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RESEARCH ARTICLE

Extensive variation in feather ornaments of Whiskered Auklets in the Aleutian Islands reflects age, sex, condition, and geography

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ABSTRACT

Both sexes of Whiskered Auklets (*Aethia pygmaea*) display the most elaborate feather ornaments of any seabird: a slender black forehead crest, and 3 bilaterally symmetrical pairs of white facial plumes (superorbital, suborbital, and auricular). We studied patterns of ornament variation in 796 banded individuals (147 of known sex, 254 of known age from 1 to 16 years) during 1992–2009 at Buldir Island (principally), and 3 other Aleutian Islands (Davidof, Ulak, and Egg) in Alaska, USA. As expected for socially selected traits, ornaments were more variable across individuals than anatomical traits in size but with only slightly male-biased sexual dimorphism. Body condition index increased from age 1 to 3 years but changed little thereafter. Even within birds ≥4 years old, ornament size was positively related to body condition index. Subadults (one-year-olds) had smaller ornaments than adults (age 2–16 years) but there was no further change in ornament size as adults aged and no evidence of senescence even in the oldest birds (>8 years old). Nonetheless, overall ornament size varied from year-to-year at Buldir and was correlated with indices of both ocean climate and auklet productivity in the preceding 2–5 years. From Buldir to Egg Island (1,266 km), the size of both anatomical and ornamental traits increased by 5–15% except for bill depth, which was largest in birds from Buldir and Egg at opposite ends of the Aleutian breeding range. This study is one of few to examine patterns of ornament variation in a long-lived, socially monogamous bird, even though such patterns are crucial to understanding the relationship between sexual selection and life history.

Keywords: age, Alcidae, Aleutian, dimorphism, feather ornaments, sexual selection, social selection, variation, seabird

LAY SUMMARY

- Whiskered Auklets, a small seabird, were measured over an 18-year period (1992–2009) in the Aleutian Islands, Alaska, to examine relationships between the size of their facial feather ornaments and their sex, age, body condition, annual productivity, and geographical distribution, as well as ocean climate.
- Males were slightly larger than females in all traits measured.
- The size of all feather ornaments increased from 1 to 2 years of age but remained stable thereafter, with no decline in the oldest birds (≥8 years old).
- Feather ornament size was correlated with a body condition index in adult birds, and this index was the best predictor of ornament size.
- Across years, average feather ornament size was also correlated with ocean climate and reproductive success during the previous 2–5 years.
- Feather ornament size increased from west to east at the 4 islands that we sampled across a 1,266 km expanse of the Aleutian Islands.

La amplia variación en los ornamentos de plumas de *Aethia pygmaea* en las Islas Aleutianas refleja la edad, el sexo, la condición y la geografía

RESUMEN

Ambos sexos de *Aethia pygmaea* exhiben los ornamentos de plumas más elaborados de cualquier ave marina: una delgada cresta negra en la frente y tres pares de plumas faciales blancas bilateralmente simétricas (superorbital, suborbital y auricular). Estudiamos los patrones de variación de los ornamentos en 796 individuos anillados (147 de sexo conocido, 254 de edad conocida de 1 a 16 años) durante 1992-2009 en la Isla Buldir (principalmente) y otras tres Islas Aleutianas (Davidof, Ulak y Egg) en Alaska, EEUU. Como era de esperar para los rasgos seleccionados socialmente, los ornamentos fueron más variables en tamaño entre individuos que los rasgos anatómicos, pero con un dimorfismo sexual ligeramente sesgado hacia los machos. El índice de condición corporal aumentó desde el año 1 hasta el año 3, pero cambió poco a partir de entonces. Incluso en aves de ≥4 años, el tamaño del ornamento se relacionó positivamente con el índice de condición corporal. Los subadultos (de un año de edad) presentaron ornamentos más pequeños que los adultos (2 a 16 años de edad), pero no hubo más cambios en el tamaño del ornamento a medida que los adultos envejecieron y no hubo evidencia de senescencia incluso en las aves más viejas (>8 años de edad). No obstante, el tamaño general de los ornamentos varió de un año a otro en la Isla Buldir y se correlacionó con los índices tanto del clima oceánico como de la productividad de *A. pygmaea* considerando los 2 a 5 años anteriores. De la Isla Buldir a la Isla Egg (1.266 km), el tamaño de los rasgos anatómicos y ornamentales aumentó entre 5-15%, excepto para la profundidad del pico, que fue mayor en las aves de Buldir y Egg en los extremos opuestos del área reproductiva de las Aleutianas. Este estudio es uno de los pocos que examina los patrones de variación de los ornamentos en un ave longeva y socialmente monógama, a pesar de que dichos patrones son cruciales para comprender la relación entre la selección sexual y la historia de vida.

Palabras clave: Alcidae, Aleutianas, ave marina, dimorfismo, edad, ornamentos de plumas, selección sexual, selección social, variación

INTRODUCTION

Elaborate avian feather structures displayed during the breeding season have been shown to be important for both species and individual recognition (Shields 1977)—as well for mate choice, signaling social status, and sensory functions—and are thus influenced by natural and sexual selection (Andersson 1994; Seneviratne and Jones 2010). The relationship between feather ornaments and sexual selection has received particular attention (Andersson 1994). Sexual dimorphism in ornaments may reflect differences in the influence of sexual and natural selection on males vs. females but the relationship between a variety of display traits and sexual selection continues to receive intense scrutiny (e.g., Cally et al. 2021; Hernández et al. 2021). When sexual selection acts similarly in males and females, as in some monogamous species, both sexes may display similar ornaments (sexually monomorphic) that are favored by mutual mate choice and mating preferences (e.g., Jones and Hunter 1993; Kraaijeveld et al. 2004), whereas polygynous species usually have highly male-biased sexual dimorphism with elaborate and variable male ornaments and displays (e.g., Andersson 1982; Petrie et al. 1991).

Sexually selected ornaments are widely believed to signal an individual's health and viability to potential mates (viability indicator hypothesis; Andersson 1994), but they may also be arbitrary traits favoured by sensory exploitation (Ryan 1990) or be a result of a "Fisherian" coevolutionary runaway process (Lande 1981; Kirkpatrick 1982). However, any mechanism that produces a costly display trait is likely to lead to a correlation with condition, health etc. mediated by cost (Balmford and Read 1991). Both the Fisherian and sensory exploitation mechanisms could certainly produce costly condition-correlated displays. Thus, the only experimental result refuting any of these hypotheses would be discovery of a completely arbitrary trait favoured by mate choice but not linked to condition, health etc. (rejecting viability indicator, consistent with Fisherian and sensory exploitation). Identifying such "arbitrary" traits via negative evidence is problematic. Nevertheless, the viability indicator model suggests that ornament expression would vary with body condition, health, and age with the maximal expression occurring in mid-life when individuals are most vigorous, with lesser expression in young and old individuals, as well as in individuals in poor health. Similarly, ornament expression within populations should vary with environmental conditions across years if those environmental conditions influence health and body condition. Despite almost four decades of interest in the plumage ornaments of birds, few long-term studies have investigated ornament variation in relation to these factors in monogamous, sexually monomorphic bird species, especially with respect to variation within individuals as they age.

Auklets (family Alcidae, tribe Aethiini) include five socially monogamous, planktivorous seabird species endemic to the North Pacific and adjacent Okhotsk and Bering Seas, some displaying elaborate feather and colorful bill ornaments during the breeding season (Jones 1999). Four of the 5 auklets (Least *Aethia pusilla*, Crested *A. cristatella*, Whiskered *A. pygmaea*, and Parakeet Auklet *A. psittacula*) display elaborate facial feather ornaments comprising filoplumes (including curling forehead crests and white filoplumes; Jones 1999; Jones et al. 2000; Seneviratne and Jones 2008). The feather ornaments of these 4 auklets 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 and Montgomerie 1992; Hunter and Jones 1999). The fifth, closely-related Cassin's Auklet (*Ptychoramphus aleuticus*) is in a different genus, lacks these filoplumes, and is coincidently highly nocturnal in its social and sexual activities (Jones 1999).

Feather ornaments of *Aethia* auklets grow to full size from January to April each year (Byrd and Williams 2020), and are then displayed during courtship activities in May to June. Field experiments using taxidermic mounts with manipulated ornaments provided some evidence for mutual mate preferences by Least Auklets based on their white facial plumes and bill colour (Jones and Montgomerie 1992) and by Crested Auklets based on their forehead crest (Jones and Hunter 1993; Jones and Hunter 1999). Similarly, we found some evidence for a heterospecific preference for crest ornaments in Least Auklets, a prediction of the sensory exploitation model (Jones and Hunter 1998). In addition, Seneviratne and Jones (2008, 2010) showed experimentally that Whiskered and Crested auklet filoplume ornaments serve a mechanosensory function in addition to their use in courtship displays. It has not been possible to duplicate those mating preference experiments for Whiskered Auklets due to their low density on the surface at colony sites and their largely nocturnal activity on land at Buldir where copulation and courtship display take place in daylight at sea (Hunter and Jones 1999). Thus, the role of the feather ornaments as sexually selected display traits in this species has been presumed based on comparative evidence (Jones 1999).

Whiskered Auklets have a slender black forehead-crest (apparently homologous to Crested Auklets' crest), 3 pairs of white facial plumes (similar to the less elaborate facial plumes of Least and Crested Auklets), a red bill, and a faint citrus-like plumage odor (Jones 1999; Seneviratne and Jones 2008). They nest in rock crevices, roost year-round on land, are partly nocturnal, and are socially monogamous, but have the most elaborate adornments of any seabird (Jones 1999; Hunter and Jones 1999; Hunter et al. 2002; Schacter and Jones 2018; Figure 1). The question remains as to how the variation in Whiskered Auklet ornaments might relate to their function.

