ornamental traits. Our finding that remating was related to male plumage color and ornaments is consistent with the idea that remating is influenced by female choice. Pairs that reunited also bred earlier in the season and had higher reproductive success than pairs with experienced individuals breeding together for the first time. We also found evidence that failure to breed in a given year increased the probability of subsequent divorce. [Behav Ecol 1991;2:249-257]

In birds, both plumage color (Hill, 1990; Högglund et al., 1990) and ornaments (Andersson, 1982; Möller, 1989; Smith and Montgomerie, 1991) have been shown to be important in mate choice. Because ornaments are decorative and often complex morphological traits that are displayed during courtship (Darwin, 1871), plumage color may also be considered an ornamental trait. Changes in such traits before the breeding season—when plumage color becomes brighter and ornaments become more elaborate—have long implicated sexual selection as the mechanism responsible for such elaboration (Darwin, 1871), but only recently has convincing evidence in support of this hypothesis been presented. Most of this evidence comes from manipulative experiments in the laboratory and the field that have shown that females prefer brighter plumages or more elaborate ornaments (Andersson, 1982; Hill, 1990; Högglund et al., 1990; Möller, 1989; Smith and Montgomerie, 1991). Although these preferences should also be manifest in unmanipulated populations, they are, for a variety of reasons, often more difficult to observe and quantify.

Natural patterns of both assortative and disassortative mating (where individuals of similar or dissimilar phenotypes, respectively, mate more often than expected by chance; Burley, 1983) and remating (the tendency to retain a mate from a previous breeding season; Rowley, 1983) can result from mate preferences. Among birds, for example, assortative mating related to plumage polymorphism has been described in parasitic jaegers (Stercorarius parasiticus; O’Donald, 1983; but see Furness, 1987) and snow geese (Chen caerulescens; Cooke and Cooch, 1968), and in both species mating preferences have been implicated as the mechanism responsible. Such assortative patterns are only revealed, of course, when there is variation in both males and females in the traits of interest. Until now, no one has looked for assortative mating with respect to ornamental traits in birds, possibly because these are often expressed and variable only in males.

Because some birds maintain long-term pair
bonds that can last for many breeding seasons (Rowley, 1983), mate choice may also involve an annual decision to remate with, or divorce from, the mate of the previous season. For some birds, remating is actively favored because there are reproductive advantages to reuniting with a previous mate (Rowley, 1983). Among the many studies of remating in birds, several concerning seabird species have shown that established pairs have higher reproductive success than pairs breeding together for the first time (e.g., Coulson, 1966; other examples in Rowley, 1983). However, the effects of plumage polymorphism or ornamentation on remating potential have received little attention so far.

In this paper, we examine mating and remating patterns in least auklets (Aethia pusilla) with respect to both plumage color and head ornamentation. Least auklets are small (75–100 g), monogamous seabirds of the Bering Sea region. During the breeding season (May–August), they congregate at dense colonies situated on talus slopes and boulder-strewn shorelines. Their clutch size is one, and both parents provision the chick in its nesting crevice for nearly 4 weeks before the chick departs from the colony (Piatt et al., 1990a; Roby and Brink, 1986a). Before they arrive at breeding colonies in early May, least auklets moult into a strikingly variable summer plumage with three kinds of ornamentation on their heads: white facial plumes on their foreheads and auricular area, a colorful bill with a light tip, and a knoblike ornament at the base of the culmen (Bédard and Sealy, 1984). Least auklets are also variable in plumage color, which varies continuously on the underparts from unmarked white to nearly black among adults. Plumage color tends to lighten with age within individuals, light-plumaged birds being dominant over those with dark plumage (Jones, 1990a).

Using model presentation experiments, we previously found that plumage color functions for status signaling on the breeding colony in least auklets (Jones, 1990a) and that both sexes performed more intense courtship displays to models with extensive facial plumes (Jones, 1990b; Jones and Montgomerie, in press). Thus, these traits should be important in inter-and intrasexual selection, respectively.

