

Patterns of variation in ornaments of Crested Auklets *Aethia cristatella*

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We investigated patterns of variation of feather and bill ornaments of Crested Auklets *Aethia cristatella*, a monogamous seabird, based on 963 individuals measured in the years 1990 to 1998. Three prominent ornaments were displayed: a forehead crest, composed of 11–31 curved feathers averaging about 40 mm in length, bilaterally symmetrical white auricular plumes on the sides of the head behind the eyes, averaging about 30 mm in length, and brightly coloured semi-circular rictal plates at the corners of the bill. As in other putative sexually selected traits, auklet ornaments were more variable across individuals than non-ornamental traits. Crest length and auricular plume length were positively correlated within individuals but not across years. Among the traits measured there was evidence for slight sexual dimorphism for the auricular plume and rictal plate ornaments and for culmen length and tarsus (males were slightly larger than females) but not for the crest ornament. Breeding adult females and males had greater crest and plume ornament expression than non-breeding adults. Paradoxically, females' crests and rictal plates were more variable than males' crests and rictal plates. Based on independent samples, the expression of feather ornaments and rictal plate varied among years between 1990 and 1998. Crested Auklet ornaments did not vary in concert with the ornaments of Whiskered *Aethia pygmaea* and Least Auklets *Aethia pusilla* during this period. Crested Auklet subadults had smaller ornaments than adults. Based on adults remeasured after an interval of one to seven years, the size of individuals' feather ornaments increased with age. We found no relationship between auricular plume length and asymmetry. Male auricular plumes and female crests were weakly correlated with body condition.

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Many bird species display elaborate ornaments including feather structures such as facial plumes, crests, and tail streamers and bare part ornaments such as bill plates, knobs and wattles during their breeding seasons. These ornaments vary in expression between the sexes, across age classes, and among individuals (Andersson 1994). Several studies have documented high levels of variation in these sexually selected ornamental traits compared to morphological traits thought to be under other forms of natural selection (Alatalo et al. 1988, Jones and Montgomerie 1992, Evans and Barnard 1995). This variation has been hypothesized to result

from a combination of: (1) lack of stabilizing selection on display traits (Alatalo et al. 1988), and (2) characteristics that lead them to be costly and thus correlated with individuals' health (Møller 1991). Another important aspect of ornament variation is sexual dimorphism, which reflects differences in the force of sexual selection on males versus females. Sexual selection acting directly on one sex can also indirectly result in ornament expression in both sexes as a consequence of genetic correlation (Andersson 1994). Polygynous birds have highly male biased sexual dimorphism and high variability of the male ornaments (e.g., Petrie et al. 1991),

while males and females of monogamous species may display similar (sexually monomorphic) ornaments that are favoured by mutual sexual selection (Jones and Hunter 1993, 1999). However, no study has investigated ornament variation in a monogamous sexually monomorphic bird species.

Auklets (family Alcidae, tribe Aethiini) include five socially monogamous seabird species in which both sexes display similar ornaments during the breeding season (Gaston and Jones 1998). Crested Auklets *Aethia cristatella* have a conspicuous black forehead-crest, white auricular plumes, an orange bill with accessory plates, and a citrus-like plumage odour (Jones 1993a). These ornaments are displayed by both sexes during courtship at the colony and at sea and mate choice follows from the performance of sexual displays by both members of courting pairs (Jones 1993a). The feather ornaments become greatly reduced and the brightly coloured bill plates drop off after the breeding season (Jones 1993a). Long crests are favoured by mating preferences and signal high dominance status, evidence that mutual inter- and intra-sexual selection favour the crest ornament (Jones and Hunter 1993, 1999).