To explore the potential role of Whiskered Auklet feather ornaments in social and sexual interactions, we studied the variation in these traits with respect to sex, age, body condition (based on a scaled mass index), and environmental conditions over an 18-year period at 1 breeding colony in the Aleutian Islands. We also looked for evidence of geographic variation across this species' range within the Aleutian Islands, for comparison to emerging evidence of differentiation across its entire range (Pshenichnikova et al. 2017). Our goal was not to test specific hypotheses about sexual or natural selection, which is always a challenge with observational data, but to explore patterns in the dataset as a basis for further research on ornamentation in this species. We discuss the implications of our findings in relation to likely mechanisms related to natural and sexual selection.

METHODS

Our main study site was a breeding colony at "Crested Point" (local name) on the northwest coast of Buldir Island, Alaska (Byrd and Day 1986, 52.371831°N, 175.890323°E, WGS 1984), from 1992 to 2009 where birds were mist netted at night. Birds were captured and plumes measured at this site every year, except 1999 and 2002, and always between days-of-the-year 139 (19/20 May) and 168 (17/18 June) though occasionally later in 11 years (latest = day 217, 5 August 1997). In two of those years, we also mist-netted birds on opportunistic nocturnal visits to 3 other islands within the Alaska Maritime National Wildlife Refuge (AMNWR): Davidof Island (51.961438°N, 178.336436°E) in the Rat Islands on 22 May 2006, to Ulak (52.038909°N, 175.908851°W) in the Andreanof Islands on 10 June and 15 July 2005, and to Egg Island (53.858415°N, 166.056848°W) in the Fox Islands on 17 nights from 16 June to 9 July 2005. All mist-net capture sites on all islands were on active talus deposits at the base of coastal cliffs within 10 m of the high tide mark, which are typical breeding colony sites for this species in the Aleutians (Byrd and Williams 2020).

At Buldir, we captured Whiskered Auklets using two 12-m mist nets between 00:00 and 02:30 ADT as they arrived at the nesting colony after foraging at sea (Table 1). Each evening, most captures occurred as the birds arrived in a "wave" within ~30 min after darkness fell (thus after sunset but varying with cloud cover and moon phase). Upon capture, we marked each individual with a numbered stainless-steel band, recorded its mass (±1 g) using a spring scale, and took several linear measurements using dial calipers (± 0.1 mm): tarsus length, bill depth, culmen, and the length of the crest as well as auricular, superorbital, and suborbital plumes (Figure 1).

Holding time for each bird was limited to ~30 min to minimize any stress associated with handling (Duarte 2013). We had teams of handlers (see Acknowledgements) who took the birds from the nets so that measurers could process birds as quickly as possible and we kept the bagged birds separate to reduce stress and overheating. Birds that appeared to be suffering from hyperthermia (heat stress; Cabanac and Guillemette 2001) were released immediately, sometimes before a complete set of measurements was obtained.

Tarsus was measured from the notch at the proximal end of the tarsometatarsus to the distal end of the tarsometatarsus on the underside of the foot. We measured bill depth along a line passing mid-way through the nostril from the edge of the feathering at the base of the culmen to the lowest point on the gonys, and the culmen length from the edge of the feathering at the base of the bill to the bill tip. We measured forehead crest length from the base of the black crest feathers at the skull to the tip of the longest feather, with crest flattened and straightened under slight pressure (Figure 1). Auricular plume length was measured from the point of origin of the first white feathers below and behind the eye to the tip of the longest, while holding the bird with the neck extended slightly to ensure that these plumes remained straight and parallel to

TABLE 1. Sampling of Whiskered Auklets on Aleutian Islands, Alaska, with the range of capture days in each year and the total number of capture days in brackets. Recaptures include repeated captures of the same bird in a given year. n/a = not applicable, because the island was not visited in a previous year

			First captures		Recaptures		
Year	Island	Capture days	Adults	Subadults	Within-year	Between-year	Total captures
1992	Buldir	139–172 (8)	88	6	14	n/a	108
1993	Buldir	153–195 (5)	45	16	13	34	108
1994	Buldir	154–167 (6)	12	11	7	62	92
1995	Buldir	142–164 (9)	22	30	12	55	119
1996	Buldir	152–207 (9)	24	28	29	94	175
1997	Buldir	145–217 (13)	40	20	19	76	155
1998	Buldir	133–205 (13)	24	27	1	92	144
2000	Buldir	149–195 (7)	43	18	1	50	112
2001	Buldir	146–202 (9)	26	29	2	75	132
2003	Buldir	153–160 (4)	17	7	4	34	62
2004	Buldir	154–157 (2)	9	0	0	14	23
2005	Buldir	150–156 (3)	15	5	2	17	39
2005	Ulak	161–196 (2)	34	0	3	n/a	37
2005	Egg	167–190 (17)	56	11	25	n/a	94
2006	Buldir	145–189 (10)	22	18	18	70	128
2006	Davidof	142 (1)	17	0	0	n/a	17
2007	Buldir	151–200 (8)	32	4	24	66	126
2008	Buldir	148–156 (5)	15	16	8	26	65
2009	Buldir	166 (1)	5	4	0	8	17
Totals			546	250	182	773	1753

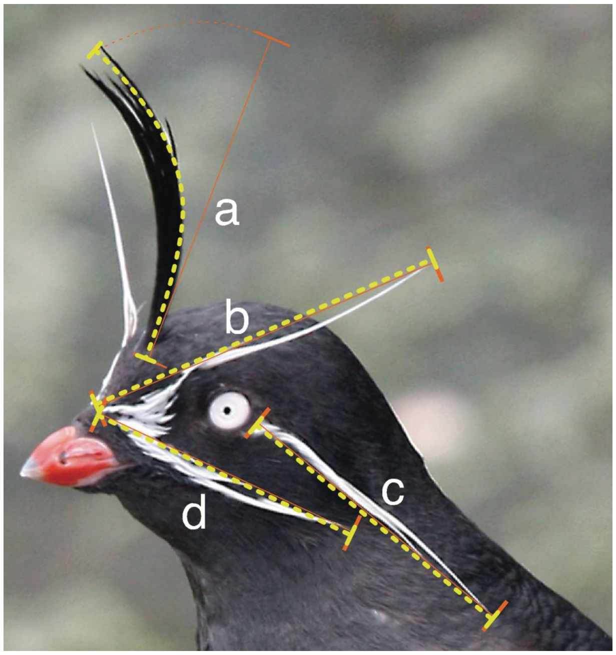

FIGURE 1. Whiskered Auklet feather ornaments of a bird photographed at Main Talus, Buldir Island on 27 June 2012 (I. L. Jones photo): (A) forehead crest, (B) superorbital plumes, (C) auricular plumes, and (D) suborbital plumes.

one another. Sub- and super-orbital plume lengths were measured from the forward-most point of origin of white feathers near the base of the bill to the tips of the longest feathers, with these straightened and parallel. We measured the bilateral auricular, superorbital, and suborbital plume lengths on the left and right sides when possible. The white facial plume measures reflect the total length of a patch of several overlapping filoplumes, while the black crest length measurement was close to the length of the longest feather in the crest. For analysis we discarded the data for a few birds whose feather ornaments were <5 mm long, indicating that those feathers had broken off rather than simply suffering from normal wear. Including those data in analyses did not affect our conclusions but too often influenced the distribution of residuals.

We scored the age of each captured bird as adult or subadult, the latter identified by extensive pale brown (due to weathering and wear) contour feathering on their forehead, chin, and neck, and similarly worn secondaries and greater coverts (Bédard and Sealy 1984; Gaston and Jones 1998; Pyle 2008). To test whether feather ornaments varied with breeding status, we examined each bird for the presence of a fully developed vascularized brood patch, indicating that it was an active breeder. We also recorded presence or absence of damage to foot webs—healed holes or tears in the webbing between the toes—that results from tick infestation at the chick stage (I. L. Jones personal observations). We reasoned that past exposure to infectious disease during early development, as indicated by web damage, might impair feather ornament expression later in life.

To ensure that the feather ornaments we were measuring were fully grown, we looked for evidence of moult.

Individuals with partly moulted ornaments were identified by the presence of a mixture of fresh blackish and worn brownish crest feathers, and mixed fresh silvery white and worn brownish auricular, super- and suborbital plumes. We also dissected a few birds found dead at the colony to check for molt as indicated by active pins. In 2000–2001, we took a 0.3 mL blood sample from the brachial vein of 102 adult and 49 subadult birds to determine their sex (91 male, 56 female) using molecular techniques described by Fridolfsson and Ellegren (1999).

All fieldwork was conducted under Animal Care Permits from Memorial University of Newfoundland and USFWS Master Banding Permit 22181 (see Acknowledgements).

Statistical Analyses

All analyses were performed using R (v. 4.1.0; R Core Team 2021). For linear mixed models (LMMs) we used the *lmer* function in the *lme4* package with bird identity as a random effect to control for multiple measurements of some individuals; for cross-correlations we used the *ccf* function in the *stats* package. For model selection, we used an information-theoretic approach, evaluating models with the corrected Akaike's Information Criterion (AIC_c) and considering all models within 2 AIC_c of the best-fitting model to be statistically supported, given the data, but correcting for uninformative parameters (Arnold 2010). We report analyses from the best-fitting models (lowest AIC_c) in the main text and all top models ($\Delta AIC_c < 2$) in a Statistical Supplement available on figshare (DOI: 10.6084/m9.figshare.14923440). Sample sizes are reported as *N* for the number of measurements and *n* for the number of individual birds.

For the bilateral feather ornaments, we focused on the larger of the 2 sides for birds where both sides were measured. In most cases we performed separate analyses on each of the 4 feather ornaments, as well as on a single variable representing overall ornament size generated by a principal components analysis. For that analysis we use the *principal* function in the psych package to calculate 2 varimax rotated components from those 4 feather ornament variables and 4 anatomical variables (body mass, culmen, bill depth, tarsus). The first rotated component (RC1) was strongly correlated with the length of the feather ornaments (r = 0.70–0.83), whereas RC2 was strongly correlated with bill depth, culmen, and tarsus (r = 0.58–0.75). Both components were moderately correlated with body mass (0.49–0.53). Thus, RC1 is a composite measure of ornament size. See Supplementary Material Table 1.2 and Supplementary Figure 1.1–1.2 for details.