Because least auklets are sexually monomorphic with respect to plumage color and ornaments, and both males and females have extensive variation in these traits (Bédard and Sealy, 1984; Jones, 1990b; Jones and Montgomerie, in press), we can now ask whether there are natural patterns of assortative mating and remating with respect to both plumage and ornamentation.

**METHODS**

**General**

I. L. J. and an assistant conducted field work at a colony of more than 10,000 least auklets near Tolstoi Point, St. Paul Island, Pribilof Islands, Alaska, USA (57°08' N, 170°17' W) during May–July of 1987, 1988, and 1989. Least auklets nested among sparsely vegetated boulders and rubble along several kilometers of shoreline at the base of a 50-m basalt cliff at this site. We conducted all banding and observations at one densely occupied 10 m × 15-m study plot on the talus slope at Tolstoi Point. Using noose carpets and mist nets, we captured and color-marked 248 birds (234 adults, 14 subadults) in 1987, 369 (306 adults, 63 subadults) in 1988, and 145 (all adults) in 1989. Because the study birds had an annual survival rate of about 0.8 (Jones IL, unpublished data), most birds were present on the plot in the 1 or 2 years after banding. We distinguished subadults (2 year olds) by their dull forehead plumage, worn flight feathers and spotted throats (Bédard and Sealy, 1984). Each auklet was given a numbered USFWS stainless-steel band and a unique combination of three durable, plastic color bands made of 0.6-mm Darvic. Upon capture, we weighed birds to the nearest 1.0 g using a Pesola spring scale and measured culmen, bill depth, wing length, and tarsus length.

To assess parental effort and breeding success, we recorded feeding trips made by all color-marked adult auklets nesting on the study plot. Marked auklets observed carrying food to a crevice were classified as breeders. Auklets that were present on the study plot throughout the nesting period but did not deliver food were classified as nonbreeders. Auklets delivering food were unambiguously identifiable by their bulging throat pouches. From these data, we estimated hatching date of each bird's chick and the likelihood that the chick survived to fledging age. Hatching date was estimated as the date that we first sighted a food delivery by either pair member (both pair members delivered food for the first time on the same day for most pairs). The feeding interval (number of days from the first to the last sighting of each bird with food) was used to assess the likelihood that a pair's chick survived to fledging age. When this interval was less than 25 days, we assumed that the nesting attempt was not successful.

**Identification of pairs**

Pairs of color-marked adults were identified by repeated association and courtship behavior before egg laying (10 May–10 June) in 1987, 1988, and 1989. Most pairs spent many
hours perching together on boulders near their nesting crevice during this period. Color-marked birds were defined as pairs if they were observed associating and courtning on at least 5 different days.

We conducted 4-h watches covering the time of peak auklet activity (1200–1600 h Alaska Daylight Saving Time; Piatt et al., 1990b; Roby and Brink, 1986a) daily from mid-May to early August from a blind at the study plot to monitor the attendance of marked birds and observe their behavior. Courtship behavior of least auklets included a variety of stereotyped vocalizations and display postures (Jones, 1990b). The courtship activity of breeding pairs was most frequent in May and early June and ceased once females had laid their eggs, even though courtship by nonbreeding pairs continued through the entire breeding season. Color-marked pairs that were breeders spent several hours courtting on the surface of the colony nearly every day during the period before laying. In each year many nonbreeding adults were present at the study plot, some paired and others unpaired but actively soliciting possible mates. Sixty-two percent (36/58) of the pairs identified were classified as breeders in 1988; 67% (35/49) were classified as breeders in 1989. Subadult (2-year-old) least auklets directed courtship displays at many individuals they encountered at the colony, but never paired successfully. We found the pair identifications to be reliable because, with few exceptions (involving aggressive competition for mates early in the season), each pair member courted only a single individual of the opposite sex, pairs always entered the same crevice, and pairs that bred initiated chick-feeding on the same day. Courtship behavior similar to that performed on land also occurred on the sea, where auklets gathered in rafts of hundreds or even thousands of birds. Copulations were observed only on the sea. Mate choice probably involved repeated courtship encounters on the colony and at sea, but we were unable to monitor the process in any detail because of the difficulty of observing individuals continuously.

