




Limited evidence that asymmetries of multiple Whiskered Auklet (*Aethia pygmaea*) feather ornaments could serve a display function

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Elaborate avian feather ornaments have proven to be enigmatic because their function is often unclear, even though they are used in courtship and social displays. Male and female Whiskered Auklets *Aethia pygmaea* display on their faces four elaborate feather ornaments that serve both courtship and mechanosensory functions: three bilateral pairs of white facial plume tracts (superorbital, suborbital and auricular) and a slender black forehead crest, each consisting of several filoplumes. We studied left–right symmetry in the three antenna-like bilateral white head plumes of 721 wild-caught marked individuals (162 of known sex, 94 of known age that were 1–16 years old) during 1992–2009. Auricular and suborbital plumes were slightly more asymmetric in subadults (1-year-olds) than in adults (≥ 2 years old) but the opposite was true for superorbital plumes. Ornament asymmetries were not sexually dimorphic, nor were they significantly related to individual body condition, body size or age, except that superorbital plume asymmetry decreased significantly with tarsus length. Relative asymmetry (scaled for ornament size) of all three ornaments was negatively correlated with plume size, as predicted by some sexual selection models, but variation in asymmetries was large and differences between left (L) and right (R) sides in most birds were probably too small to be detected visually. Marginal mean absolute asymmetries ($|L-R|$) of super- and suborbital plumes were correlated with ocean climate during the preceding year when the birds would have been moulting, suggesting that fluctuating asymmetry at the population level might be a useful index of environmental stress in this seabird. The spectacular bilaterally expressed facial plumes displayed by Whiskered Auklets provide an interesting test case for questions about asymmetry in sexually and naturally selected traits.

Keywords: *Aethia pygmaea*, Alcidae, Aleutian Islands, environmental stress, feather ornaments, fluctuating asymmetry, ocean climate, seabird, sexual selection, Whiskered Auklet.

It is widely accepted that elaborate avian feather structures result from sexual selection driven by mating preferences and social interactions that affect ornament size (e.g. tail length, Andersson 1982), colouration and their use in courtship

and social displays (Darwin 1871, Andersson 1994, Jones & Hunter 1999, Lyon & Montgomerie 2012). It has also been suggested that mating preferences might focus on structural (left–right) symmetry of traits displayed during courtship (e.g. Cuthill *et al.* 1993, Møller & Pomiankowski 1993, Watson & Thornhill 1994, Thornhill & Møller 1998). Thus, in birds, the asymmetry of ornamental

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feathers has been suggested to influence mate choice (Møller & Höglund 1991). The logic comes from the developmental phenomenon of fluctuating asymmetry (Palmer & Strobeck 1986) in which population-level deviations from bilateral symmetry across the entire phenotype result from environmental stress (Vøllestad *et al.* 1999, Bjorksten *et al.* 2000). By extension, it has been argued that individual birds with asymmetrical feather ornaments are of low quality (reflecting stress during feather growth) and thus that mate choice should favour ornament symmetry (e.g. Møller & Höglund 1991, Møller & Pomiankowski 1993). While the expected relationship between ornament asymmetry and the health and viability of individual animals has been questioned (Palmer & Strobeck 1986, Palmer 1999, Kozlov & Zvereva 2015), the notion that symmetry is attractive is widely held (Rosenthal 2017). Thus, patterns of symmetry (or lack thereof) in display traits remain of theoretical interest in ornithology and behavioural ecology (Stephenson *et al.* 2020, Graham 2021, Vijendravarma *et al.* 2022).

Empirical studies of bird feather ornaments have looked at relationships between individuals' ornament symmetries and mate choice, mating success, and individual health and quality (including parasite load and physical condition). However, the results of these studies have been mixed and frequently controversial. For example, in the Barn Swallow *Hirundo rustica*, female mate choice appears to favour males with symmetrical tail streamers (Møller 1993), and males with symmetrical tail streamers have been documented to be healthier and provide more parental care (e.g. Møller 1994). In contrast, asymmetry of similar streamer ornaments of Roseate Terns *Sterna dougallii* was not related to indices of individual quality and there was no evidence to suggest that asymmetry was correlated between mates (Palestis *et al.* 2012). Similarly, in Red-tailed Tropicbirds *Phaethon rubricauda*, tail ornaments were affected by differential timing of growth of streamers on left and right sides, but fully grown ornament asymmetry was not related to age or body condition, nor was ornament size correlated within pairs (Veit & Jones 2003, 2004). In Black Grouse *Tetrao tetrix*, asymmetries of the males' lyre-like tail ornaments and their mating success were not correlated (Rintamäki *et al.* 1997). In Red-collared Widowbirds *Euplectes ardens*, there was no relationship between symmetry of their spectacular

male tail ornaments and either tail length or body condition (Goddard & Lawes 2000). Møller and Höglund (1991) originally argued that the signal function of ornament asymmetry is demonstrated by a negative correlation between ornament size and asymmetry (see also Kimball *et al.* 1997, Aparicio & Bonal 2002), though some studies have failed to find such a pattern. Thus, relationships between sexual selection, mate choice and ornament asymmetry in birds remains generally unclear, and there are ongoing criticisms of the rigour of empirical studies (cf. Pomory 1997, Graham 2021).

The auklets (family Alcidae, tribe Aethiini) are five socially monogamous, planktivorous seabird species endemic to the North Pacific and adjacent Okhotsk and Bering Seas (Jones 1999). Four of the five auklets (Least *Aethia pusilla*, Crested *Aethia cristatella*, Whiskered *Aethia pygmaea* and Parakeet Auklet *Aethia psittacula*) display elaborate feather ornaments on the faces of both sexes, each ornament comprising several filoplumes including curling forehead crests and bilateral white filoplumes (Jones 1999, Jones *et al.* 2000, 2022a, Seneviratne & Jones 2008). Mate choice follows from the performance of mutual sexual displays of courting pairs that display their facial ornaments (Jones & Montgomerie 1992, Jones & Hunter 1993, Hunter & Jones 1999) but there is also experimental evidence that those ornaments serve a mechanosensory function unrelated to courtship behaviour (Seneviratne & Jones 2008, 2010).