We analyzed the within-year repeatability of measurements taken on individuals measured more than once to assess the measurement error resulting from the difficulty of measuring these birds in the field. To control for seasonal variation in traits, we analyzed within-year repeatabilities only for measurements within the earliest 2-week period for each bird each year controlling for year and day of the year as fixed effects. Repeatabilities were calculated using the *rpt* function in the *rptR* package.

To investigate the relationship of feather ornament expression to body condition we calculated the scaled mass index (SMI) of Peig and Green (2009). To calculate SMI we used the body mass and tarsus length of one randomly chosen measurement from each individual (see Supplementary Material Figure 1.4). In studies of birds both wing length and tarsus length have been shown to be reliable measures of body size but in our study tarsus length was measured on every bird captured and was just as repeatable as wing length (Table 2). However, auklet body mass varies daily and seasonally (Jones 1994), creating "noise" in any body-mass-based index of body condition. As a result, we expected to detect only strong biological relationships between ornaments and condition.

On finding that some of the measures of body condition (SMI), age, and progress of the breeding season were correlated with ornament size, we performed a Path Analysis (using the *lavaan* package, Rosseel 2012) to examine the relationships among these variables. Because we had measured many birds in more than one year, we calculated standardized path coefficients as the means of 1,000 iterations, each time choosing at random the measurements from one capture of each individual. We report coefficients from "completely standardized solutions" where both latent and observed variables are standardized and the magnitudes of the coefficients are directly comparable.

To investigate the relationship between feather ornament expression and both ocean climate and Whiskered Auklet demographic parameters, we performed exploratory time series analyses to look at cross correlations between current ornament sizes and past conditions that might influence feather growth. To do this, we used the *ccf()* function in the *stats* package on data across the 18 years of our study. For the analyses we looked at cross correlations with 5 ocean climate variables—Pacific Decadal Oscillation (Mantua et al. 1997), North Pacific Index (Trenberth and Hurrell 1994), Aleutian Low Pressure Index (Surry and King 2015), SLP-based NAM (Trenberth and Hurrell 1994), and Multivariate ENSO (National Center for Atmospheric Research 2019, also see Litzow et al. 2020)—and 3 measures of Whiskered Auklet demography at Buldir Island — annual productivity (number of chicks fledged per egg laid; Bond et al. 2011), timing of breeding (mean hatch date; Bond et al. 2011), and annual adult survival rate (Jones et al. 2002; Jones et al. 2007).

TABLE 2. Repeatabilities of anatomical and ornamental traits of Whiskered Auklets measured twice within a 2-week period at Buldir Island

Trait	Repeatability [95% CL]	P^a	*N* (*n*)
Anatomical			
Body mass	0.48 [0.32, 0.63]	<0.0001	196 (85)
Tarsus (mm)	0.85 [0.77, 0.92]	<0.0001	134 (85)
Wing (mm)	0.84 [0.78, 0.91]	<0.0001	300 (245)
Bill depth (mm)	0.93 [0.90, 0.97]	<0.0001	133 (85)
Culmen (mm)	0.81 [0.73, 0.90]	<0.0001	131 (84)
Plumage ornaments			
Crest (mm)	0.77 [0.66, 0.88]	<0.0001	132 (85)
Auricular (mm)	0.78 [0.66, 0.92]	<0.0001	95 (68)
Superorbital (mm)	0.91 [0.86, 0.96]	<0.0001	97 (68)
Suborbital (mm)	0.72 [0.57, 0.88]	0.0003	96 (68)

[a] 95% CL calculated by bootstrapping with 1,000 replicates. *P*-values from likelihood ratio tests.

RESULTS

Capture Summary

From 1992 to 2009 we captured, banded, and measured 796 Whiskered Auklets on 4 Aleutian Islands: 722 on Buldir, 17 on Davidof, 34 on Ulak, and 67 on Egg (Table 1). At first capture, 486 (67%) of the birds caught on Buldir were classified as adults (≥2 years old) and 235 (33%) as subadults (1 year old). Individual birds were captured and measured 1–12 times (average 2.3 times) over the years, such that 905 (56%) of all captures were of individuals marked and measured previously and 182 of those were of birds recaptured more than once in the same year. Among the 235 birds first captured and marked as subadults (1-year-olds) at Buldir, 94 were recaptured 1–15 years later so we know how old they were on recapture. All 39 birds recaptured one year after their initial capture as a subadult were classified as adults (i.e. subadult appearance lasted only for 1 year); 1 bird banded as a fledgling (September 1999) was in subadult plumage when we captured it on 3 June 2000 (i.e. subadults are 1 year old; cf Pyle 2008). Examination of ornamental feathers revealed active molt only in subadult birds, all of which showed some evidence of some growing facial feathers, a distinctive characteristic of individuals at this age (Bédard and Sealy 1984; Pyle 2008). Measurements were contributed by four observers as follows: I. L. Jones (1,116, 69%), F. M. Hunter (286, 18%), S. Seneviratne (207, 13%), and H. J. Munro (17, 1%). Because there were some significant differences among the measurers (Supplementary Material Table 2.1), we included measurer identity in all full models tested. Such differences were not unexpected given the difficult field conditions, measuring the birds at night when it was often cold, wet, and windy.

Repeatability

Within-year repeatability of feather ornament measurements (maximum of the 2 sides for bilateral ornaments) ranged from 0.72 for the suborbital plumes to 0.91 for the superorbital plumes, and for linear measurements of anatomical traits from 0.81 for culmen to 0.93 for bill depth (Table 2). Not surprisingly the repeatability of body mass was low (0.48) as this trait can change from hour to hour. Measurement error (1-repeatability; Bailey and Byrne 1990) of feather ornaments and linear measurements of other body parts traits ranged from 7 to 28%.

Sexual Dimorphism

Males were, on average, slightly larger than females for all measurements of adult birds (Table 3), with the sexual dimorphism index ranging from 1.02 to 1.03 for anatomical traits (body mass, wing, culmen, tarsus) and from 1.05 to 1.09 for ornamental plume lengths and bill depth (insets Figure 2A–D). Thus, feather ornaments and bill depth were slightly more sexually dimorphic than other anatomical traits. The differences between male and female traits were statistically significant for all anatomical traits (Table 3) and for all but crest length among the 4 ornamental traits (insets Figure 2A–D). Although males had significantly larger bill depths than females, the mean difference between marginal means was only 0.52 mm (Table 3). About 84% of adults could be reliably identified to sex using the linear measurements of their anatomical traits (culmen, wing, tarsus, bill depth) in a linear discriminant analysis (Supplementary Material Table S1.3 Figure S1.3).

Ornamental Trait Variability

All 4 ornamental traits were slightly larger (0.3–0.9 mm) in adult breeders (with brood patch) compared to presumed adult nonbreeders (no brood patch). None of those differences were significant ($P = 0.10$–0.49), so we pooled the data for all adults in all further analyses. Coefficients of variation for all four feather ornaments were high (9.9–19.1%), with little difference in variability between males and females (Table 4). Coefficients of variation for linear measurements of anatomical traits were considerably lower (2.3–7.3%), as expected for traits thought to be influenced by natural, rather than sexual, selection. All correlations among an individual

TABLE 3. Descriptive statistics—marginal mean [95% CI] *N* (*n*)—for adult males and females calculated from linear mixed models with sex, measurer, and day of year as fixed effects, and year and bird identity as random effects; bilateral facial plumes calculated from maximum of left and right plumes for each bird that had both plumes measured. SDI is calculated as male/female (Lovich and Gibbons 1992)

	Males		Females			
Trait	Mean [95% CI]	*N* (*n*)	Mean [95% CI]	*N* (*n*)	M-F (*P*) [a]	SDI
Forehead crest (mm)	39.2 [37.3, 41.0]	278 (86)	37.3 [35.3, 39.3]	195 (58)	1.85 (0.11)	1.05
Auricular plume (mm)	35.3 [34.2, 36.4]	278 (85)	33.4 [32.2, 34.6]	195 (58)	1.92 (0.003)	1.06
Superorbital plume (mm)	34.8 [33.5, 36.1]	278 (85)	32.0 [30.5, 33.6]	195 (58)	2.76 (0.008)	1.09
Suborbital plume (mm)	32.4 [31.5, 33.2]	278 (85)	30.8 [29.9, 31.8]	195 (58)	1.53 (0.004)	1.05
Bill depth (mm)	7.67 [7.58, 7.76]	278 (85)	7.15 [7.05, 7.26]	195 (58)	0.52 (<0.0001)	1.07
Culmen (mm)	9.48 [9.37, 9.59]	278 (85)	9.20 [9.07, 9.32]	195 (58)	0.28 (0.0002)	1.03
Tarsus (mm)	22.1 [21.9, 22.3]	278 (85)	21.6 [21.3, 21.8]	195 (58)	0.56 (<0.0001)	1.02
Wing (mm)	109 [108,110]	278 (58)	107 [106, 108]	195 (39)	2.31 (<0.0001)	1.02
Body mass (g)	120 [118, 123]	278 (86)	116 [114, 119]	105 (58)	4.04 (0.002)	1.03

[a] Difference between marginal means for males and females (*P*-value from Tukey post-hoc tests).