Because least auklets are sexually monomorphic in ornaments, plumage color, and body size (Bédard and Sealy, 1984; Jones, 1990a,b), color-marked individuals could not be sexed with certainty from external measurements. However, we were able to identify a large sample of males from their distinctive vocal advertising display (Jones, 1990b) and females by their association with those males.

We determined which of the color-marked pair members survived to return in years after the one in which they were first identified and determined which pair members disappeared. Least auklets are strongly philopatric to their breeding site, so birds were presumed to have died if they were in regular attendance on the study plot in one year and did not reappear there in a subsequent year. No birds that regularly attended the study plot in one year were found during careful searches of the rest of the Tolstoi Point colony in subsequent years, and no birds that failed to return in 1988 were subsequently seen 1989. Thus, we feel confident in interpreting the disappearance of a marked bird as indicating its death.

Ornamentation and plumage color variability

After each bird was captured, we photographed its head (in profile at a scale of 1:2) in color using electronic flash to provide consistent lighting. The bill color and size of facial plumes (both auricular plumes and forehead plumes) and bill ornament were later measured from the photographs. The auricular plumes were quantified in the field as the distance from the exposed base of the plumes (just below and behind the eye) to the distal end of the longest plume (i.e., auricular plume length) and quantified later from photographs as the sum of the lengths of the exposed portions of each plume feather (i.e., auricular plume score). Auricular plume length thus provides an estimate of the size of the plumes, whereas auricular plume score indicates the extent of auricular plumes covering the face. We scored the extent of forehead plumes using a standard grid marked on transparent Plexiglas, placed over the forehead of each bird in the photographs. This forehead plume score was the count of grid intersections (out of 100 possible) that were over white plumage feathers rather than over the dark gray forehead plumeage. We quantified the bill color by scoring Jet Black (see Smith, 1975, for color descriptions) as 0, Burnt Sienna as 1, Crimson as 2, and Poppy Red as 3 for five areas of the bill. Bill color score is the sum of these five values, so an entirely bright red bill would score 15, and an entirely black bill would score 0. We measured the bill ornament height (above the culmen) directly from the photographs. The average bill ornament was about 2 mm high and, like all other least auklet ornaments, varied greatly among individuals (see Jones, 1990b, for further details on all ornament measures).

To ensure that the variation in ornament size among individuals was greater than that within individuals between years, we calculated the intraclass correlation coefficient ($r_i$; Zar, 1984), or repeatability, of each measure based on data from birds measured in both 1988 and 1989. All repeatabilities were positive and
significantly different from zero (Table 1). Thus, ornament variation within individuals was significantly less than variation among individuals (Table 1), and the ornament size of each individual was similar from year to year.

To score their highly variable plumage color, we photographed the underparts of all birds captured in 1988 and 1989 and scored the extent of dark spotting using a grid marked on transparent Plexiglas. This grid covered >90% of each auklet's breast on the photograph, and the number of grid intersections over dark versus white plumage was counted (out of 100 intersections). This plumage color score was expressed as the count of intersections over dark feathering and thus represents the proportion of each bird's breast with dark plumage. Each bird was also assigned to a plumage color category in the field (see Jones, 1990a, for details) by the density of dark spotting on the underparts as follows: 0 = immaculate (0% dark); 1 = lightly spotted (1%-20% dark); 2 = intermediate (21%-50% dark); 3 = heavily spotted (51%-80% dark); or 4 = dark (>80% dark). We also estimated body condition of marked birds as the residual mass from the model I regression of mean mass on tarsus length.

Statistical analyses

Only pairs with individuals of known sex were included in the analyses. Unless otherwise noted, data are from 1988 and 1989. We pooled data from these 2 years in most analyses, but in each case there was no qualitative difference in the patterns found in each year taken separately (see below). When pooling data over the 2 years, we used only data from 1988 when we had data from the same pair in both years. Descriptive statistics are presented as mean ± SE. We used model II (reduced major axis) regressions throughout because both variables were continuous and measured with error (see McArdfle, 1988).