Whiskered Auklets have a single slender black forehead crest and three pairs of conspicuous, bilateral, white facial plumes (Jones 1999; Fig. 1). These are some of the most elaborate adornments of any seabird (Hunter & Jones 1999, Jones 1999, Hunter *et al.* 2002, Schacter & Jones 2018, Jones *et al.* 2022a) and variation in the sizes of those feather ornaments correlates with sex, body condition, environmental conditions and geography (Jones *et al.* 2022a). Here we quantified variation in structural left–right asymmetry of these bilateral white facial plumes to examine: (i) the frequency distributions of asymmetries and correlations between different ornaments' asymmetries, (ii) the relationship between asymmetry and size of each ornament as predicted by some sexual selection models (e.g. Møller & Höglund 1991), (iii) relationships between asymmetries and the age, sex, size, body condition and breeding status of

individuals, as well as variation in asymmetry over the breeding season and across years, and (iv) relationships between average fluctuating asymmetry of each ornament at the population level and measures of environmental stress in the two previous years when growth of ornaments during moult might have been affected.

We hypothesized that, if Whiskered Auklet feather ornament asymmetry serves as a quality indicating signal, (i) smaller ornaments would be more asymmetrical, (ii) subadults would be more asymmetrical than adults, (iii) asymmetry would correlate negatively with body condition, (iv) non-breeding birds would be more asymmetrical than breeders (assuming that non-breeders were less preferred as mates) and (v) average population-level fluctuating asymmetry would increase with environmental stress (e.g. Palmer & Strobeck 1986, Vøllestad *et al.* 1999, Bjorksten *et al.* 2000).

METHODS

We measured Whiskered Auklets captured using mist-nets at night at a breeding site at 'Crested Point' on the northwest coast of Buldir Island, Aleutian Islands, Alaska (52°22'17.70"N, 175°53'23.95"E), from 1992 to 2009 (cf. Jones *et al.* 2022a). This species nests in rock crevices, roosts year-round on land, is partly nocturnal and is socially monogamous. Upon capture, we marked each individual with a numbered stainless steel ring, recorded its mass (± 1 g, using a spring scale)

and took linear measurements (± 0.1 mm, using dial callipers) of tarsus length, bill depth, culmen length and the maximum lengths of the black forehead crest and the bilateral white auricular, super-orbital and suborbital plumes on the left and right sides (Fig. 1). Our measures of white facial plumes quantified the longest dimension of tracts of several overlapping filoplumes (i.e. size of composite ornaments; Fig. 1). Our measurement of length of the black crest length quantified length of the longest feather in the crest (feather ornament measurement methods described in detail by Jones *et al.* 2022a). Due to time constraints, we did not measure left and right sides of wings and tarsi to determine whether asymmetries in these traits, which are not the focus of sexual selection, are more symmetrical than the facial plumes, as documented by Møller and Höglund (1991) for 32 species of passerine birds. Holding time for each bird was limited to about 30 min to minimize stress associated with handling (Duarte 2013). Birds that appeared to be suffering from hyperthermia (heat stress; Cabanac & Guillemette 2001) were released promptly, occasionally before we obtained a complete set of measurements. We scored the age of each bird as adult or subadult (1 year old). Subadults were identified by extensive pale brown (due to moult, weathering and wear) contour feathering on their forehead, chin and neck, and similarly worn secondaries and greater coverts (Bédard & Sealy 1984, Gaston & Jones 1998, Pyle 2008). Ninety-four individuals first captured

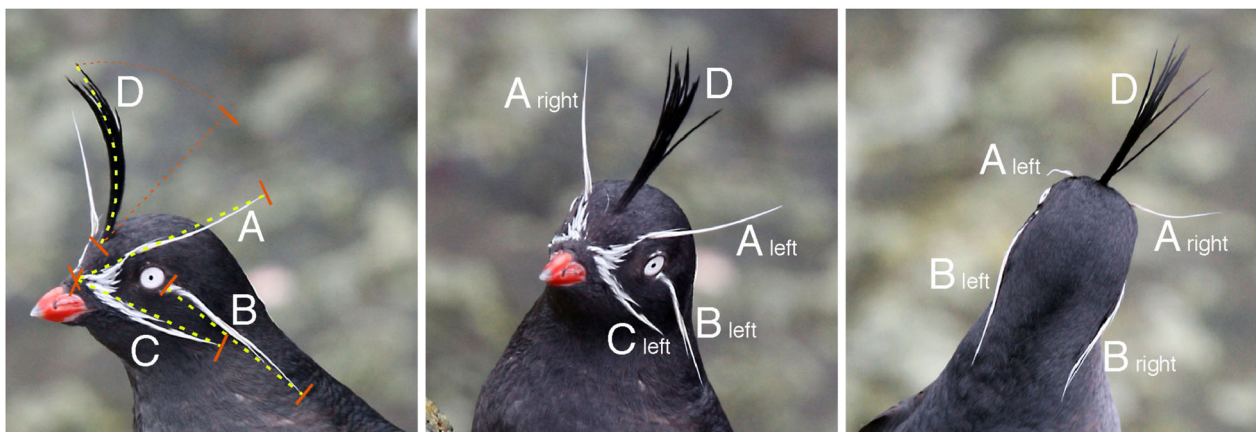


Figure 1. Feather ornaments of an adult Whiskered Auklet photographed at Main Talus, Buldir Island, Alaska (I. L. Jones photo, 27 June 2012), showing their appearance from different angles of view, and how they were measured: (A) superorbital plumes, (B) auricular plumes, (C) suborbital plumes and (D) forehead crest.

as subadults were recaptured 1–15 years later, so we knew their age each time they were captured (Jones *et al.* 2022a).

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. In 2000–2001, we also took 0.3 mL of blood from the brachial vein of 113 birds captured as adults and 49 captured as subadults to determine their sex using a molecular technique (Fridolfsson & Ellegren 1999). Birds that were not sexed by this method were scored as ‘unknown’ sex. Fieldwork was conducted under Animal Care Permits from Memorial University of Newfoundland and USFWS Master Banding Permit 22181.