TABLE 4. Coefficients of variation (CV) calculated from one randomly chosen measurement for each adult

Trait	Male CV (*n*)	Female CV (*n*)	Compare CVs
Maximum auricular plume	9.9 (75)	10.5 (50)	F > M
Maximum superorbital plume	19.1 (77)	16.3 (51)	M > F
Maximum suborbital plume	10.5 (75)	11.3 (47)	F > M
Crest	12.6 (86)	12.9 (58)	F > M
Bill depth	4.5 (76)	4.1 (47)	M > F
Culmen	5.5 (76)	4.1 (47)	M > F
Tarsus	3.2 (79)	3.5 (58)	F > M
Body mass	6.8 (86)	7.3 (58)	F > M
Wing	2.7 (36)	2.3 (27)	M > F

adult bird's feather ornaments were moderate and similar (r = 0.47–0.52), whereas the correlations between those ornaments with anatomical traits except bill depth were weak at best (r = 0.02–0.41) and only the correlation between culmen and suborbital plume length was significant after Bonferroni correction (Table 5). All four plumage ornaments were weakly and significantly correlated with bill depth (r = 0.18–0.28) but most of the other correlations between ornaments and anatomical traits were weak ($r < |0.10|$).

Variation with Age, Body Condition (SMI), and Tick Infestation

The feather ornaments of subadults (1 year old) were smaller than those of adults (≥2 years old; Figure 2). By age 2, most birds' ornamental plumes had reached their maximum length with relatively little year-to-year fluctuation in ornament size as the birds aged (Figure 2). The best-fitting model for each of the ornamental traits included age category (subadult vs. adult) as a significant predictor. The index of body condition (SMI) increased from age 1 (subadults) to age 4 but then remained more or less constant through the rest of the bird's life (Figure 3). Thus, all subsequent full models included age as a predictor to control for any age effects. Each of the 4 feather ornaments also increased in size with the index of body condition (Figure 4), with similar standardized effect sizes though only significant for the super- and suborbital plumes (Table 6). Thus, feather ornament size was a predictor of condition during the breeding season, even though those ornaments were grown 4–6 months previously. Conversely, none of the anatomical traits were associated with condition (Table 6), even though some of the rhamphotheca (which would influence bill depth and possibly culmen length) and the feathers of the wing are shed and regrown following the breeding season each year (Byrd and Williams 2020). Despite the sometimes, extensive damage to the birds' foot webs due to nestling stage tick infestations, the presence of web holes in birds captured as subadults and adults had no significant effect on either body condition (SMI) or the size of any of the ornaments (LMMs, $P > 0.08$).

Because feather ornament size seemed to vary with breeding status (breeding or not), adult age, day of the year, and body condition (SMI), we used these 4 variables in a Path Analysis to quantify their interrelationships. To conduct that analysis, we assumed that adult age, day of the year, and condition might influence ornament size, that adult age and day might also influence condition and breeding status, and that condition, day of the year, and ornament size might influence breeding status. The analysis shows a moderate correlation between body condition (SMI) and ornament size, more than 10 times the magnitude of the correlations between age and either body condition (SMI) or ornament size (Figure 5). Breeding status, in turn, was approximately equally correlated with age, body condition (SMI), and day of the year. Thus, adult birds that were breeders each year were more likely to be older, to be in better

TABLE 5. Repeated measures correlations (above diagonal) among Aleutian Island Whiskered Auklet ornaments and anatomical traits of adult birds (>1 year old), with *P*-values below the diagonal. Sample sizes of individuals are shown, with 1–12 measurements per individual. Significant correlations in bold, after Bonferroni correction for multiple analyses; *P*-values are uncorrected

Trait (*n*)	Crest	Auricular	Superorbital	Suborbital	Culmen	Tarsus	Wing	Bill depth
crest (568)	–	**0.51**	**0.52**	**0.47**	0.08	0.03	0.06	**0.21**
Auricular (436)	**<0.0001**	–	**0.51**	**0.52**	0.02	**–0.10**	0.23	**0.28**
Superorbital (488)	**<0.0001**	**<0.0001**	–	**0.50**	0.12	–0.08	–0.03	**0.18**
Suborbital (437)	**<0.0001**	**<0.0001**	**<0.0001**	–	**0.14**	0.05	0.41	**0.25**
Culmen (451)	0.06	0.56	0.006	**0.001**	–	–0.07	0.24	0.09
Tarsus (509)	0.39	0.03	0.06	0.31	0.11	–	0.30	–0.01
Wing (256)	0.46	0.16	0.77	0.01	0.14	0.005	–	0.40
Bill depth (462)	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	0.04	0.76	0.01	–

TABLE 6. Relationships between the Whiskered Auklet body condition index (SMI) and plumage ornaments, and bill depth. For the 3 facial plumes that were measured on both sides of the face, the models predict the maximum length of the 2 sides. Effects of SMI are from best-fitting models with SMI included as a fixed effect (standardized) and individual identity as a random effect in all models. Significant effects of SMI in bold.

Response	Std beta [95% CL]	*P*	*N* (*n*)
Crest (mm)	0.42 [–0.12, 0.95]	0.13	203 (93)
Auricular (mm)	0.39 [–0.07, 0.85]	0.09	171 (85)
Superorbital (mm)	**0.67 [0.25, 1.10]**	**0.002**	192 (92)
Suborbital (mm)	**0.43 [0.08, 0.78]**	**0.02**	171 (85)
Overall ornament size (RC1)	**0.19 (0.12, 0.25)**	**<0.001**	171 (85)
Bill depth (mm)	0.005 [–0.03, 0.03]	0.77	182 (86)
Culmen (mm)	0.01 (–0.04, 0.06)	0.72	182 (86)
Wing length (mm)	–0.05 (–0.70, 0.60)	0.88	63 (46)

body condition, to be caught later in the season, and to have larger facial plume ornaments than nonbreeding adults.

Year-to-Year Variation

The overall size of facial plume ornaments (RC1) varied significantly across the 18 years of this study (Figure 6D), as did the size of the super- and suborbital plumes but not the crest or auricular plume. Bill depth and tarsus length also varied significantly across years, but culmen, wing length, and body mass did not. Cross correlations among the sizes of individual ornaments were highest and significant only with ornaments measured in the same year (Figure 6I, Supplementary Material Figure 4.1), suggesting that the size of ornaments varied more or less in concert from year to year. With respect to ocean climate, the highest cross-correlations were between overall ornament size (RC1) and the Pacific Decadal Oscillation and multivariate ENSO indices 3 and 5 years earlier (Figure 6F, G). With respect to Whiskered Auklet demographic variation at Buldir, the only significant cross correlation was between overall ornament size and the number of chicks fledged per egg laid 1 and 3 years previously (Figure 6H, Supplementary Material Figure 4.2).

Geographic Variation

All feather ornaments varied significantly in size across the four study sites, generally increasing in average size from west to east (Figure 7) in models controlling for tarsus length (as a measure of body size), day of the year, and year. For the three facial plumes, the birds from Egg Island, the easternmost site, were 9–13% larger than birds from Buldir Island, the westernmost site, and their crests were 25% larger. Three anatomical traits (culmen, wing, and tarsus) varied in the same fashion from west to east, with the smallest birds at Buldir and the largest at Egg Island (Figure 7). Island-to-island variation in bill depth showed a different pattern as birds from Buldir had the largest bill depth, slightly deeper than those from Egg Island and significantly deeper than birds from Ulak (Figure 7). Despite that variation in average linear measurements, there were only slight differences in average body mass among the islands (linear model, LLR χ^2 = 3.9, P = 0.27), and birds from Buldir were on average the heaviest.

DISCUSSION

Whiskered Auklets' feather ornaments exhibited about 2–5 times as much variability as non-ornamental traits (Table 4), as expected from a comparison of sexually and naturally selected traits for other auklet species (Jones and Montgomerie 1992; Jones et al. 2000) and for birds in general (Alatalo et al. 1988). High individual variability is considered to be characteristic of traits that are a product of social selection (e.g., for individual recognition) or sexual selection (for courtship and mate choice). Thus, we conclude that Whiskered Auklet feather ornaments are display traits, as has been experimentally indicated for similar ornaments of Crested (Jones and Hunter 1993, 1999) and Least auklets (Jones and Montgomerie 1992). Such field experiments were not feasible in our study site at Buldir because the number of Whiskered Auklets active during daylight was too small (cf. Byrd and Williams 2020).

These feather plumes have also been shown experimentally to have a (naturally selected) sensory function used underground in their constricted rock crevice breeding habitat on coastal cliffs and talus slopes (Seneviratne