In order to comprehend ornament function, it is essential that we understand patterns of ornament variation. We quantified Crested Auklet ornament variation for comparison with other evidence on the role of sexual selection in auklet ornament evolution, and for comparison with other avian studies of sexually selected ornaments. We evaluated correlations among ornaments to assess whether they might have a single function or multiple functions. We quantified the relative amount of variation expressed in ornaments versus other morphological traits to test whether Crested Auklet ornaments show similar variation to the extravagant traits of polygynous bird species. To assess the relative force of sexual selection on males and females we quantified ornament sexual dimorphism and the relative amount of variation expressed in male and female ornaments. To assess ornaments' roles as either fixed or

flexible signals of viability we attempted to estimate the effects of age and year on their expression. To evaluate whether ornament symmetry might play a role in sexual selection we tested for an inverse relationship between size and asymmetry of their bilateral auricular plumes. Finally, we tested whether ornaments reflected individuals' body condition as predicted by viability indicator models of sexual selection.

Methods

Fieldwork was carried out at a colony of more than 100000 Crested and other auklets at Buldir Island, Aleutian Islands, Alaska (52°2'N, 175°5'E; Byrd and Day 1984, Byrd et al. 1983) during mid-May to early July of 1990–1998.

Auklets were captured using noose carpets set on the colony surface within a 100 m² study area containing more than 1000 nesting pairs (Table 1). We believe noose carpets selected breeding and non-breeding auklets randomly from the population. Each captured auklet was given a numbered stainless steel leg band and a unique combination of three plastic colour bands. Upon capture, birds were weighed to the nearest 1 g using a spring scale, sexed using bill shape (Jones 1993b) and the following measurements were taken by ILJ or FMH, or both: bill depth (from the proximal base of the culmen to the angle of the gonys), culmen length, rictal plate height (on the right side, from its mid-point along the cutting edge of the bill near the gape to its highest point), tarsus length (on the right leg, from the mid-point of the tibiotarsal joint to the blunt end of the tarsometatarsal joint on the underside of the foot), crest length (length of the longest straightened crest shaft), and the auricular plume length (from the exposed proximal end of the plumes just below the eye to the end of the longest plume) to the nearest 0.1 mm using calipers. Incomplete sets of measurements were obtained when individual birds had to be released quickly to prevent them from overheating (e.g., when

Table 1. Summary of Crested Auklet captures at Buldir Island, 1990–1998.

Year	New birds		Retraps		Total captures
	Adults	Sub-adults	Within year	Between year	
1990	200	7	5	–	212
1991	120	9	1	9	139
1992	113	0	1	17	131
1993	36	1	0	10	47
1994	0	0	0	11	11
1995	58	3	6	11	78
1996	116	6	6	22	150
1997	122	5	2	21	150
1998	198	5	30	71	304
Totals	963	36	51	172	1222

several birds were caught simultaneously). Crest length was measured from 1991 onwards and auricular plumes were measured on the right side only from 1990 to 1991 and both right and left sides were measured 1992 to 1998. We used the right side measurement (1990–1991) and the mean value of left and right auricular plume measurements (1992–1998) to index auricular plume expression. Some birds begin to shed parts of their bill ornaments during chick rearing and individuals captured in this condition were excluded from analysis. Other than 36 birds captured in a distinctive sub-adult plumage (two-year olds; Bédard and Sealy 1984), characterized by worn brownish flight feathers and greater coverts and dull orange bills, none of the individuals measured in our study were of known age. Because of the large size of the colony, few individuals were recaptured and measured more than once within or between years (Table 1). Repeatability and measurement error of our ornament measures were calculated on birds measured twice within a year, and on birds measured by both ILJ and FMH either consecutively or within a year to compare inter-measurer measurement reliability. We caught and measured Least Auklets (for protocol see Jones and Montgomerie 1992) during 1990–1998 on the same plot used for Crested Auklet captures. We captured and measured Whiskered Auklets at night using mist-nets at Buldir Island during 1992–1998.

To determine whether the feather ornaments were moulting (i.e., growing) during the breeding season we examined 25 fresh corpses of adults killed by gulls. We checked the bases of the crest and auricular plume feathers for evidence of growing feathers in pin.

To quantify crests more fully, we clipped the crests (by cutting off all elongated feathers at their points of attachment) from 25 adults and counted the number of crest shafts and measured the length of each shaft. We examined the relative length of crest feathers to evaluate the usefulness of our single measure of crest length (length of longest feather).