RESULTS

Mating patterns

There were significantly more matings be-

<table>
<thead>
<tr>
<th>Ornamental trait</th>
<th>$r$</th>
<th>SE</th>
<th>$F$ ratio (df)</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Auricular plume length</td>
<td>.735</td>
<td>0.051</td>
<td>6.56 (81,82)</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Auricular plume score</td>
<td>.581</td>
<td>0.075</td>
<td>3.78 (77,78)</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Forehead plume score</td>
<td>.412</td>
<td>0.092</td>
<td>2.40 (81,82)</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Bill color score</td>
<td>.523</td>
<td>0.081</td>
<td>3.20 (81,82)</td>
<td>&lt;.0001</td>
</tr>
<tr>
<td>Bill ornament height</td>
<td>.448</td>
<td>0.093</td>
<td>2.76 (74,75)</td>
<td>&lt;.0001</td>
</tr>
</tbody>
</table>

* $r$, the intraclass correlation coefficient; Zar, 1984.

tween birds of similar plumage color and fewer matings between birds of different plumage color than expected by chance ($x^2 = 7.47, df = 2, p = .02$; Table 2). The greatest deviation from random mating resulted from excess pairing among birds of pale plumage (Table 2). For this analysis we used data on plumage color categories estimated in the field rather than from plumage color scores determined from photographs (see Methods) because the sample size of photographed pairs was too small for analysis. Data from 1988 and 1989 were also pooled because there was no difference between years in the frequencies of matings among the various plumage color categories ($x^2 = 3.15, df = 2, p = .21$). We calculated expected values by assuming random matings among the birds of each plumage color category in the sample of mated pairs. We conclude from this analysis that there was assortative mating with respect to plumage color in this population of least auklets.

There was also assortative mating in relation to body size, indicated by the significant positive correlation between male and female tarsus lengths within pairs ($r = .54, p = .01, n = 50$; Figure 1). Because there were no significant correlations between tarsus length and plumage color or any of the five ornaments studied ($r = .02-.13, p = .13-.83, n = 203$ adults in each case), we conclude that assortative mating by body size was independent of assortative mating with respect to these other traits. However, tarsus length did increase with age (increased between 1988 and 1989 in 80 adults measured in both years, $r = .645, df = 79, p < .0001$), so this pattern of assortment could have resulted from an age correlation within pairs (see Reid, 1988).

Before looking for evidence of deviations from random mating in relation to auklet ornaments, we used analysis of covariance to check for differences between years in the relationships between male and female ornaments within pairs. None of these relationships differed significantly between years (ANCOVAs, $p > .05$ for each year-by-trait interaction), so pairs from both 1988 and 1989 (no individual included more than once) were pooled for further analysis. Auklets mated dis-
Table 2
Evidence for assortative mating in least auklets with respect to plumage color in 1988 and 1989

<table>
<thead>
<tr>
<th>Plumage categories of mated pairs</th>
<th>A × A</th>
<th>A × B</th>
<th>B × B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of pairs observed at Tolstoi</td>
<td>18</td>
<td>28</td>
<td>39</td>
</tr>
<tr>
<td>Expected with random mating</td>
<td>12.5</td>
<td>40.2</td>
<td>32.4</td>
</tr>
<tr>
<td>Deviation from expected (%)</td>
<td>+44</td>
<td>−30</td>
<td>+20</td>
</tr>
</tbody>
</table>

*Plumage categories pooled so that all expected values were >5. A includes categories 0 (white) and 1 (lightly spotted); B includes categories 2 (intermediates) and 3 (heavily spotted birds).*

assortatively by auricular plume score (Table 3; Figure 2) but did not mate significantly differently from random for any other ornament (Table 5). Thus, birds of either sex with limited auricular plumage tended to have mates with extensive plumage (Figure 2).

Remating and divorce

When both members of a pair survived to the next year, approximately 65% reunited (i.e., paired with the same individual; Table 4). Eight of the 15 pairs identified in 1987 remained together for all 3 years of the study. Our observations indicate, however, that nearly half (41% in 1988, 49% in 1989) of auklets paired in 1 year found a new mate in the following year, either because of the death of a mate or divorce. When both members survived to the next year, about 35% divorced (i.e., both pair members survived and returned to the colony but the pair did not remate; Table 4). In 1989, when we had the largest sample (16) of divorced individuals on the colony, 75% (12/16) of them mated with other auklets, whereas 25% (4/16) failed to obtain a mate.