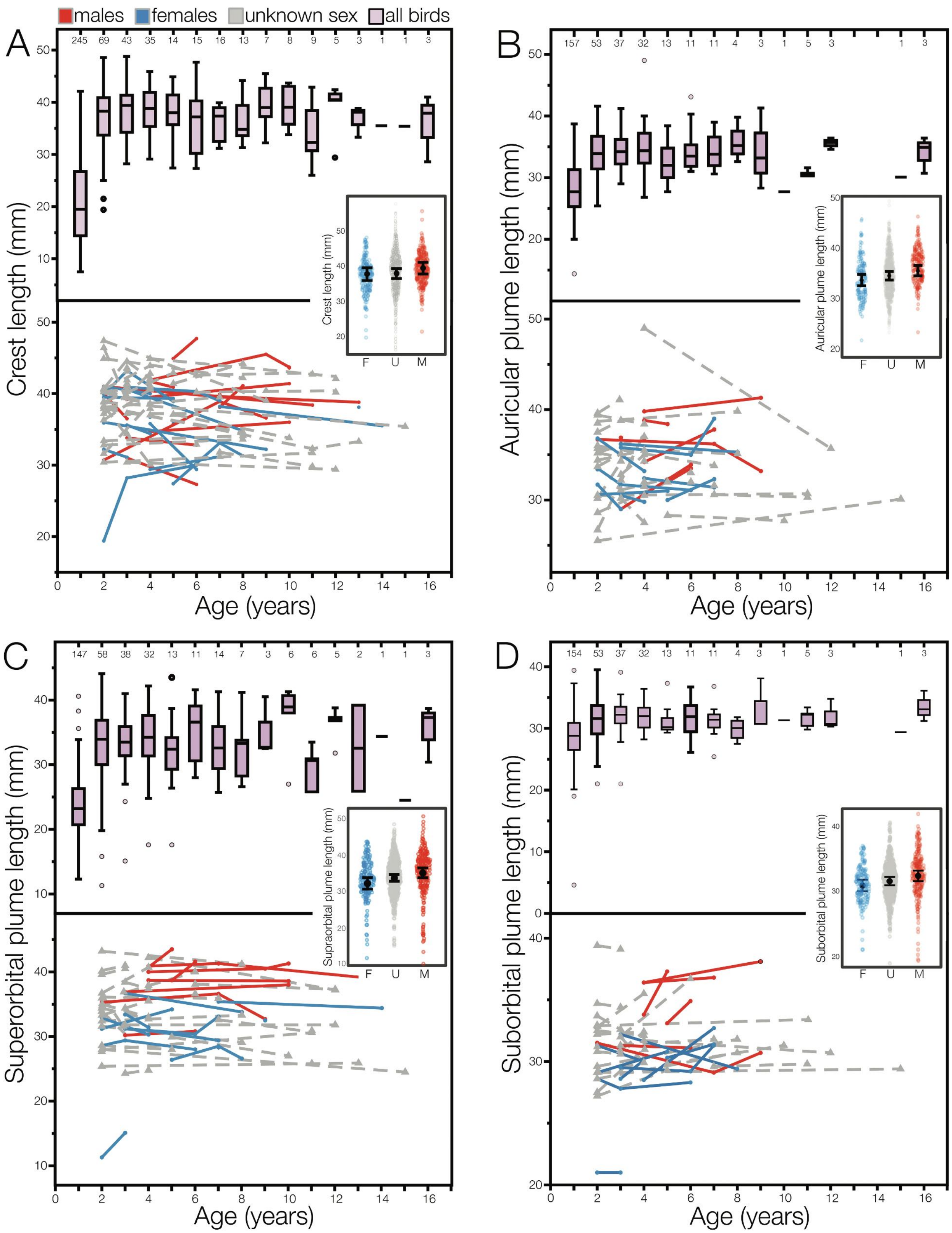

FIGURE 2. Whiskered Auklet feather ornament expression in relation to age and sex. In each pane the top graph shows Tukey box plots for each age, for all birds, regardless of sex (sample sizes below the top axis). Insets show all of the raw data for adult males (M), females (F), and birds of unknown sex (U), with marginal means ± 95% CL for each group (see Table 3 for model details and sample sizes). Bottom graph in each pane shows the ornament size for each individual that was measured in different years as adults (>1 year old). (A) Crest length. (B) Maximum auricular plume length. (C) Maximum superorbital plume length. (D) Maximum suborbital plume length.

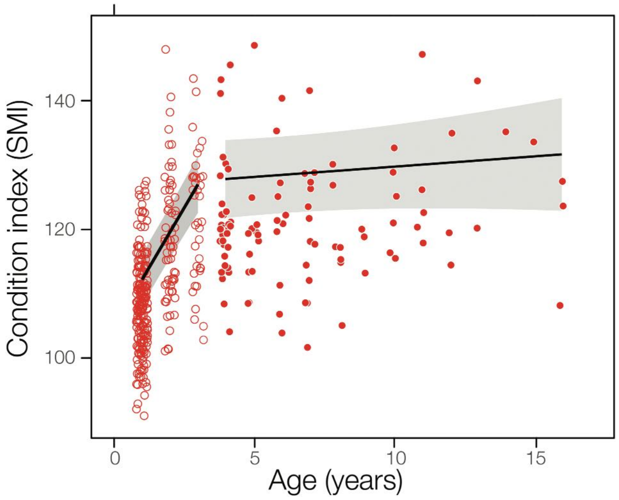

FIGURE 3. Variation in Whiskered Auklet body condition (SMI) in relation to age. Average condition increased with age until age 3 (open circles), then remained constant for the rest of life (closed circles). Predicted regressions ± 95% CL are plotted for each group, from models controlling for sex, measurer, and day of the year as fixed effects, and both year and bird identity as random effects. Sample sizes (measurements, birds): ages 1–3 (306, 240), ages ≥ 4 (101, 61). See Jones et al. (2021) for statistical details..

and Jones 2008, 2010). With 3 sets of protruding facial filoplumes and a forehead filoplume crest, Whiskered Auklets are well equipped to navigate a darkened maze configured similar to the rock crevices where they nest. These different filoplume ornaments were also all about the same average length (Table 3) and protruded about equally away from the birds' heads (I. L. Jones personal observations), consistent with their use as sensors in dark crevices. Filoplumes, characterized by their sensory function, also serve as display ornaments in a variety of other bird species (Seneviratne and Jones 2010; Kane et al. 2018). Intriguingly, Kane et al. (2018) showed experimentally an acoustic sensitivity of peacock's filoplume crest ornament. Whiskered Auklets are nocturnal and communicate with loud vocalizations in situations where vision is restricted. Taken together, these findings indicate a dual function for these facial feather ornaments (display and sensory) as sensory function would not appear to predict the high individual variability observed in these ornamental feathers, which is more typical of a display trait.

The slight male-biased sexual dimorphism (2–9%; Table 3) in both ornamental and anatomical traits matched the pattern previously described for Least and Crested auklets (Jones and Montgomerie 1992; Jones et al. 2000). Nevertheless, in our main study population on Buldir, size dimorphism was slightly greater in the feather ornaments than in anatomical traits (Table 3), consistent with the ornaments' function in sexual and social displays as males appear to take a more active role in courtship displays than females (e.g., Hunter and Jones 1999; Bond et al. 2020; Jones 2020).

The positive correlations between ornaments within individual adults (Table 5), suggest that different feather ornament types were grown in concert during the annual molt. These similar correlation coefficients and the similar sizes of these four ornaments are not consistent with an individual recognition function (Dale et al. 2001), as identity signals are expected to provide the most information when their traits are only weakly correlated. Alternatively, high correlations and structural similarity among traits argues for the sort of signal redundancy (Møller and Pomiankowski 1993) that is thought to characterize sexually-selected traits, especially when each of those traits is correlated with condition (Figure 4).

While there was a large increase in feather ornament size between 1- and 2-year-olds, ornament size did not increase further with age, and there was no evidence of senescence in ornament expression even in the oldest birds (Figure 2). Like the other *Aethia* auklets, average longevity in this species is about 8–9 years (Jones et al. 2007; Bond et al. 2020). We studied 28 individuals >7 years old, where senescence might be expected but we found no evidence of a decline in body condition (SMI) or ornament size (Figures 2 and 3). In addition, although Whiskered Auklets have delayed plumage maturation, there was no indication that ornaments function as reliable indicators of age among adult birds (cf. Balbontín et al. 2011).

The age-related pattern of sexually selected ornamental trait expression across the life span is potentially useful for understanding the function of these enigmatic traits, yet few studies have quantified this for long-lived wild birds. The Red-tailed Tropicbird's (*Phaethon rubricauda*) elongated tail streamer length was not related to age among 372 known-age individuals 3–22 years old (Veit and Jones 2003, 2004), similar to our finding for Buldir Whiskered Auklets. For shorter-lived species, the pattern apparently may be different. For example, in the well-studied Barn Swallow (*Hirundo rustica*), male tail ornament size steadily increased with age in males but not females (2,143 individuals, 2–6 years old; Balbontín et al. 2011). Similarly, the eye-comb ornament of male Black Grouse (*Lyrurus tetrix*), increased steadily in size with age, but the length of the lyre tail ornament stabilized after 1 year and body colouration showed only a weak age relationship (164 individuals, 1–6 years old; Kervinen et al. 2015). For a more complete understanding of the function of such sexually selected ornamental traits and their relation to life history, far more information is needed on how they relate to age, especially in long-lived species. Given the difficulty of obtaining these data, it may be some time before this matter is clarified.

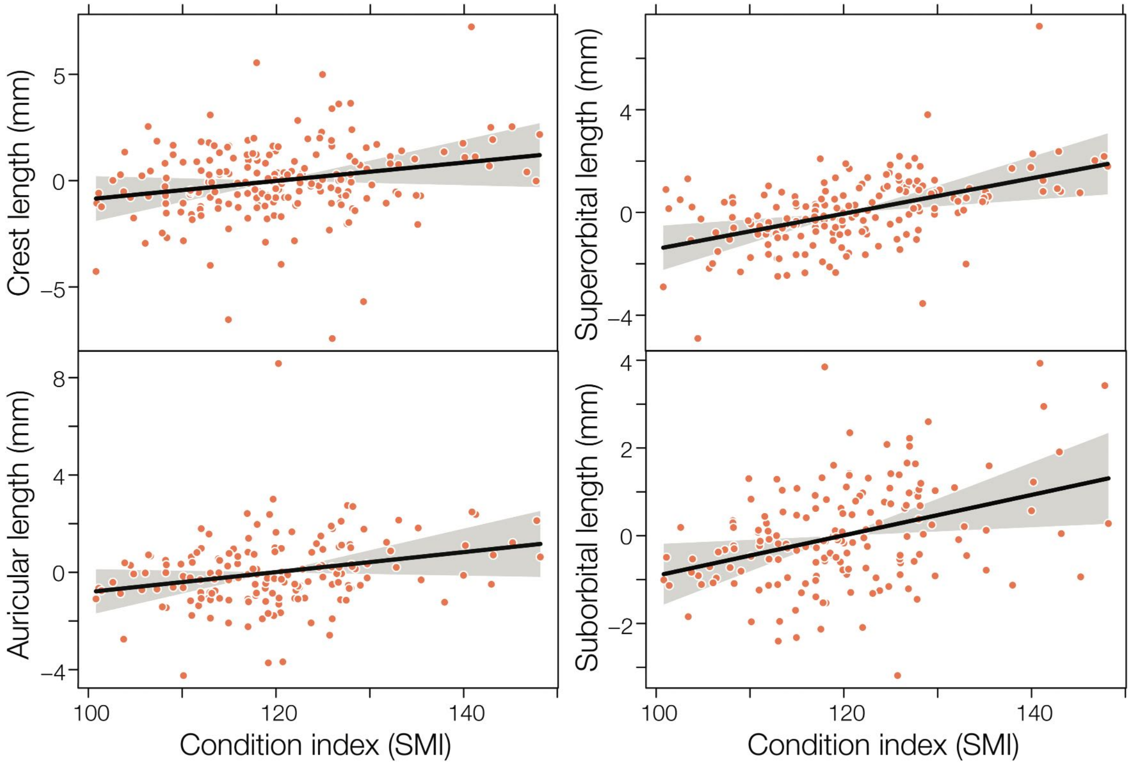

FIGURE 4. Variation in Whiskered Auklet feather ornaments in relation to body condition (SMI). Each graph for bilateral plumes shows predicted regressions (±95% CL) for the maximum of the two sides in birds where both sides were measured (see Table 6 for models and sample sizes).