Statistical analyses

We calculated ornament asymmetry in two different ways. First, for all analyses of individual variation, we calculated ‘relative asymmetry’ as the absolute value of the difference between the two sides divided by the size of that ornament, defined as the mean of the two sides (Palmer & Strobeck 1986, Møller & Höglund 1991). Relative asymmetry ($(L-R)/\text{size}$) accounts for the effects of Weber’s Law, whereby the magnitude of perceived differences is proportional to the size of the perceived object (e.g. van der Helm 2010), in this case Whiskered Auklets’ conspicuous white facial ornaments. Relative asymmetry is therefore most appropriate when assessing signal potential of an ornament. Secondly, for the analysis of population-level relationships to annual covariates (ocean climate and demographic parameters), we used absolute asymmetry as recommended by Palmer and Strobeck (1986) and Graham (2021). We also calculated ‘absolute asymmetry’ (a measure of fluctuating asymmetry) as the absolute value of the difference between the two sides ($|L-R|$) as a measure of fluctuating asymmetry. Thus, we were focusing here on actual measured asymmetry, irrespective of the birds’ ability to perceive differences between left and right sides. When analysing population-level absolute asymmetries, we removed outliers identified by Grubb’s test (as recommended by Niemeier *et al.* 2019, Graham 2021).

We used R (v.4.2.2; R Core Team 2022) for all analyses (Jones *et al.* 2022b). For linear mixed models (LMMs), we used the *lmer* function in the

lme4 package (Bates *et al.* 2015), standardizing continuous predictors and square-root-transforming asymmetries to satisfy model assumptions (see Supporting Information section 4 for details). Residuals from LMMs were not normally distributed when those response variables were not transformed, whereas square-root-transformations of both absolute and relative asymmetries provided reasonable fits to normality. LMMs reported here are full models, with day of the year, age class, sex, body mass, tarsus length, measurer identity and ornament size tested as fixed effects, and bird identity as a random effect to control for repeated measurements of individuals within and between years. In these models, body mass (controlling for tarsus length) is used as a measure of body condition (Schulte-Hostedde *et al.* 2005). We entered ornament size in those models to help control for measurement error, as we found that this increased with ornament size. Graham (2021) recommended calculating asymmetry as $|\log L - \log R|$ to control for size scaling, but that did not completely control for ornament size effects and complicated the models and the presentation of results, while resulting in similar conclusions.

To calculate repeatabilities, we analysed measurements of birds captured twice within a 14-day period in any year, using the *rpt* function in the *rptR* package (Stoffel *et al.* 2017) to calculate bootstrapped estimates based on 1000 iterations. In each model, we included measurer identity, year and ornament size as fixed effects and bird identity as a random effect.

For time series analyses, we used the *ccf* function in the *stats* package. We limited that analysis to cross-correlations between current-year absolute asymmetries and annual covariates (climate and demographic) in the preceding 4 years. We reasoned that ocean climate only in the preceding year or two might conceivably influence the growth of feathers during the annual moult in the December–April period preceding our measurements (Byrd & Williams 2020, Jones *et al.* 2022a). As estimates of population-level fluctuating asymmetry each year, we calculated marginal means from LMMs (controlling for other variables in the models) using the *emmeans* function in the *emmeans* package. In these analyses, we examined cross-correlations between the average marginal asymmetry at the population level and (i) six ocean climate variables that are often assumed to be related to environmental stress: Pacific Decadal

Oscillation (Mantua *et al.* 1997), two North Pacific Indices (NPI1 during the preceding November–March and NPI2 during the previous 12 months; Trenberth & Hurrell 1994), Aleutian Low Pressure Index (Surry & King 2015), Sea Level Pressure-based Northern Annular Mode index (SLP-based NAM, Trenberth & Hurrell 1994) and Multivariate El Niño Southern Oscillation (National Center for Atmospheric Research Staff 2019, but see also Litzow *et al.* 2020), and (ii) three demographic indices from this Whiskered Auklet population: annual survival rate (calculated from mark–recapture data), annual productivity (proportion of chicks fledged) and mean hatch date (see Hunter *et al.* 2002 and Jones *et al.* 2007 for details).

RESULTS

Capture summary

For this study, we captured, ringed and measured 721 Whiskered Auklets during all but one breeding season from 1992 to 2009 (cf. Jones *et al.* 2022a); no birds were captured in 2002 and only one in 1999 (Jones *et al.* 2022b). Over the years, 379 birds were captured and measured more than once (average 2.3 times, range 1–12 times) and 78 of those birds were captured more than once in the same year. Thus, our dataset comprises 1626 captures during 17 breeding seasons. On first capture, 485 (67%) birds were identified as adults (≥ 2 years old) and 236 (33%) as subadults (1 year old). Examination of ornamental feathers revealed active moult only in subadult birds, all of which showed evidence of some growing facial feathers, a distinctive characteristic of 1-year-olds at this age (Bédard & Sealy 1984, Pyle 2008, Jones *et al.* 2022a). A total of 533 (74%) of the 721 birds captured had both sides of all their ornaments measured during at least one capture. Among the 236 birds first captured and marked as subadults (1-year-olds), 94 were recaptured 1–15 years later, so we know how old they were on recapture. Of the 162 birds that we sexed using molecular methods, 66 were females and 96 were males.