To quantify sexual dimorphism, we compared ornament size between samples of adult males and females. Few sub-adults were captured and the gender of these individuals could not be determined from external appearance (Jones 1993b). We also compared the ornament size between breeders (identified by a full brood patch during the incubation period, 25 May–25 June, or by the presence of food for chick provisioning in the sublingual pouch between 25 June and 25 July), and non-breeders (absence of a full brood patch during the incubation period).

To quantify population level variation in ornament expression, we compared ornaments of adults among the years 1990–1998 ($n = 9$ years), based on one set of measurements (at first capture) from each individual. Because none of the birds measured (other than 31 birds caught as subadults) were of known age, we were

unable to directly quantify age-related differences in ornaments. However, to investigate how ornament expression varied as marked individual adults aged, we compared the change in ornament size among individuals remeasured one to seven years after their initial measurement. If ornament expression remained fixed after individuals reach adulthood, we expected no directional change in ornament size after initial measurement. If ornaments increased steadily with age, we expected an increase in the change in ornament size with increasing numbers of years following initial measurement. Using individuals measured by ILJ during the seasonal period of mass stability, we regressed body mass on tarsus for males and females separately (because of gender differences in body mass and shape) and used the residuals as indices of body condition for comparison with ornament expression.

Results

Ornament measurement

Our measurements provided a robust quantification of ornament variation over an 8-year period. More than 100 Crested Auklets were measured in each of 1990–1992 and 1996–1998, fewer in the years 1993–1995 (Table 1). Sub-adults comprised 3% of captures, retraps within years comprised 4% of captures, and retraps between years 14% of captures.

Crested Auklets displayed conspicuous ornaments that could be reliably measured. We found no evidence of moult of ornamental feathers during the breeding season. Repeatability of measurements within measurer was high, particularly for ornaments (0.88–0.97) and measurement error (ME) low (3.1–12.0%; Table 2). Repeatability between measurers was high for the crest (0.91) and plume ornaments (0.89) but low for tarsus length (0.21). Crests were composed of narrow (c. 1–1.5 mm wide) forward-curving feathers varying continuously in length, with 10–12 visually prominent feathers supported by shorter less obvious feathers (Fig. 1). Based on crests cut from 25 adults, crests were composed of 20 (range 11–31) feathers. Crests tended to have several (3–4) shafts close to the length of the longest feather (Fig. 1), suggesting that our measure of longest crest shaft was reflective of overall crest length. There was a strong correlation between the length of the longest crest feather and the combined length of all other feathers ($r = 0.57$, $df = 24$, $p = 0.003$). Crest expression within individuals within a year was fixed (i.e., crest shape or conspicuousness could not be adjusted using musculature), although individuals' crests did vary in appearance due to wind, precipitation, dirt and occasionally damage resulting from fights. There was evidence for correlations among ornaments and other morphological traits within individuals (Table 3). Within both males and females, there were significant

Table 2. Within- and inter-measurer repeatabilities of Crested Auklet ornament and tarsus measures.

Ornament	ME (%) ^a	r _I	SE	F	df within, between	P
Within measurer						
Forehead crest length	5.4	0.95	0.03	35.9	27,13	<0.0001
Auricular plume length	7.8	0.92	0.04	24.3	29,14	<0.0001
Rictal plate height	5.8	0.94	0.03	33.7	23,11	<0.0001
Culmen length	3.1	0.97	0.02	63.7	29,14	<0.0001
Tarsus length	12.0	0.88	0.06	15.9	29,14	<0.0001
Between measurers						
Forehead crest length	9.2	0.91	0.04	20.5	33,16	<0.0001
Auricular plume length	11.4	0.89	0.05	16.5	33,16	<0.0001
Rictal plate height	–	–	–	–	–	–
Culmen length	10.3	0.95	0.05	18.5	33,16	<0.0001
Tarsus length	78.8	0.21	0.23	1.5	33,16	0.2

^a ME: measurement error, the proportion of within-individual variation to total variation, $ME = MS_{\text{within}} / (s_{\lambda}^2 + MS_{\text{within}}) \times 100\%$ (Bailey and Byrnes 1990).

positive correlations between crest and auricular plume, indicating that individuals with large crests had long facial plumes and vice versa. However, rictal plate bill ornament size was not correlated with feather ornament size.