We also tested whether divorces were more likely to occur after pairs failed to breed successfully. Breeding pairs [37% divorce rate (16/66) between 1988 and 1989] were significantly less likely to divorce than nonbreeding pairs [69% divorce rate (18/26) between 1988 and 1989; log-likelihood ratio test, $G = 16.0, p = .0002$]. Similarly, successful breeding pairs [27% divorce rate (8/22) between 1988 and 1989] were less likely to divorce than unsuccessful breeding pairs [44% divorce rate (24/56) between 1988 and 1989], but this difference was not significant ($G = 2.8, p = .10$). Thus, there was some evidence that lack of reproductive success led to subsequent divorce, particularly when pairs did not attempt to breed in a given year.

We also tested whether individuals that divorced suffered a cost with respect to timing of breeding or reproductive success when they remarried compared to birds that reunited with their previous mate. Members of pairs breeding in 1988 that subsequently divorced (i.e., did not reunite in 1989) bred significantly later in 1989 (July hatch dates, reunited pairs: 5.0 ± 3.4 days; pairs with one divorcee: 8.6 ± 6.6 days; $t = 2.86, df = 62, p = .006$). These divorced birds were also less likely to breed successfully (chick fledging success = 44%, $n = 18$) compared to reunited pairs (97%, $n = 46$; $G = 24.4, p < .001$). Furthermore, members of pairs that divorced were in poor condition in 1989 (residuals = −0.5 ± 3.8 g) compared to pair members that reunited (2.2 ± 4.2 g; $t = 2.04, df = 43, p = .047$).

We found that ornaments explained a small but significant (multiple regression, $R^2 = 0.07, p < .02, n = 133$) proportion of the variability in individual adults' body condition in 1988, and adults had greater expression of ornaments than subadults (Jones, 1990b). Given that ornamentation may reflect an individual's age and body condition (auricular plume length explained a small (about 5%) but significant proportion of the variation in body condition in 1988; Jones, 1990b), we tested whether divorce was related to the relative ornamentation of pair members. We quantified relative ornamentation within pairs for each ornament as the measure from the pair member with the smaller ornament divided by the measure from the member with the larger ornament. We then compared the relative or-

![Figure 1](image-url)

Relation between body size (tarsus length) of male and female auklets within pairs 1988 and 1989 ($r = .34, p = .01, n = 50$ pairs). The equation for the model II regression shown is $y = 0.1x + 0.99x$. 

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nament between pairs that divorced and those that reunited between 1988 and 1989, but there was no relationship between relative ornamentation and likelihood of divorce (Mann-Whitney U tests, \( p > .05 \) for each ornament).

There were, however, significant differences between reunited and divorced pairs in average ornament size. Pairs with large facial plumes were less likely to divorce than pairs with small plumes (mean auricular plume length, reunited pairs: 18.1 ± 1.7 mm; divorced pairs: 15.88 ± 2.9 mm; \( t = 2.26, df = 21, p = .04 \)). There was a similar, but not statistically significant, trend in mean auricular plume scores (reunited pairs: 35.4 ± 4.8; divorced pairs: 27.4 ± 12.5; \( t = 1.26, df = 18, p = .20 \)). To examine whether this effect occurred in one or both sexes, we looked at the relationship between pair fidelity (from year to year) and male and female plume ornaments separately. Pair fidelity was related only to male plume ornaments: males that divorced had significantly smaller auricular plume length (15.4 ± 4.9 mm) than males that reunited with their mate of the previous year (18.1 ± 1.7 mm; \( t = 2.18, df = 27, p = .04 \)).