Frequency distributions of asymmetries

Eight (0.2%) of the 3426 measured asymmetries were especially large because one side was <5 mm long, suggesting that feathers on the shorter side

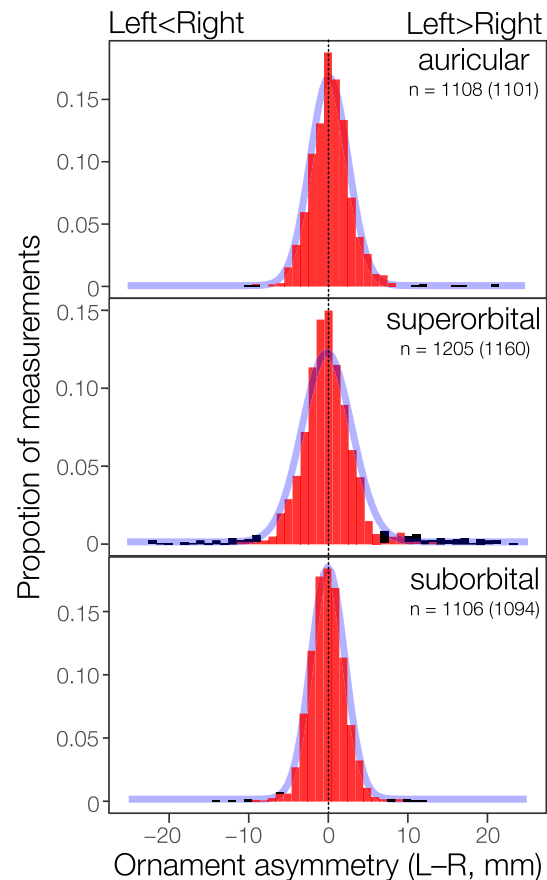


Figure 2. Whiskered Auklet feather ornament asymmetry (left side – right side) to show actual differences between the two sides. Except for data from eight plumes ≤ 5 mm long, all data are shown including outliers (black bars) and repeated measurements of individual birds (n = number of measurements with and without outliers). Blue lines show normal distributions calculated from the mean and sd for the data excluding outliers (black bars).

were broken and not the result of differential growth. These eight asymmetries were excluded from all further analyses. Based on raw data from all birds, there was no evidence for any directional asymmetry (L–R) regardless of whether outliers were excluded (Fig. 2, Fig. S1).

Simply counting the number of left- and right-side biases on first capture of each adult bird, including outliers, revealed no evidence of a left: right side bias for any of the bilateral ornamental plumes: auricular (163:147; binomial test, $P = 0.39$), superorbital (167:173; $P = 0.79$), suborbital (164:147; $P = 0.36$). These patterns demonstrate clear evidence for fluctuating asymmetry (Palmer & Strobeck 1986) in these ornaments.

Despite this, the direction of asymmetries in recaptured individuals was more often on the same side from 1 year to the next than expected by chance (binomial tests of same: different sides compared with random expectation of 1:1): auricular = 145:116 ($P = 0.08$), superorbital = 157:89 ($P < 0.001$), suborbital = 148:98 ($P < 0.001$) (Fig. 3). We also identified 64 outliers (using Grubb's test) that Niemeier *et al.* (2019) and Graham (2021) recommend be removed before analyses of fluctuating asymmetry. With those removed, the distributions of asymmetries of all three ornamental plumes were normal upon visual inspection (Fig. 2). When outliers were included, the distributions of auricular and suborbital plume measurements were decidedly leptokurtotic (auricular = 6.1, superorbital = 5.9, suborbital = 3.4; compared with kurtosis = 3.0 for a normal distribution), and superorbital plumes had many more extreme asymmetries (outliers) than either auricular or suborbital plumes (Fig. 2). Unless otherwise noted, all analyses of relative asymmetry included these outliers. Asymmetries > 5 mm (about 15% of mean ornament size) were conspicuous to the naked eye (I.L. Jones and F.M. Hunter pers. obs.) and these comprised 5.1% of the measurements of the auricular plumes, 14.2% of superorbital plumes and 3.3% of suborbital plumes.

Repeatabilities (R) of multiple asymmetry measurements of birds re-measured within any 2-week period were statistically significant and high for superorbital plumes ($R = 0.88$, 95% CI 0.83–0.94, $P < 0.001$, $n = 140$ measurements of 68 birds) but moderate for both auricular ($R = 0.32$, 95% CI 0.13–0.60, $P = 0.02$, $n = 124$ measurements of 60 birds) and suborbital plumes ($R = 0.47$, 95% CI 0.31–0.69, $P = 0.0003$, $n = 126$ measurements of 61 birds). These repeatabilities translate to measurement errors of 12%, 68% and 53%, respectively (Bailey & Byrnes 1990).

Asymmetries in relation to traits of individual birds

In LMMs for each type of bilateral white ornamental plume (Table 1), fixed effects explained only a small proportion of the variation in the magnitude of relative asymmetry (marginal $R^2 \leq 0.15$ in each case). For both auricular and suborbital plumes, the magnitude of relative asymmetries was larger in subadults than in adults but the difference for suborbital plumes was

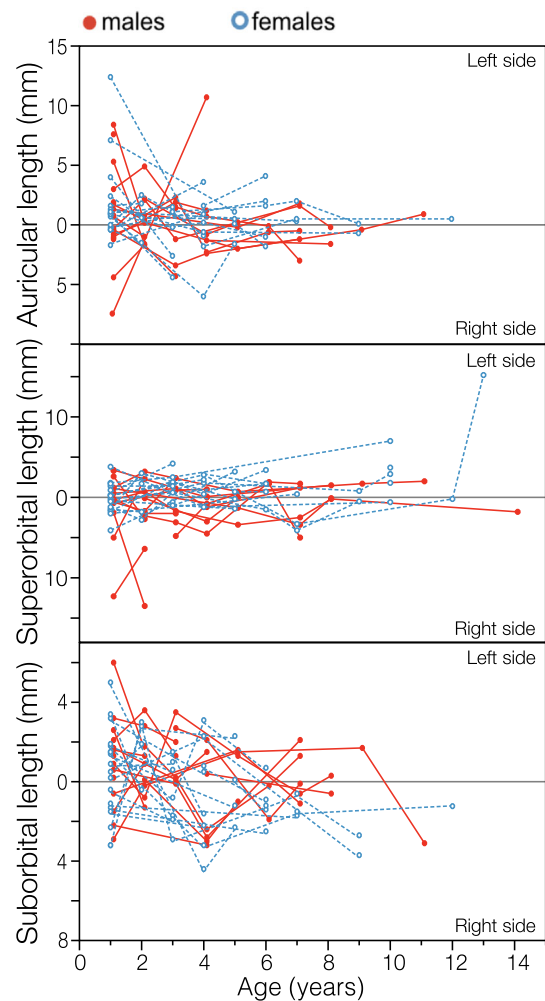


Figure 3. Length of left and right sides of individual Whiskered Auklets' bilateral ornamental auricular, superorbital and suborbital plumes as the birds aged.

particularly small and not significantly different from zero. Moreover, the relative asymmetry of superorbital plumes was significantly larger in adults than in subadults, counter to expectations. In each case, the difference in the mean relative asymmetries of adults and subadults was small and the variation within each age category was large, with no clear relationship of asymmetry to actual age measured in years (Figs 3 and 4, see also Table S7 and Fig. S2).