As for Least and Crested auklets (Jones and Montgomerie 1992; Jones et al. 2000), there were moderate positive correlations between ornament size and an index of body condition (SMI) for the 4 Whiskered Auklet feather ornaments (Figure 4). A Path Analysis showed that body condition (SMI) was much more important than an individual's age or the stage of the breeding season in predicting ornament size, and that ornament size was a moderate predictor of adult breeding status (Figure 5). Here our body condition index was based on a single mass measurement for each individual from a mixed sample including breeders arriving to begin their incubation shifts, a few breeders departing after completing their incubation shifts, as well as adult nonbreeders prospecting on the site. Moreover, our index of body condition (SMI) is based on body mass which is known to vary daily and seasonally within individual auklets (Jones 1994) is thus a source of unexplained variation. Thus, while the relationships between ornament size and body condition (SMI) were relatively weak, they may reflect a less variable measure of individual quality (i.e. "viability indicator hypothesis"; Andersson 1994) that could be useful to individuals choosing mates.

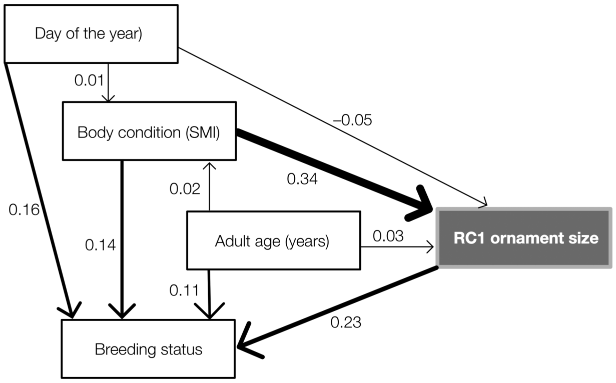

FIGURE 5. Standardized path analysis coefficients for the relationships among adult age, breeding status, body condition (SMI), day of the year, and overall ornament size (RC1). Line thickness indicates the relative magnitude of each effect. Mean coefficients calculated from randomly sampling one capture from each individual and repeating this 1,000 times (*n* = 58–77 birds per analysis). See also Supplementary Material Figure S3.1 for similar results without age as a predictor in the model and thus much larger sample size.

Climate-forced annual and decadal variation in North Pacific oceanography (captured by large-scale climate indices; Hallett et al. 2004) determines ocean productivity and food supply for seabirds, fish, and other marine predators (Trenberth and Hurrell 1994). For Whiskered Auklets at Buldir, annual adult survival was correlated with the ALPI ocean climate index (Jones et al. 2007). Similarly, there was some annual variability in the feather ornaments in the Buldir population, with the different

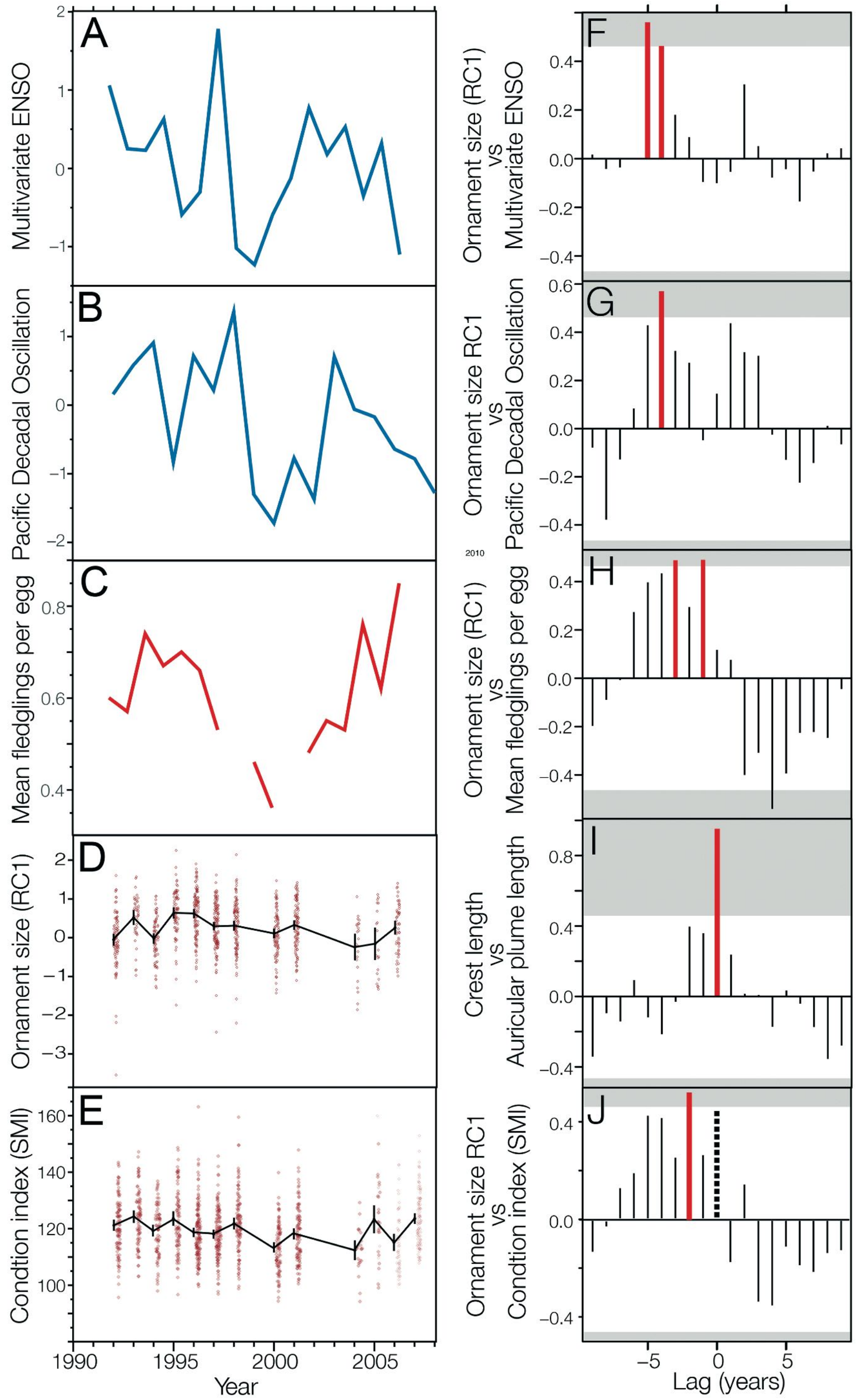

FIGURE 6. (A–E) Year-to-year variation in Whiskered Auklet feather ornaments in relation to environmental conditions, auklet productivity and body condition (SMI) during 1992–2008 and (F–J) cross correlations from time series analyses, with the lag indicating the difference between ornament size in the current year and the environmental, productivity, or condition variable in previous and future years. (A, B) Measures of North Pacific climate; (C) average number of chicks fledged per egg laid; (D, E) predicted ±95% CL overall ornament length (RC1) and condition (SMI), respectively, including all of the data (red symbols) for all adults each year, from a model controlling for day of the year, age, sex, and measurer as fixed effects and bird identity as a random effect; (F, G) overall ornament size (RC1) vs. measures of North Pacific climate; (H) RC1 vs. average number of chicks fledged per egg laid; (I) crest length vs. auricular plume length; (J) ornament size (RC1) vs. condition (SMI). Vertical lines on the right-hand graphs show magnitude of cross-correlation coefficients, with significant correlations in red. The dashed line in (J) shows the within-year correlation, which is significant in a LMM (Table 6). Grey shading indicates regions of significant cross correlations.

ornaments varying in a correlated fashion across years and correlated with the Pacific Decadal Oscillation and multivariate ENSO ocean climate indices (Figure 6F and G) that are associated with ocean primary productivity and thus the abundance of zooplankton potentially available to foraging Whiskered Auklets. Because the Whiskered Auklet facial plume length results from growth during the preceding winter and spring, a correlation between ornament expression and prey abundance, and thus ocean productivity in past years, was expected. We also found some evidence for annual variability in the feather ornaments correlating with productivity of Whiskered Auklets at Buldir 1 and 3 years previously (Figure 6H). Higher productivity indicates that those earlier years were associated with greater ocean productivity, a factor that might influence body condition and the growth of new feathers in the coming winter (Figure 6J). These finding make sense in relation to connections among the variations in ocean productivity forced by ocean climate, the life cycles of Whiskered Auklet's zooplankton prey, and the timing or ornamental feather growth. Euphausiid and other crustacean prey of Whiskered Auklets (Byrd and Williams 2020) have multi-year life cycles (Kim et al. 2009), so their winter availability as suitable prey might be expected to lag by 1–5 years following climate driven episodes of peak productivity.