There were no significant ornament differences between reunited and divorced females (e.g., mean auricular plume length, reunited females: 17.8 ± 3.3 mm; divorced females: 17.3 ± 2.6 mm; \( t = 0.46, df = 28, p = .65 \)). Ornaments were also related to pairing success because auklets that were pair members had larger facial plumes than unpaired birds in 1988 (mean auricular plume length, paired birds: 17.5 ± 3.0 mm; unpaired birds: 16.3 ± 2.9 mm; \( t = 2.45, df = 163, p = .02 \)). There was a similar but not statistically significant trend in 1989 (mean auricular plume score, paired birds: 33.6 ± 10.9 mm; unpaired birds: 30.3 ± 9.9 mm; \( t = 1.36, df = 127, p = .18 \)). Note that auricular plume length and auricular plume score are measures of the size of the same ornament.

Because overall plumage color of least auklets tends to lighten with age and functions for status signaling in aggressive encounters (Jones, 1990a), we also examined the relationship between plumage color and year-to-year pair fidelity. There was a significant difference between the mean plumage color score of reunited (8.8 ± 12.4) and divorced pairs (31.8 ± 3.6; \( t = 3.28, df = 3, p = .05 \)). As a plumage color score of 0 would be a white bird and a score of 100 a black bird, this analysis indicates that pairs with light plumage were less likely to divorce. As with ornaments, it was the plumage color of the male pair members that mattered (mean plumage color scores, reunited males: 11.6 ± 6.7; divorced males: 41.8 ± 13.7; \( t = 5.49, df = 11, p = .0002 \)). There was no significant difference in plumage-color scores between reunited (20.0 ± 12.9) and divorced females (21.2 ± 15.8; \( t = 0.15, df = 10, p = .89 \)).

**DISCUSSION**

**Mating patterns**

The most interesting mating patterns that we found were (1) the significant trend toward disassortative mating with respect to auricular plume score (Figure 2) and (2) the absence of assortative mating patterns for any other ornament (Table 3). Disassortative mating is a relatively rare pattern (see review in Findlay, 1987); it has been documented only a few times in birds and seldom in other animals. Probably the best-studied example is the disassortative mating with respect to head plumage color in the white-throated sparrow (Zonotrichia albicollis) first described by Lowther (1961). Disassortative mating for plumage color has also been described in polymorphic rock doves (Columba livia) in England (Murton et al., 1978). To the best of our knowledge, no other examples of disassortative mating for plumage characters have been described. The remaining case of disassortative mating in birds in-

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**Table 3**

Correlations between male and female ornaments within pairs

<table>
<thead>
<tr>
<th>Ornament</th>
<th>( r )</th>
<th>( p )</th>
<th>( n )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Auricular plume length</td>
<td>.02</td>
<td>.88</td>
<td>54</td>
</tr>
<tr>
<td>Auricular plume score</td>
<td>-.35</td>
<td>.01*</td>
<td>47</td>
</tr>
<tr>
<td>Forehead plume score</td>
<td>.15</td>
<td>.32</td>
<td>46</td>
</tr>
<tr>
<td>Bill color score</td>
<td>.01</td>
<td>.92</td>
<td>54</td>
</tr>
<tr>
<td>Bill ornament height</td>
<td>.22</td>
<td>.12</td>
<td>58</td>
</tr>
</tbody>
</table>

* Significant at a table-wide level of \( p = .05 \) using a sequential Bonferroni analysis to minimize type I error (see Rice, 1989).
Table 4
Remating patterns in least auklets in 1988 and 1989

<table>
<thead>
<tr>
<th>Breeding pairs identified in previous year</th>
<th>1988</th>
<th>1989</th>
</tr>
</thead>
<tbody>
<tr>
<td>Both pair members alive</td>
<td>15</td>
<td>66</td>
</tr>
<tr>
<td>Both pair members disappeared</td>
<td>12 (80%)*</td>
<td>43 (65%)</td>
</tr>
<tr>
<td>One pair member disappeared</td>
<td>1 (7%)</td>
<td>4 (6%)</td>
</tr>
<tr>
<td>Pair reunited</td>
<td>2 (13%)</td>
<td>19 (29%)</td>
</tr>
<tr>
<td>Divorced</td>
<td>8 (53%) (57%)</td>
<td>27 (41%) (63%)</td>
</tr>
<tr>
<td></td>
<td>4 (27%) (55%)</td>
<td>16 (24%) (37%)</td>
</tr>
</tbody>
</table>

* Numbers in parentheses indicate percent of breeding pairs identified in previous year.

volves a weak negative correlation for beak width in an island population of the song sparrow (*Melospiza melodia*; Smith and Zach, 1979).