Variation of ornaments compared to other traits

Crest, auricular plume, and rictal plate ornaments had higher coefficients of variation than non-ornamental traits (Table 4). Crest length (range 8.1 mm–58.0 mm) and auricular plume length (range = 15.4 mm–41.3 mm) were the most conspicuously variable traits whereas culmen (range = 10.1 mm–13.4 mm) and tarsus lengths (range = 25.8 mm–32.1 mm) were relatively invariant.

Sexual dimorphism

Crested Auklet males and females had similar ornament expression. We evaluated sexual dimorphism of three ornaments and three traits that reflect body size (Table 4). Mean male crest length was slightly longer (1 mm) than mean female crest length but this difference was not statistically significant at a tablewise level of 0.05. The indices of sexual dimorphism for tarsus and mass were slightly male-biased, but we found no evidence that males had either absolutely or relatively (to body size) larger crests than females (Table 4). Among the traits measured there was also slight sexual dimorphism for the auricular plume and rictal plate ornaments and for culmen length. Inter-sexual differences in culmen and rictal plate size were consistent with previously documented differences in bill shape and size (Jones 1993b). We found evidence for inter-sexual differences in ornament variability: female crests (variance ratio test, $F_{274,269} = 1.6$, $P < 0.0002$) and rictal plates (variance ratio test, $F_{209,251} = 1.4$, $P =$

0.007) were significantly more variable than male crests and rictal plates (Table 4). There was no difference in variation of auricular plumes between the sexes (variance ratio test, $F_{314,303} = 1.0$, $P = 0.7$).

Among adults, breeding females had different ornament expression from non-breeding females, consistent with ornaments reflecting quality differences. Breeding adult females had longer crests than non-breeding females ($t = 5.2$, $df = 147$, $p < 0.0001$). For breeding and non-breeding males, the difference in crest length was non-significant ($t = 1.8$, $df = 169$, $p = 0.07$). Breeding birds had longer auricular plumes than non-breeders (males, $t = 2.8$, $df = 166$, $p = 0.006$; females, $t = 1.3$, $df = 147$, $p = 0.2$). The opposite trend was reflected in rictal plates, for which non-breeding adults of both sexes had larger rictal plates than breeding adults (males, $t = 5.5$, $df = 152$, $p < 0.0001$; females, $t = 4.3$, $df = 120$, $p < 0.0001$).

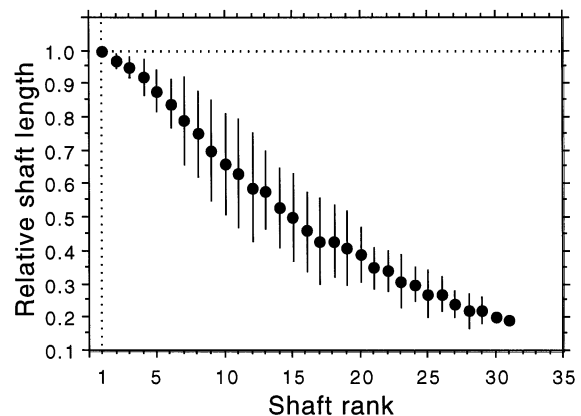


Fig. 1. The relationship between the crest shaft rank (i.e., 1 = longest crest shaft feather, 10 = tenth longest crest shaft feather) on x-axis and the relative length of each crest shaft compared to the longest shaft (i.e., 1 = same length as longest shaft, 0.5 is half the length of the longest shaft; mean proportions \pm 95% confidence limits) on the y-axis for $n = 25$ crests.

Table 3. Correlation matrix for adult male and female Crested Auklet ornaments and morphological traits (r for males/ r for females; $n = 242$ males and $n = 202$ females measured).