Whiskered Auklets exhibit geographic variation in size and other traits across their range, the most conspicuous reported feature of this being size, with birds from Aleutian Islands (51–54°N, 178°W–172°E) smaller than birds from Kurile Islands (45–49°N, 149–154°E) with the largest birds breeding population further northwest at isolated St.-Jonah (Iona) Island (56°N, 143°E) in the Sea of Okhotsk (Feinstein 1959; Pshenichnikova et al. 2017). Within the Aleutians, the breeding range of this species spans >1,500 km east to west, with a pattern of increasing size from west to east (2 mm in wing, 1 mm in tarsus; Figure 7) that due to our limited sample sizes for two sites requires further examination. Whiskered Auklets might be expected to exhibit local genetic and morphological differentiation because they are less dispersive than other *Aethia* auklet species (e.g., at Buldir their population appears to be year-round resident on the island; Schacter and Jones 2018). If Whiskered Auklet populations are generally as sessile as they are at Buldir, more such undiscovered variation among the isolated Aleutian, Commander Islands, Kurile Islands, Penzhina Bay, and Iona Island areas (Figure 7) is likely to be revealed. In relation to behavioral variation across the breeding range, we also note that, although Whiskered Auklets were netted at night for this study, they exhibit diurnal activity at the Main Talus colony on Buldir Island (Figure 1) where Least and Crested Auklets are abundant (Byrd et al. 1983; I. L. Jones personal observations). Similar diurnal activity occurs at Iona Island, also in the presence of nesting Least and Crested Auklets (Pshenichnikova et al. 2017).

Conclusion

In summary, we quantified patterns of variation of Whiskered Auklet feather ornaments (Figure 1) from direct measurements of birds made during 1992–2009 in the Aleutian Islands. Whiskered Auklets were difficult to handle and measure—they arrived at our nets en masse and individuals could only be held for a limited time—so few individuals could be measured repeatedly. In addition, the feather ornaments themselves were challenging to measure, being complex and flexible (Figure 1). White facial plume ornaments were composite traits of multiple overlapping feathers, so our measurement was of a group of overlapping feathers rather than a single more readily comparable feather. Because sex could not be reliably determined from measurements alone, we depended on the relatively small sample (22% of individuals) we were able to sex with molecular techniques for comparisons of males and females. Nonetheless, our study spanned 18 years (1992–2009), the sample of birds measured was large (Table 1), our measurements were repeatable (Table 2), and we obtained measurements from 4 sites spanning 1,266 km across this species' range in the Aleutian Island chain.

Whiskered Auklets display a highly variable set of elaborate facial feather ornaments that have multiple functions both for social and sexual displays as well as for sensing a constricted nesting environment in dark crevices (confirmed by a variety of experimental and comparative evidence). Only a few other studies have examined such variation in elaborate ornamental feather traits with respect to both age and annual variation. Thus, we now know, at least for Whiskered Auklets, that these ornaments do not change as adults age, and that annual variation probably reflects body condition that is influenced by ocean productivity before the annual moult. Despite these patterns, the link between birds' ornaments and life history is still uncertain and will require more careful experiments in the field.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithology* online.

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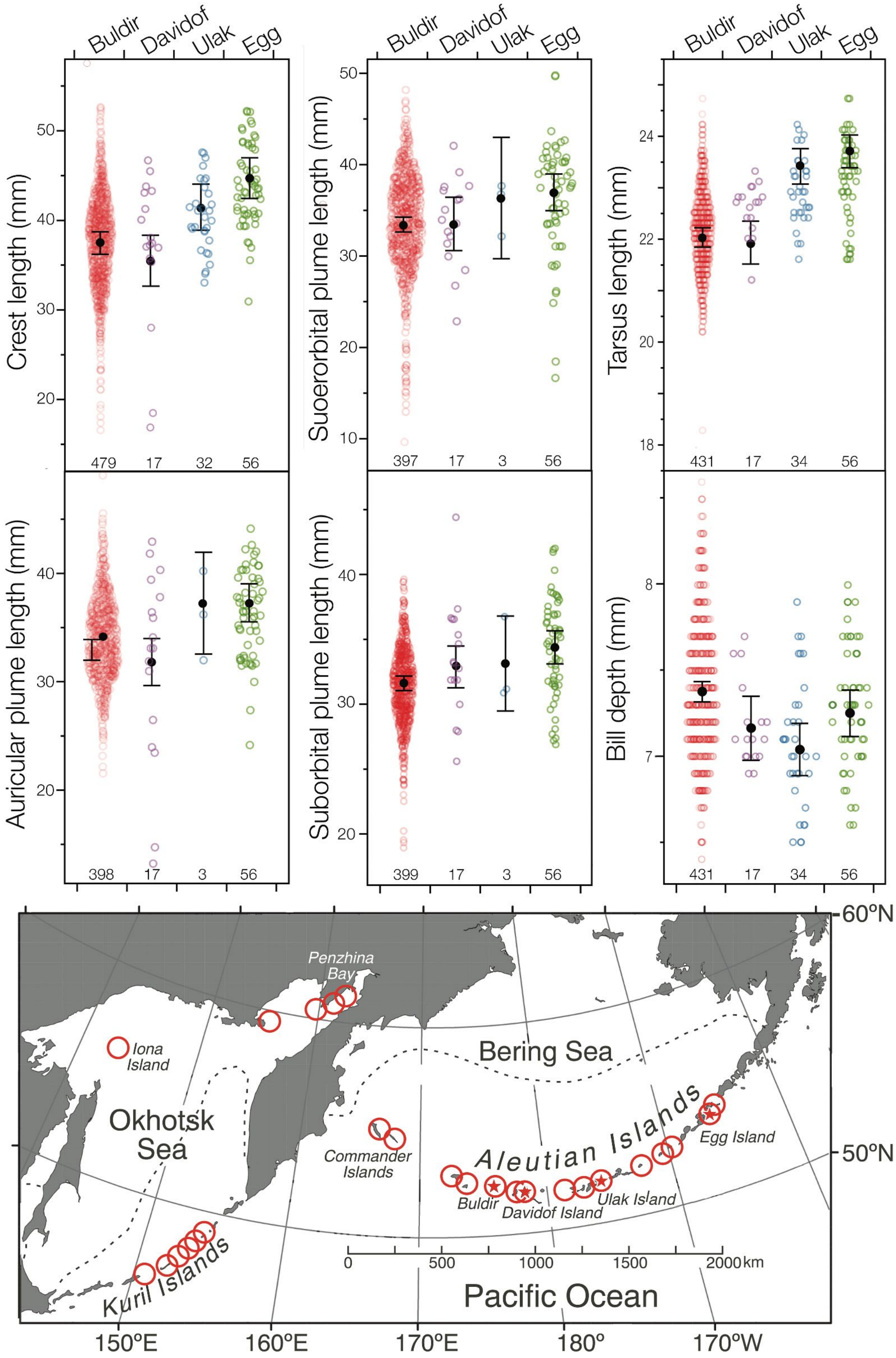

FIGURE 7. Variation in Whiskered Auklet ornamental and anatomical traits across 4 Aleutian Islands (red stars on map). For each island, measurements of all adult birds measured by I. L. Jones are shown, with the point estimate ± 95% CL of the marginal means from models controlling for day of the year, tarsus length as an index of body size, and both year and bird identity as random effects. Sample sizes shown are the number of individual adults measured. On the map, all known Whiskered Auklet breeding colonies are indicated with red circles (after Gaston and Jones 1998).

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Ethics statement: Our research was conducted under U.S. federal Master Banding Permit #22181 held by I. L. J., in compliance with the animal care regulations of the Institutional Animal Care Committee at Memorial University of Newfoundland, and with permission from AMNWR to conduct research in wilderness areas of the refuge. The authors declare no conflicts of interest. The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

Author contributions: I. L. J. and F. M. H. conceived the study and conducted fieldwork; S. S. S. conducted fieldwork and J. C. W. conducted fieldwork and facilitated AMNWR logistic support; R. M. led the statistical analysis; I. L. J. and R. M. wrote the first draft of the paper, and all authors contributed to and approved the final manuscript.

Data deposits: Analyses reported in this article can be reproduced using the data provided by Jones et al. (2021).

LITERATURE CITED

Alatalo, R. V., Höglund, J., and A. Lundberg (1988). Patterns of variation in tail ornament size in birds. Biological Journal of the Linnean Society 34:363–374.

Andersson, M. (1982). Female choice selects for extreme tail length in a widowbird. Nature 299:818–820.

Andersson, M. (1994). Sexual Selection. Princeton University Press, Princeton, NJ, USA.

Arnold, T. W. (2010). Uninformative parameters and model selection using Akaike's information criterion. The Journal of Wildlife Management 74:1175–1178.

Bailey, R. C., and J. Byrnes (1990). A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. Systematic Biology 39:124–130.

Balbontín, J., F. de Lope, I. G. Hermosell, T. A. Mousseau, and A. P. Møller (2011). Determinants of age-dependent change in a secondary sexual character. Journal of Evolutionary Biology 24:440–448.

Balmford, A., and A. F. Read (1991). Testing alternative models of sexual selection through female choice. Trends in Ecology and Evolution 6:274–276.

Bédard, J., and S. G. Sealy (1984). Moults and feather generations in the Least, Crested and Parakeet Auklets. Journal of Zoology 202:461–488.

Bond, A. L., I. L. Jones, W. J. Sydeman, H. L. Major, S. Minobe, J. C. Williams, and G. V. Byrd (2011). Reproductive success of planktivorous seabirds in the North Pacific is related to ocean climate on decadal scales. Marine Ecology Progress Series 424:205–218.