Like the other reports of disassortative mating in birds, we have no convincing explanation for the mechanism that might have led to this pattern in least auklets. Indeed, a pattern of assortative mating might have been expected because we found experimental evidence for a mating preference in both sexes for model birds with more extensive facial plumes in this population. Both males and females performed more frequent sexual displays to models with accentuated plumes (plumes manipulated to increase auricular plume length and score to the maximum that naturally occurs) compared to the same models with average plumes (Jones, 1990b; Jones and Montgomerie, in press). During our model presentations, however, we could not record the auricular plume score of the choosing birds, so we were unable to assess the strength of preference relative to the bird's own plume size.

Our model presentation experiments tend to rule out two explanations for disassortative mating that involve only mating preferences. First, a pattern of disassortment could occur if birds with limited plumes preferred those with extensive plumes and vice versa (our model presentation experiments showed no evidence of such preferences). Second, this pattern could also result from preferences of males and females for different-sized ornaments (also not supported by model presentation experiments). Thus, the pattern of disassortative mating must have resulted from other factors that governed matings, such as differential access or availability of potential mates to each other, related to plumage size. As we have no data to properly address this question, and the mechanism producing disassortative mating remains unknown.

One possible mechanism that could produce disassortative mating, however, can probably be ruled out. Although the size of all auklet ornaments increased significantly between subadult and adult age groups (test, $t = 5.6-14.4$, df = 269–296, $p = .0003–.0001$), there was no relation between ornament size and age among adults (>2 years old, $t$ tests, $t = 0.50-1.46$, df = 76–81, $p > .05$; Jones 1990b; Jones and Montgomerie, in press). Thus, the disassortative mating, which occurs within the adult age class, appears not to have been the result of a prevalence of matings between older and younger adults. Other evidence suggests that pairing occurs between birds of similar age (see below).

We found evidence for assortative mating by plumage color in this population, as indicated by an excess of matings between individuals of similar plumage phenotypes and fewer matings between birds of dissimilar plumage color than expected by chance. We believe that this mating pattern, unlike the disassortative pattern with respect to auricular plume score, was related to a pattern of assortative mating by age. Least auklet plumage lightens with age, even among adults (Jones, 1990a), so pairing among birds of similar plumage color suggests a prevalence of matings and rematings among similar-age individuals. Assortative mating related to plumage color and age could have resulted from several mechanisms: (1) initial random pairing of young birds of similar age followed by remating (Reid, 1988), (2) pairing of birds determined by social dominance status, leading indirectly to pairing of birds of similar status, age, and plumage color, (3) homotypic preferences related to plumage color (Burley, 1983), leading to pairing of birds of similar color and thus leading indirectly to pairing of birds of similar age, or (4) differential access of birds of different age and plumage color to one another as potential mates. Any one, or a combination of several, of these mechanisms could have led to the observed pattern of assortative mating.

At present, our data do not permit us to critically test all of these hypotheses. However, the first mechanism can be rejected because pair stability is low in least auklets (due
to high frequencies of divorce and mortality) compared to long-lived seabird species (Rowley, 1983). Even low frequencies of divorce or pair splitting substantially reduce the correlation of age within pairs that can result from initial pairing of birds of similar age (Reid, 1988). Thus, the pattern of assortative mating probably did not result from random initial pairing among least auklets of similar age.

Positive assortment related to plumage color must have resulted from the influence on pairing of social dominance, homotypic preferences, or differential access. In model presentation experiments, pale-plumaged auklets approached pale models more closely than did intermediate-plumaged auklets (Jones, 1990a), a result consistent with the existence of a homotypic mating preference and consistent with the importance of social status. However, there was no difference in the frequency of courtship displays directed at pale versus darkened models (Jones, 1990a), suggesting that social status, rather than an active mating preference, may be the most important factor in determining this mating pattern. Since pale-plumaged birds were socially dominant (Jones, 1990a), a mating prevalence for pale plumage could lead to pairings and re-pairings among experienced and socially dominant birds. This would likely be selectively advantageous because there is intense competition for nesting sites, which may limit breeding opportunities in least auklets (Roby and Brink, 1986b). We have too few data to assess the fourth proposed mechanism to explain the assortative mating pattern, the differential availability or access of potential mates of differing plumage color. A test of this hypothesis would require a detailed investigation of the availability of unmated birds of each plumage color during the breeding season. This mechanism could work if, for example, auklets with relatively pale plumage arrive at the colony and pair earlier in the season than birds with darker plumage.