Similarly, the magnitude of relative asymmetries of auricular and superorbital plumes was significantly larger in breeders than in non-breeders (but not for suborbital plumes, which showed the opposite, but non-significant, pattern) but the differences in mean asymmetries were again very

Table 1. Summary of results from LMMs to predict the magnitude of relative asymmetries for each of the ornamental plumes of Whiskered Auklets, outliers included.

Predictors	Auricular	Superorbital	Suborbital
(Intercept)	0.199 (0.168–0.230) < 0.001	0.242 (0.197–0.286) < 0.001	0.214 (0.184–0.244) < 0.001
Subadults – adults ^a	0.051 (0.023–0.079) < 0.001	–0.057 (–0.095 to –0.019) 0.003	0.014 (–0.013 to 0.040) 0.32
Breeders – non-breeders ^a	0.044 (0.013–0.059) 0.002	0.036 (0.009–0.064) 0.01	–0.004 (–0.026 to 0.018) 0.73
Day of the year	–0.036 (–0.012 to 0.004) 0.30	0.0004 (–0.009 to 0.010) 0.93	–0.001 (–0.008 to 0.007) 0.82
Tarsus length (mm)	–0.004 (–0.012 to 0.004) 0.35	–0.011 (–0.022 to 0.001) 0.07	–0.004 (–0.012 to 0.004) 0.30
Body mass (g)	0.001 (–0.007 to 0.010) 0.81	0.009 (–0.003 to 0.020) 0.14	–0.004 (–0.012 to 0.004) 0.34
Sex (male – female) ^a	–0.0004 (–0.026 to 0.025) 0.98	0.012 (–0.031 to 0.054) 0.59	0.021 (–0.004 to 0.046) 0.09
Sex (unknown – female) ^a	0.001 (–0.020 to 0.022) 0.93	0.028 (–0.007 to 0.064) 0.12	0.006 (–0.015 to 0.027) 0.56
Mean ornament size (mm)	–0.013 (–0.022 to –0.004) 0.004	–0.073 (–0.086 to –0.061) < 0.001	–0.014 (–0.022 to –0.006) < 0.001
Measurer (ILJ – FMH) ^a	–0.016 (–0.033 to –0.001) 0.07	–0.009 (–0.030 to 0.012) 0.38	0.002 (–0.014 to 0.018) 0.83
Measurer (SS – FMH) ^a	–0.008 (–0.078 to 0.061) 0.81	0.008 (–0.027 to 0.044) 0.65	–0.024 (–0.091 to 0.043) 0.48
Number of birds	517	559	516
Number of measurements	1020	1107	1019
Number of measurers	3	3	3
R ² marginal/conditional	0.04/0.19	0.15/0.53	0.04/0.20

Coefficients for day of the year, body mass, tarsus and ornament size were standardized and can be compared directly with one another. Bird identity was included as a random effect in each model to control for multiple captures of many of the birds. Relative asymmetries were square-root-transformed to normalize residuals (see also Table S3). Values in bold indicate at least weak evidence in support of a trend. ^aEstimates are for the differences indicated.

small (Table 1). With respect to the relative asymmetries in the ornaments of individual birds, there was no evidence from any of the bilateral plumes to support (i) any seasonal variation (day of the year), (ii) any positive effects of condition (using body mass controlling for tarsus length as a condition index; Schulte-Hostedde *et al.* 2005) or (iii) any difference between the sexes except for some weak support for males having slightly larger relative asymmetry of suborbital plumes than females (Table 1).

Larger birds (as measured by tarsus length) had smaller relative asymmetries for all three ornaments, but the relationship was statistically significant only for superorbital plumes (Table 1).

Correlations among ornament asymmetries

There was no evidence for any correlations among the magnitudes of relative asymmetries across the three white ornamental plume types within individuals ($P > 0.47$ for the relationships between relative asymmetries in each LMM; Table S3). There was also no evidence that any of the relative asymmetries were related to the length of birds' black ornamental forehead crests (LMMs, $P > 0.24$ in each case; Table S5).

Correlations between ornament size and asymmetry

Larger ornaments were more symmetrical, reflected in the negative relationships between ornament size (mean of left and right sides) and relative asymmetry for all three ornaments (Table 1, Fig. 5). It has been argued that negative relationships between asymmetry and ornament size might be the result of substantial measurement error (see Graham 2021 for details), as there was for our measurements of auricular and suborbital plumes. For superorbital plumes, however, measurement error was relatively small (12%) and the standardized estimate for the effect of ornament size on the relative asymmetry of superorbital plumes was more than five times the standardized estimates for that of auricular and suborbital plumes (Table 1).