Bond, A. L., I. L. Jones, S. Seneviratne, and S. Bin Muzaffar (2020). Least Auklet (*Aethia pusilla*), version 1.0. In Birds of the World (A. F. Poole, Editor). Lab of Ornithology, Cornell Ithaca, NY, USA. https://doi.org/10.2173/bow.leaauk.01

Byrd G. V., R. H. Day, and E. P. Knudtson (1983). Patterns of colony attendance and censusing of auklets at Buldir Island, Alaska. The Condor 85:274–280.

Byrd, G. V., and R. H. Day (1986). The avifauna of Buldir Island, Aleutian Islands, Alaska. Arctic 39:109–118.

Byrd, G. V., and J. C. Williams. (2020). Whiskered Auklet (*Aethia pygmaea*), version 1.0. In Birds of the World (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.whiauk.01

Cabanac, A. J., and M. Guillemette (2001). Temperature and heart rate as stress indicators of handled Common Eider. Physiology and Behaviour 74:475–479.

Cally, J. G., D. Stuart-Fox, L. Holman, J. Dale, and I. Medina (2021). Male-biased sexual selection, but not sexual dichromatism, predicts speciation in birds. Evolution 75:931–944.

Dale, J., D. B. Lank, and H. K. Reeve (2001). Signaling individual identity versus quality: A model and case studies with Ruffs, queleas, and House Finches. The American Naturalist 158:75–86.

Duarte, L. M. G. (2013). Impacts of Capture and Handling of Wild Birds. Ph.D. thesis, Cardiff University, Cardiff, UK.

Feinstein, B. (1959). Geographic variation in the Whiskered Auklet. The Auk 76:60–67.

Fridolfsson, A.-K., and H. Ellegren (1999). A simple and universal method for molecular sexing of non-ratite birds. Journal of Avian Biology 30:116–121.

Gaston, A. J., and I. L. Jones (1998). The Auks. Oxford University Press, Oxford, UK.

Hallett, T. B., T. Coulson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and B. T. Grenfell (2004). Why large-scale climate indices seem to predict ecological processes better than local weather. Nature 430:71–75.

Hernández, A., M. Martínez-Gómez, R. Beamonte-Barrientos, and B. Montoya (2021). Colourful traits in female birds relate to individual condition, reproductive performance and male-mate preferences: A meta-analytic approach. Biology Letters 17:20210283.

Hunter, F. M., and I. L. Jones (1999). The frequency and function of aquatic courtship and copulation by Least, Crested, Whiskered and Parakeet Auklets. The Condor 101:518–528.

Hunter, F. M., I. L. Jones, J. C. Williams, and G. V. Byrd (2002). Breeding biology of the Whiskered Auklet (*Aethia pygmaea*) on Buldir Island, Alaska. The Auk 119:1036–1051.

Jones, I. L. (1994). Mass changes of Least Auklets *Aethia pusilla* during the breeding season: Evidence for programmed loss of mass. Journal of Animal Ecology 63:71–78.

Jones, I. L. (1999). Assessing the role of sexual selection in adaptive radiation of the auklets (Alcidae, Aethiini). In Proceedings of the 22nd International Ornithological Congress, Durban, South Africa (N. J. Adams, and R. H. Slotow, Editors). University of Natal, Durban, South Africa.

Jones, I. L. (2020). Crested Auklet (*Aethia cristatella*), version 1.0. In Birds of the World (A. F. Poole and F. B. Gill, Editors). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.creauk.01

Jones, I. L., and R. D. Montgomerie (1992). Least Auklet ornaments: Do they function as quality indicators? Behavioural Ecology and Sociobiology 30:43–52.

Jones, I. L., and F. M. Hunter (1993). Mutual sexual selection in a monogamous seabird. Nature 362:238–239.

Jones, I. L., and F. M. Hunter (1998). Heterospecific mating preferences for a feather ornament in Least Auklets. Behavioral Ecology 9:189–192.

Jones, I. L., and F. M. Hunter (1999). Experimental evidence for mutual inter- and intrasexual selection favouring a Crested Auklet ornament. Animal Behaviour 57:521–528.

Jones, I. L., F. M. Hunter, and G. Fraser (2000). Patterns of variation in ornaments of Crested Auklets (*Aethia cristatella*). Journal of Avian Biology 31:119–127.

Jones, I. L., F. M. Hunter, and G. J. Robertson (2002). Annual adult survival of Least Auklets (Aves, Alcidae) varies with large-scale climatic conditions of the North Pacific Ocean. Oecologia 133:38–44.

Jones, I. L., F. M. Hunter, G. J. Robertson, J. C. Williams, and G. V. Byrd (2007). Covariation among demographic and climate parameters in Whiskered Auklets (*Aethia pygmaea*). Journal of Avian Biology 38:450–461.

Jones, I. L., F. M. Hunter, S. S. Seneviratne, J. C. Williams, and R. Montgomerie (2021). Data from: Extensive variation in feather ornaments of Whiskered Auklets in the Aleutian Islands reflects age, sex, condition, and geography. Ornithology 139:ukab082. https://doi.org/10.5061/dryad.jq2bvq89p

Kane, S. A., D. Van Beveren, and R. Dakin (2018). Biomechanics of the Peafowl's crest reveals frequencies tuned to social displays. PLoS One 13:e0207247.

Kervinen, M., C. Lebigre, R. V. Alatalo, H. Siitari, and C. D. Soulsbury (2015). Life-history differences in age-dependent expressions of multiple ornaments and behaviors in a lekking bird. The American Naturalist 185:13–27.

Kim, H. S., A. Yamaguchi, and T. Ikeda (2009). Abundance, biomass and life cycle patterns of euphausiids (*Euphausia pacifica, Thysanoessa inspinata* and T. *longipes*) in the Oyashio region, western subarctic Pacific. Plankton Benthos Research 4:43–52.

Kirkpatrick, M. (1982). Sexual selection and the evolution of female choice. Evolution 36:1–12.

Kraaijeveld, K., J. Gregurke, C. Hall, J. Komdeur, and R. A. Mulder (2004). Mutual ornamentation, sexual selection, and social dominance in the Black Swan. Behavioral Ecology 15:380–389.

Lande, R. (1981). Models of speciation by sexual selection on polygenic traits. Proceedings of the National Academy of Sciences USA 78:3721–3725.

Litzow, M. A., M. E. Hunsicker, N. A. Bond, B. J. Burke, C. J. Cunningham, J. L. Gosselin, E. L. Norton, E. J. Ward, and S. G. Zador (2020). The changing physical and ecological meanings of North Pacific Ocean climate indices. Proceedings of the National Academy of Sciences USA 117:7665–7671.

Lovich, J. E., and J. W. Gibbons (1992). A review of techniques for quantifying sexual size dimorphism. Growth, Development, and Aging 56:269–281.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis (1997). A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069–1079.

Møller, A. P., and A. Pomiankowski (1993). Why have birds got multiple ornaments? Behavioural Ecology and Sociobiology 32:167–176.

National Center for Atmospheric Research Staff (Editors). (2019). The Climate Data Guide: Multivariate ENSO Index. https://climatedataguide.ucar.edu/climate-data/multivariate-enso-index

Petrie, M., T. Halliday, and C. Sanders (1991). Peahens prefer peacocks with elaborate trains. Animal Behaviour 41:323–331.

Peig, J., and A. J. Green (2009). New perspectives for estimating body condition from mass/length data: The scaled mass index as an alternative method. Oikos 118:1883–1891

Pshenichnikova, O. S., A. V. Klenova, P. A. Sorokin, N. B. Konyukhov, A. V. Andreev, S. P. Kharitonov, V. A. Zubakin, Y. B. Artukhin, and C. R. Schacter (2017). Population differentiation in Whiskered Auklets *Aethia pygmaea*: Do diurnal and nocturnal colonies differ in genetics, morphometry and acoustics? Journal of Avian Biology 48:1047–1061.

Pyle, P. (2008). Identification Guide to North American Birds, Part II: Anatidae to Alcidae. Slate Creek Press, Bolinas, CA, USA.

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rosseel, Y. (2012). lavaan: An R package for structural equation modeling. Journal of Statistical Software 48:1–36.

Ryan, M. (1990). Sexual selection, sensory systems and sensory exploitation. Oxford Surveys in Evolutionary Biology 7:157–195.

Schacter, C., and I. L. Jones (2018). Confirmed year-round residence and land roosting of Whiskered Auklets (*Aethia pygmaea*) at Buldir Island, Alaska. The Auk: Ornithological Advances 135:706–715.

Seneviratne, S., and I. L. Jones (2008). Sensory function for elaborate facial ornamentation in a crevice-dwelling seabird. Behavioural Ecology 19:784–790.

Seneviratne, S. S., and I. L. Jones (2010). Origin and maintenance of mechanosensory feather ornaments. Animal Behaviour 79:637–644.

Shields, W. M. (1977). The social significance of avian winter plumage variability: A comment. Evolution 31:905–907.

Surry, A. M., and J. R. King (2015). A new method for calculating ALPI: The Aleutian Low Pressure Index. Canadian Technical Report of Fisheries and Aquatic Sciences 3135: v + 31 p. https://open.canada.ca/data/en/dataset/4bb821ce-bef7-46d3-95d2-064065f1bda4

Trenberth, K. E., and J. W. Hurrell. (1994). Decadal atmosphere-ocean variations in the Pacific. Climate Dynamics 9:303–319. https://climatedataguide.ucar.edu/climatedata/north-pacific-np-index-trenberth-andhurrellmonthlyandwinterandhttps://climatedataguide.ucar.edu/climate-data/hurrell-wintertime-slp-basednorthernannular-mode-namindex

Veit, A. C., and I. L. Jones (2003). The function of tail streamers of Red-tailed Tropicbirds (*Phaethon rubricauda*) as inferred from patterns of variation. The Auk 120:1033–1043.

Veit, A. C., and I. L. Jones (2004). Timing and patterns of growth of Red-tailed Tropicbird (*Phaethon rubricauda*) tail streamer ornaments. Ibis 146:355–359.