Remating and divorce

Least auklets appear to be intermediate in mate fidelity between long-lived seabirds (where fidelity is nearly the rule) and shorter-lived, north temperate passerines (where most individuals switch mates each year; Rowley, 1983). However, because the data on remating in alcids are scanty, we can only speculate as to whether least auklets' mate fidelity is relatively high or low among the Alcidae. At about 35%, the divorce rate of least auklets is greater than that described for other alcids like Atlantic puffins (Fratercula arctica) at 8% (Ashcroft, 1979) and black guillemots (Cepphus grylle) at 5%–7% (Asbirk, 1979; Petersen, 1981). Given that murres (Uria spp.) also have high mate fidelity (divorce rate near zero; Birkhead et al., 1985), it appears that least auklet mate fidelity is relatively low. Combined with the mortality rate, divorces led to almost half the adult population being required to find a new mate each year, a factor that undoubtedly favored the intense competition for mates that occurred in the period before laying each spring.

As occurs in several other species, least auklet pairs that bred together the previous season had greater success (through earlier breeding and greater fledging success) than experienced birds that were breeding together for the first time. This could represent a source of strong selection for mate fidelity in this species and poses the question of why the divorce rate is relatively high if there is such a cost. As only a little over half the adult least auklet population managed to breed each year at St. Paul Island (Jones II, unpublished data), many individuals must have had mates that were somehow unable to meet the demands of breeding. For these individuals, divorce might improve the chances of obtaining a higher-quality mate and ultimately improving breeding success. Divorce could thus be either a behavioral strategy to improve fitness or a nonselected consequence of the pair members leaving the colony earlier after reproductive failure (failed breeders left the colony up to 1 month earlier than successful breeders). The data available to address this question are equivocal: although both nonbreeding and unsuccessful breeding pairs had a high divorce rate, the differences were not statistically significant from the divorce rate of successful breeders. Work on other bird species has also supported the idea that divorce follows reproductive failure (Rowley, 1983).

The positive relationship between male ornaments and pair fidelity begs the question, Why were pairs in which the males had small ornaments in 1988 more likely to divorce? The answer may be an interaction among male preference, body condition, and ornament size. In 1988, facial plumes were significantly correlated with individual body condition (Jones, 1990b). Thus, short-plumed males were likely to have made less satisfactory mates than long-plumed males, leading to divorce of pairs with short-plumed males. We do not know if divorces resulted from active mate choice for a more ornamented partner in the next season. However, the greater remating success of more-highly-ornamented males could represent a force of sexual selection favoring the ornaments involved. Our finding that the likelihood of remating was related to male plumage color and ornaments is consistent with the
idea that remating is at least partly controlled by female choice.

Taken together, the patterns of mating and remating in least auks are consistent with the observations that plumage color (Jones, 1990a) and head ornaments (Jones, 1990b; Jones and Montgomerie, in press) influence status signaling and mating preferences, respectively, in this species. We found that auks of both sexes performed more sexual displays toward models with large plumes, consistent with a generalized preference for mates with large plumes. The fact that both assortative and disassortative patterns were observed suggests that the interaction between status signaling, mate choice, and the availability of mates with differing degrees of ornamentation in auks may be complex. Because it is not possible to infer mechanisms from assortment patterns alone (Burley, 1983), more studies like this are needed before we can make any general statements about the relation between assortative mating patterns and sexual selection. Even in auks, more work will be needed before both the process and the adaptive significance of these mating patterns can be fully understood.

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REFERENCES


Jones and Montgomerie • Least auklet mating patterns