	Auricular plume	Rictal plate	Culmen	Tarsus
Forehead crest	0.160*/0.211**	-0.016/-0.219**	0.008/-0.218**	0.024/-0.110
Auricular plume		0.001/-0.080	0.082/-0.142*	-0.030/0.094
Rictal plate			0.020/0.234**	0.288***/0.246***
Culmen				0.106/0.270***

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Ornament variation among years and within individuals due to age

Crests varied in expression among years between 1990 and 1998 based on measurements of adults (sexes combined, ANOVA, $F_{5,468} = 33.3$, $P < 0.0001$, Fig. 2). Male (ANOVA, $F_{7,294} = 7.0$, $P < 0.0001$) and female (ANOVA, $F_{7,281} = 3.2$, $P < 0.003$) auricular plumes and male (ANOVA, $F_{6,254} = 7.4$, $P < 0.0001$) and female (ANOVA, $F_{6,207} = 8.3$, $P < 0.0001$) rictal plate ornaments also showed significant variability among years (Fig. 2). Crest and auricular plume ornament expression was not correlated across years ($r = 0.41$, $p = 0.33$, $n = 8$ years). Ornament expression and reproductive performance were not related (correlations between ornaments and hatching, fledging and overall reproductive success across years, $r = -0.14$ – 0.57 , $p = 0.20$ – 0.79 ; note that because we only had $n = 9$ years of data our analysis would only detect strong trends).

Adults had significantly longer crests (mean adult-subadult difference = 6.1 mm, $t = 3.7$, $df = 593$, $p = 0.0003$), auricular plumes (mean difference = 2.1 mm, $t = 2.8$, $df = 876$, $p = 0.005$) and rictal plates (mean difference = 0.7 mm, $t = 3.2$, $df = 576$, $p = 0.002$) than subadults (two-year olds), in all years of the study. The largest subadult crest measured (41 mm) was close to the mean adult crest length (40 mm), suggesting that ornament expression increased with age. Further measurements of known age individuals would be required to test this unequivocally. Based on 48 adults (> two years old) whose crests were remeasured one or two years after an initial measurement, there was no change in crest size (paired $t = 0.54$, $df = 47$, $p = 0.6$; Fig. 3). However, individuals whose crests were remeasured after three or more years did have larger crests at second measurement (paired $t = 3.0$, $df = 21$, $p < 0.003$; Fig. 3). Auricular plumes increased in length after both one- or two-year (paired $t = 0.8$, $df = 63$, $p = 0.04$) and three- to seven-year periods (paired $t = 1.8$, $df = 40$, $p < 0.0004$). These increases paralleled a trend in increasing ornament size across years (Fig. 2). Remeasured rictal plates and tarsi did not change significantly in size.

Male auricular plumes (but not crests or rictal plates) were weakly but significantly correlated with our index of body condition across individuals ($r = 0.18$, $r^2 =$

0.03, $p = 0.02$, $n = 183$). Female crests (but not auricular plumes or rictal plates) were weakly but significantly correlated with body condition across individuals ($r = 0.23$, $r^2 = 0.05$, $p = 0.01$, $n = 122$).

Auricular plume ornament measurement asymmetry

Crested Auklets' auricular plumes exhibited measurement asymmetry (a difference between right- and left-side measurements, mean = 2.3 ± 0.1 SE mm, range = 0–17.5 mm). Because individuals' plumes were measured only once at each capture, we were not able to quantify the relative importance of fluctuating asymmetry, measurement error, and feather damage in determining this asymmetry (Palmer and Strobeck 1986, Swaddle et al. 1994). However, we found no relationship between ornament length and ornament asymmetry as reported in some previous studies (Fig. 4). There was no evidence of a relationship between these measures ($n = 427$ adults, $r^2 = 0.001$, $P = 0.5$). Asymmetries of < 1 mm may be attributable to measurement error (see Table 2).

Discussion

Male and female Crested Auklets display similar elaborate feather and bill ornaments during courtship. These are much more variable than non-ornamental morphological traits, consistent with these traits being the product of sexual selection (Andersson 1994). This possibility is supported for the crest ornament by our previous work in which we found evidence that Crested Auklet crests were subject to inter- and intra-sexual selection because: (1) males and females expressed mating preferences for long crests in an experiment (Jones and Hunter 1993, 1999) and, (2) crest size was correlated with dominance within both sexes under natural conditions and experimental manipulations of crest size confirmed that large crests function as a badge of status (Jones and Hunter 1999). Experimental evidence for mating preferences focusing on Crested Auklets' auricular plume ornament is lacking but it seems probable that this ornament is also favoured by sexual selection because experiments previously showed evidence for

Table 4. Variation of ornaments and morphological traits of adults in relation to gender.