Correlations between fluctuating asymmetry and ocean climate

Of the six ocean climate variables that we analysed, mean absolute asymmetries of auricular and suborbital plumes in this population were significantly negatively correlated ($r > -0.45$) only with the North Pacific Index (Trenberth &

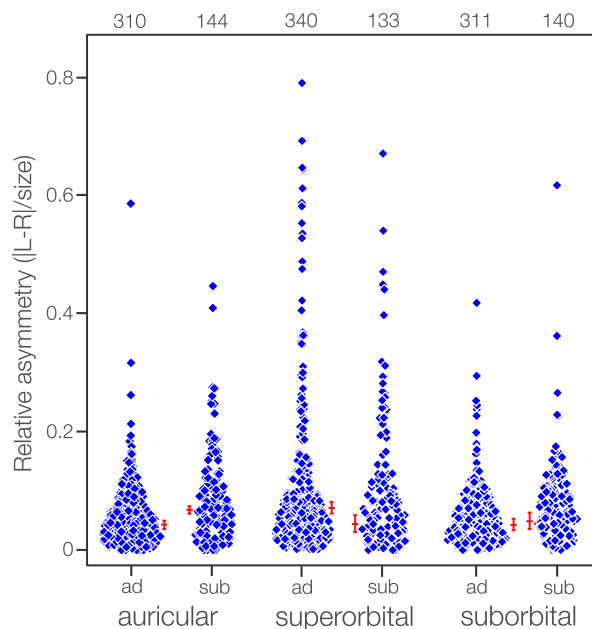


Figure 4. Relative asymmetries of auricular, superorbital and suborbital plumes of adult and subadult (1-year-old) Whiskered Auklets when first captured (blue diamonds). Means and 95% CI (red lines), calculated by back-transforming (i.e. squaring) marginal means for adults and subadults from the models in Table 1; sample sizes are given at the top.

Hurrell 1994) during the preceding year (Fig. 6), when the birds would have been moulting and growing those feathers. The mean absolute asymmetry of auricular plumes was also significantly but positively correlated with the Aleutian Low Pressure Index (Surry & King 2015) in the preceding year (Fig. 6). There was no evidence ($P > 0.05$ in each case) in support of the other 14 cross-correlations between the absolute asymmetries of ornamental plumes and ocean climate in the preceding year (Fig. S6).

Correlations between fluctuating asymmetry and whiskered auklet demography

Only the annual survival rate in this population (Jones *et al.* 2007) was significantly correlated with mean absolute asymmetries during the current and preceding year (Fig. 6). Thus, the absolute asymmetries of superorbital and suborbital plumes were negatively correlated with annual survival to the current year, as might be expected if asymmetry is higher in birds suffering higher levels of stress. However, survival to the current year was also

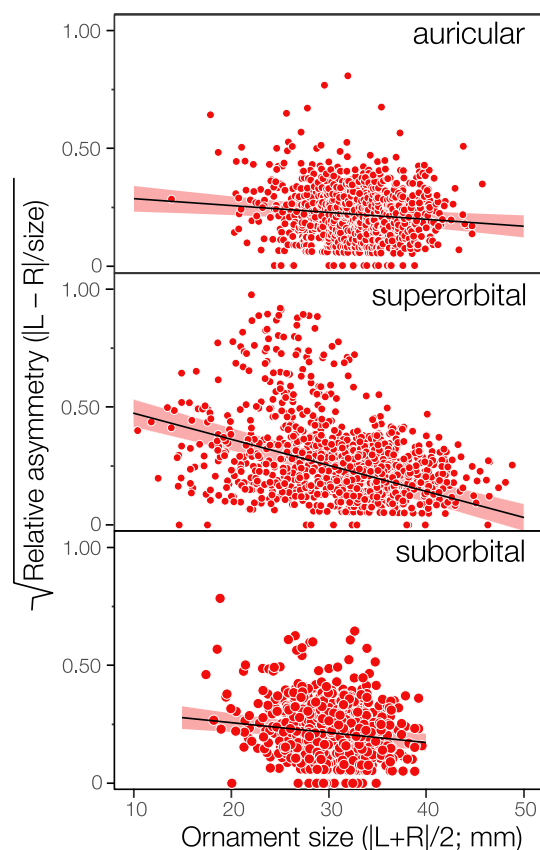


Figure 5. Relationships between square-root-transformed relative asymmetries and ornament sizes for each of the bilateral plumes as predicted from the models in Table 1, controlling for sex, age category, day of the year, breeding status, measurer, tarsus length and body mass, as well as multiple measurements per individual. See also Figure S5.

positively correlated with the absolute asymmetry of auricular plumes in the preceding year, counter to expectations. None of the other 12 cross-correlations between absolute asymmetry and survival in the current and preceding 4 years was statistically significant, nor were any of the 30 such correlations with population productivity or hatch date (Fig. S7).

Extreme asymmetries

The few very short plumes (≤ 5 mm long, and apparently broken) that we removed from the dataset were evenly divided between left ($n = 4$) and right sides ($n = 4$) and across the three facial plume ornaments (two in auricular and three each in super- and suborbital plumes). Two of those apparently broken plumes were on the left