Trait	Males (mean \pm SE, n)	CV	Females (mean \pm SE, n)	CV	SD ^a (m/f)	t, df, p
Forehead crest (mm)	40.7 \pm 0.4, 265	0.133	39.7 \pm 4, 270	0.172	1.03	2.0, 533, 0.04
Auricular plume (mm)	30.2 \pm 0.2, 290	0.130	28.6 \pm 2, 285	0.141	1.06	4.8, 573, <0.0001 ^b
Rictal plate (mm)	5.2 \pm 0.1, 246	0.172	4.5 \pm 0.1, 204	0.239	1.16	7.9, 448, <0.0001 ^b
Culmen (mm)	12.4 \pm 0.04, 281	0.053	11.7 \pm 0.04, 281	0.054	1.06	13.1, 560, <0.0001 ^b
Tarsus (mm)	29.4 \pm 0.1, 251	0.043	28.7 \pm 0.1, 243	0.036	1.02	6.8, 492, <0.0001 ^b
Mass (g)	267.9 \pm 1.3, 214	0.072	253.0 \pm 1.5, 175	0.077	1.06	7.5, 387, <0.0001 ^b

^a SD: Sexual dimorphism index (male trait size/female trait size).

^b Significant differences at a tablewide $p < 0.05$, using sequential Bonferroni analysis.

mating preferences for Least Auklet's *Aethia pusilla* homologous auricular plumes (Jones and Montgomerie 1992). Together these results suggest that male and female Crested Auklets display similar mutually sexually selected ornaments with attributes comparable to the elaborate morphological ornaments of some male birds that have been the focus of recent studies (e.g., Petrie et al. 1991, Andersson 1992, Møller 1994).

The minimal sexual dimorphism and similar function of male and female Crested Auklet feather ornaments are consistent with there being a nearly identical balance point in males and females between the sexually selected benefits of displaying the ornaments and the energetic and social costs of producing and maintaining them. Male and female Crested Auklet ornaments have similar mutually sexually selected functions and the expression of ornaments in females is not merely a consequence of a genetic correlation between the sexes (e.g., Lande and Arnold 1985). This is consistent with similar sexual behaviour, parental effort and foraging ecology of male and female Crested Auklets (Gaston and Jones 1998). The slight tendency for greater ornament expression by males (Table 4) could be related to one or more of the following factors: (1) marginally higher mating success benefits of ornament expression to males (e.g., attributable to male-female differences in ornament function related to intra-sexual competition, Jones and Hunter 1999); (2) enhanced variation in male mating success via extra pair copulations, Hunter and Jones unpubl.); (3) differences between males and females in ability to produce or bear the ornament (i.e., differential costs); (4) differences between males and females in costs of mate choice (Johnstone et al. 1996); or (5) natural or sexual selection for slightly male-biased sexual overall body size dimorphism. Future investigation of subtle differences between the sexes in mating behaviour and costs of ornament expression could shed light on this question.

Our most striking finding was the greater variability of the crest and rictal plate ornaments within females compared to within males. In sexually dimorphic species with highly ornamented males it is usually the male ornaments that show greater variability than the homologous traits in females (Alatalo et al. 1988), because

the female traits have not undergone costly exaggeration. Inter-sexual difference in variation in Crested Auklet crests is paradoxical because the ornaments of males and females are similar in size. Previously we found that Crested Auklet female-female social interactions were mediated principally by subtle signaling involving the crest ornament whereas male-male interactions were more likely to involve overt aggression (Jones and Hunter 1999). We believe that greater variability of female crests may be related to the greater importance of crest size as a status signal in females, even though their ornaments are similar in size to males.

Although we were unable to confirm that Crested Auklets' bilaterally symmetrical auricular plume ornaments exhibit fluctuating asymmetry *per se*, our results have some bearing on the issue of the relationship of sexual selection and ornament asymmetry. Møller and Höglund (1991) predicted that elaborate bilaterally symmetrical ornaments that honestly indicate individual quality and are costly to produce would show a

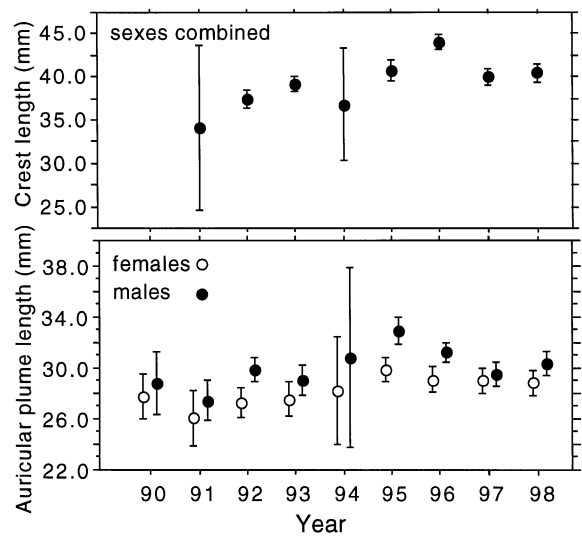


Fig. 2. Variation in crest and auricular plume ornament expression according to year of adult Crested Auklets at Buldir, 1990–1998 (means = 95% confidence limits).

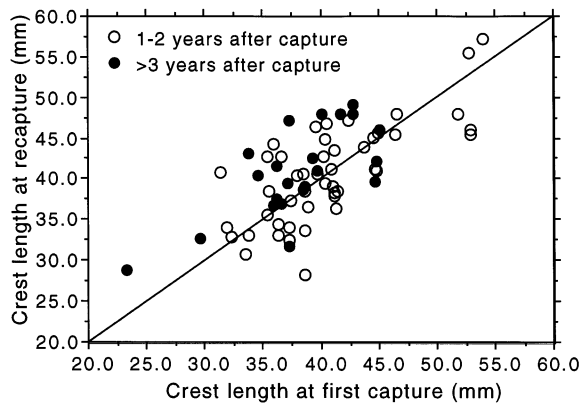


Fig. 3. Plot of crest length at first capture versus length at subsequent recaptures, based on 70 individuals measured twice (line indicates 1:1, i.e., no change in ornament size).

negative relationship between degree of asymmetry and ornament size. This is based on the logic that high quality individuals should be able to produce an ornament that is both large (because they can bear the production costs of a larger ornament) and symmetrical (because symmetry reflects individuals' ability to withstand environmental stress; Parsons 1990). Crested Auklet auricular plumes exhibited asymmetries of up to 17.5 mm, well outside our level of measurement error, yet we found no evidence of a negative relationship between ornament size and symmetry (Fig. 4). The best explanation for this result may be that the auricular plume ornament is a poor indicator of individual quality in which neither size nor symmetry relate to individuals' overall condition.

We found evidence for significant population-wide fluctuation in ornament size among years during 1990–1998. We also found evidence that ornament expression increased with age. Thus, inter-annual variation in ornament expression could have resulted partly from changes in the auklet population's age structure. This

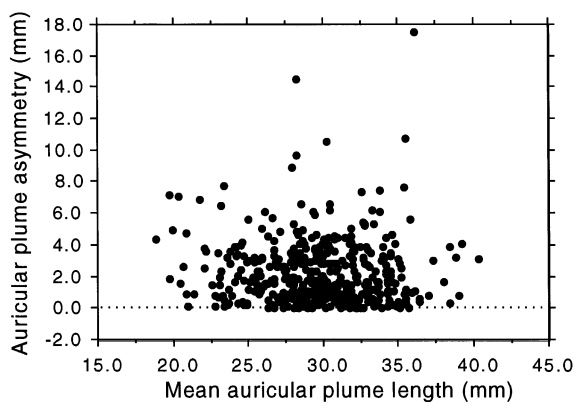


Fig. 4. Plot of mean length (of left and right) auricular plumes versus auricular plume measurement asymmetry.