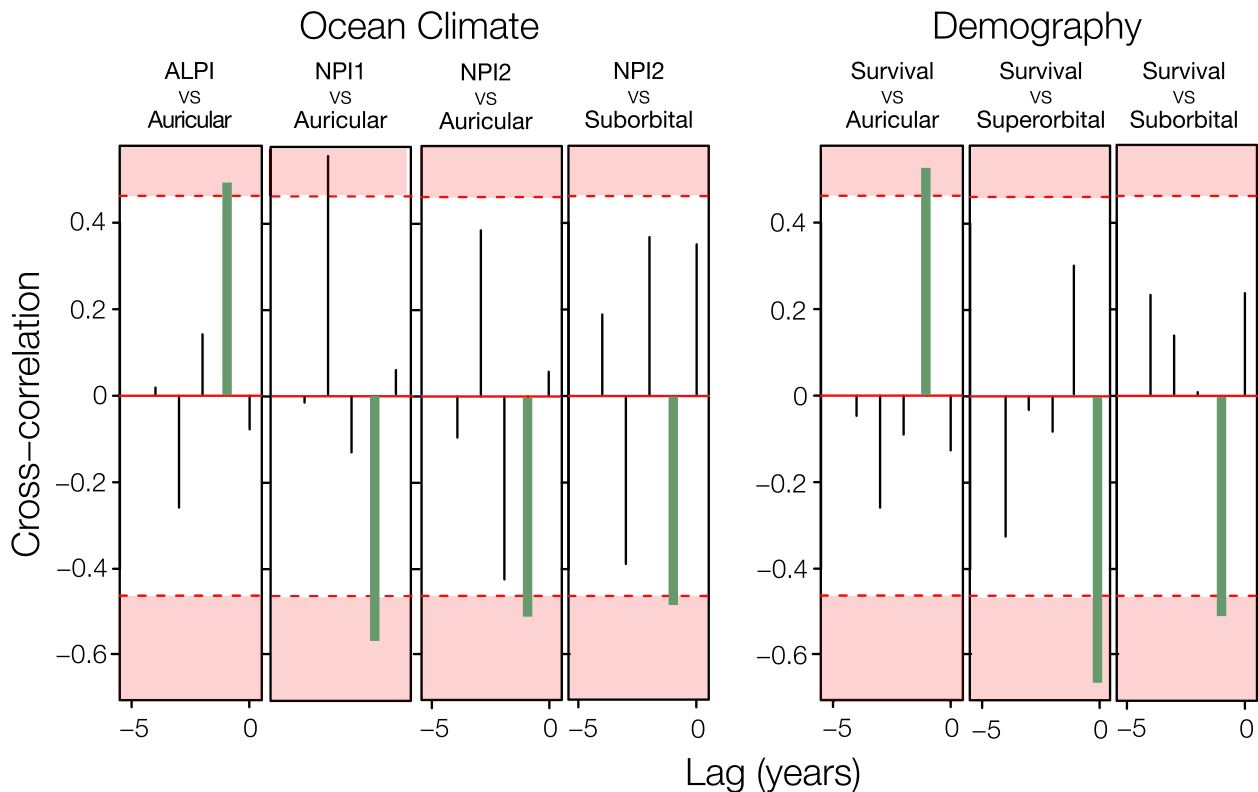


Figure 6. Significant cross-correlations between annual marginal means of absolute asymmetries of Whiskered Auklet ornamental plumes and both ocean climate indices (ALPI = Aleutian Low Pressure Index; NPI1 and NPI2 = North Pacific Indices) and demographic parameters. Green lines indicate correlations supported by at least moderate evidence ($P < 0.05$, shaded red regions).

suborbital and the right auricular plumes of the same bird, and two others were in the left suborbital and superorbital plumes of the same bird.

In addition, there were 64 plume lengths identified as outliers (using Grubb's test) on one to six captures of 36 birds and many of those may also have been broken or very worn (Fig. S1). Most of those outliers ($n = 45$) were in superorbital plumes, the most exposed of the bilateral plumes (Figs 1 and 2), but they were not longer than the other two bilateral ornamental plumes. Overall, these outliers occurred on only a single capture of 22 individuals, with the remaining 42 outliers found on two to six captures of 14 individuals.

There was no evidence of bias in the distribution of outliers with respect to sex (outliers occurred on four males and seven females, from a sample of 96 males and 66 females; Fisher's Exact test, $P = 0.21$) but there was strong evidence that adults were more likely to have outliers than were subadults. Thus, outliers occurred on 33 birds measured as adults and four

measured as subadults, from a sample of 578 measured as adults and 237 measured as subadults (Fisher's Exact test, $P = 0.02$). Exclusion of outliers from statistical models influenced coefficients for some predictors even though outliers represented $< 1\%$ of the 7077 plumes measured (Table S8). Nonetheless, these outliers had no effect on the conclusions we drew from the models reported above.

DISCUSSION

If Whiskered Auklet ornament asymmetry is a display indicator relevant to mate choice, we hypothesized that we would find variation in asymmetry related to age, breeding status, body size, body condition and ornament size, all of which are often considered to be indices of individual 'quality'. There was strong evidence (discussed in detail below) for relative asymmetry decreasing with ornament size for all three plumes (Fig. 5) and weak evidence for superorbital plume asymmetry

decreasing with body size (tarsus length). Nonetheless, we argue that there was limited evidence for signal function for ornament asymmetry in Whiskered Auklets.

We acknowledge that an ideal experimental design for this study would have been multiple remeasurements of every individual at every capture and recapture, as that would have allowed for even better control of measurement error. However, this was not possible in our study of free-living wild seabirds that could be held only briefly in captivity due to the stress associated with handling (Duarte 2013). Although all our measurements of facial plumes were significantly repeatable, there was considerable measurement error for auricular and suborbital plumes, as expected in a field study of these difficult-to-measure traits each comprising several filoplumes (cf. Jones *et al.* 2022a). Nonetheless, we have no reason to believe there was systematic bias in those measurements. Thus, this type of measurement error simply added noise to our analyses, resulting in reductions in the amount of variance explained by the models. For that reason, the patterns that we report (Table 1) are likely to be supported by more evidence than our models would indicate. Moreover, effects of measurement error on parameter estimates are minimized when samples sizes are relatively large (see, for example, fig. 1 in Silvestro *et al.* 2015), as they were in our study ($n = 721$ Whiskered Auklets measured).

Ornament asymmetry vs. age, breeding status and body condition

Despite the statistically significant patterns for age and breeding status (Table 1, Fig. 4), we consider it unlikely that these ornament asymmetries could often be useful to the birds as indicators of age, size, dominance or quality as potential mates, for three reasons. First, the difference in mean asymmetries between adults and subadults was small (Figs 3 and 4) and only significant in the expected direction for auricular plumes when controlling for other variables in LMMs (Table 1). Moreover, the overlap between age categories was large (Figs 3 and 4, Table S7, Fig. S5), superorbital plumes showed the opposite pattern, and adults are conspicuously different from subadults in other ways that are much easier to assess visually (Pyle 2008, Jones *et al.* 2022a). Although we could visibly detect asymmetries > 5 mm, the bilateral

ornaments are on opposite sides of the head, making smaller differences difficult to assess visually. Secondly, it might be expected that birds breeding in a given year are higher quality as mates than those that fail to breed (Hunter *et al.* 2002). Thus, breeding birds would be expected to have more symmetrical ornaments, whereas we found the opposite (i.e. larger asymmetries) for auricular and superorbital plumes, and no evidence of a pattern for suborbital plumes. Thirdly, there was no evidence that relative asymmetries of any of these bilateral ornaments were related to body condition (Table 1), contrary to the predicted negative relationship. We are well aware that our index of body condition is only one of many possible measures, so this subject deserves some further investigation. Nonetheless, in contrast to our results here for relative symmetries, we have previously found that the sizes of all three of these white feather ornaments were significantly positively correlated with body condition, and thus that ornament size rather than symmetry may constitute a more reliable indicator of condition in this species (Jones *et al.* 2022a).