variation was also consistent with some form of large scale variation in the marine environment that determined ornament expression by affecting individuals' ability to grow their ornaments prior to the breeding season during March and April (see Bédard and Sealy 1984). The wintering area(s) of the Crested Auklet population of Buldir Island are remote and unknown, so we are at present unable to identify any environmental variables that could have been important. Furthermore, a large marked population of known age birds would be required to fully reveal the relative importance of age and year quality effects in determining ornament variation. Unfortunately, none of our marked birds were of known age and we did not have any other evidence of population age structure. However, the observation that the Crested, Whiskered *Aethia pygmaea* and Least Auklet populations' ornaments did not vary in concert across years suggests that the processes that determine inter-annual ornament variation vary independently among different auklet species.

Overall, despite the fluctuation of population ornament size among years, we found little evidence that Crested Auklet ornaments correlated with body condition or other measures of individual viability. This may not be too surprising, because our measures of condition were made during June, while the ornaments are grown months before during late winter (Bédard and Sealy 1984). Nevertheless, further methods of assessing individual differences that could relate to ornament expression need to be explored. For example, haematocrit has recently been identified as a useful measure of individuals' quality and has been found to correlate with Barn Swallow *Hirundo rustica* ornaments (e.g., Saino et al. 1997). Furthermore, individuals' display traits may reflect their measured immune response (e.g., Dufva and Allander 1995, Saino and Møller 1996) and thus indicate health. Thirdly, individuals' survival ability as determined from capture-mark-recapture analyses may provide an ultimate measure of viability that relates to ornament expression.

Møller and Pomiankowski (1993) addressed the question of why some birds have multiple ornamental traits and proposed three hypotheses: (1) the multiple message hypothesis, which suggests that different ornaments signal different aspects of individual quality; (2) the redundant signal hypothesis, which suggests that combinations of several ornaments most reliably signal overall individual quality; and (3) the unreliable signal hypothesis, which suggests that multiple ornaments do not signal condition, are cheap to produce and bear, but are maintained by weak mating preferences. Pomiankowski and Iwasa (1998) also considered the possibility that multiple ornament evolution could be the result of runaway selection for arbitrary ornaments. Our study does not provide a definitive test of these hypotheses. However, several lines of evidence point to

the unreliable signal hypothesis as the best explanation for auklet ornaments. Although ornament expression did fluctuate from year to year, we found little evidence that Crested Auklets ornaments acted as strong signals of quality because of the weak correlations between ornaments and body condition. This result mirrors the results of a previous study of Least Auklet ornaments (Jones and Montgomerie 1992). Crested Auklet ornaments consist of feathers and keratin amounting to less than a gram on a bird averaging about 260 g in body mass, so their energetic costs of production are likely to be small. Furthermore, because the ornaments are smoothly contoured with the bird's body form (auricular plumes and rectal plate) or flexible enough to lie flat against the head during flight in the air and underwater (the forehead crest), the aero- and hydrodynamic drag costs of the ornaments are also likely to be low (A. L. R. Thomas, unpublished data) compared to some other bird ornaments (e.g., Evans and Thomas 1992). In addition, results of experiments on mating preferences of Least Auklets showed that they have a heterospecific mating preference for forehead crests, an ornament they do not naturally express (Jones and Hunter 1998), evidence that auklet ornament preferences may be at least in part arbitrary with respect to choice for a high quality partner. Together, these aspects of auklet preferences and ornaments suggest that their multiple ornaments are unreliable viability indicators. However, these results are enigmatic because despite the apparent low costs of production and maintenance of auklet ornaments, they show high levels of variability in expression similar to the costly sexually selected ornaments of other bird species (Alatalo et al. 1988). Normally, this variation in sexually selected traits is ascribed to variability across individuals (usually males) in ability to produce these extravagant and costly traits. If auklet ornaments and similar multiple ornaments of other bird species are indeed cheap to produce and bear, this leaves open the question of what factors are responsible for their remarkable variability. Future work needs to investigate the cryptic costs of such less extravagant but highly variable adornments in birds.

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