The relative asymmetries of the three bilateral ornaments were not significantly correlated within individuals (Table S4). Thus, these asymmetries would have conveyed inconsistent information about individual birds. Absence of correlations among ornament asymmetries was not expected, as environmental stress is expected to drive fluctuating asymmetry across multiple traits in individuals because of its broad interference with developmental processes (Palmer & Strobeck 1986). Whiskered Auklet feather ornaments grow in winter but the precise timing of growth of the different sets of replacement facial plumes has not been measured. If the different ornaments were normally grown at different times, they could have regularly experienced different environmental stresses and thus would not necessarily have correlated asymmetries. We also recognize that these low correlations among ornament asymmetries in Whiskered Auklets could have partly resulted from stochastic processes, both naturally occurring (e.g. breakage and wear) and related to measurement error, without a direct link to an individual's health or to environmental stress. Thus, the patterns of asymmetry that we documented stand in contrast to patterns of variation in size of Whiskered Auklet feather ornaments that showed strong correlations across ornaments within

individuals and correlations with age, body condition and breeding status (Jones *et al.* 2022a). The direction of asymmetries of single ornaments in recaptured individuals was more often on the same side from one year to the next than expected by chance. Such non-random patterns of asymmetry from year to year might not be expected for fluctuating asymmetry. To the best of our knowledge, such changes in the direction of asymmetry in re-grown traits has not previously been measured in any animal species, and deserves further investigation.

Ornament asymmetry vs. size

Møller and Höglund (1991) originally argued that the best evidence for ornament symmetry indicating the quality of individuals, and thus potentially favoured by sexual selection, is a negative correlation between ornament size and asymmetry. As a result, high-quality individuals are expected to have ornaments that are both larger and more symmetrical than low-quality individuals. Kimball *et al.* (1997) reported this pattern in only one of several ornamental traits examined in Red Junglefowl *Gallus gallus* but other studies have failed to find such a pattern (Polak & Starmer 2005, Bartoš *et al.* 2007, Yosef *et al.* 2018). As noted by Graham (2021), however, the error inherent in measurement of feather ornaments is problematic for any comparison of asymmetry between large and small ornaments. For example, if measurement error is relatively greater for smaller ornaments, these might appear to be more asymmetrical than larger ornaments. Our impression when taking Whiskered Auklet measurements in the field was that smaller ornaments were easier to measure (I. L. Jones and F. M. Hunter pers. obs.), which could have lessened any associated error.

Our results showed the predicted negative relationship between ornament size and relative asymmetry (Fig. 5). Even so, the left–right differences in plume lengths were so variable at all plume sizes that birds preferring mates with low levels of asymmetry, for example, would have been as likely to get a mate with either small or large ornaments (Fig. S4), contrary to our previous finding that larger ornaments were more likely to influence mating (Jones *et al.* 2022a). In addition, the difference in predicted mean asymmetries of the smallest and largest superorbital plumes was so small (~0.1 mm) that we would not expect them to be easily detectable to birds during courtship

interactions (cf. Swaddle 1999). Thus, for Whiskered Auklet ornaments, the size–symmetry relationship was clearly in the expected direction (Møller & Höglund 1991) but the biological relevance of this asymmetry as a viability indicator is unclear. By comparison, variation in the size of Whiskered Auklet feather ornaments was in the range 1.7–4.0 mm (5–12% of mean size) and thus more visible and consistent with social signal function (table 3 in Jones *et al.* 2022a). Nevertheless, some individuals had ornamental plume asymmetry of 5–10 mm that was visible to us in the field (cf. Fig. 1, Fig. S5) and could have affected those birds' attractiveness to potential mates. This possibility could be tested with field experiments involving manipulated ornaments.

Seneviratne and Jones (2008, 2010) previously showed experimentally that Whiskered and Crested Auklet facial plumes serve a sensory function wherein these protruding filoplumes allowed birds to navigate better by touch in confined spaces. This is related to the nocturnal activity of Whiskered Auklets and their year-round use of confined rock crevices in heaps of fallen talus and on coastal cliffs (Schacter & Jones 2018, Byrd & Williams 2020). The most obvious expectation related to asymmetry is that the birds' subterranean behaviour and use of plumes for sensing would lead to wear and tear on these feathers, and probably to breakage and differential wear through the life of the feather (i.e. a functionally derived asymmetry not related to feather growth). However, we found no evidence for a seasonal effect (day of the year) on relative asymmetries of these ornamental plumes (Table 1). In relation to our measurements, this underlines the concern that the pattern detected for superorbital plumes might relate to feather wear as much as to developmental processes related to fluctuating asymmetry in the strict sense (Palmer & Strobeck 1986). The effects of these asymmetries on the birds' abilities to sense their nesting environment are unknown and an additional experiment similar to that of Seneviratne and Jones (2008), with one side manipulated, would be required to investigate this further.

Comparison with feather ornament asymmetries of other bird species

Møller and Höglund (1991) reported absolute and relative asymmetries for non-ornamental (mainly wing lengths) and ornamental traits (mainly tail

streamers) of males and females in 16 pairs of closely related (co-familial) passerine bird species. One species in each pair was sexually monomorphic and the other had extravagant feather ornaments (15 tail, one wing) in males. For ornaments, they reported mean relative asymmetry as 0.035 (95% CI 0.022–0.048) for males and 0.019 (95% CI 0.009–0.028) for females (data extracted from their fig. 1). In contrast, Whiskered Auklets showed no differences in ornament asymmetries of males and females, but mean relative asymmetries as much as an order of magnitude higher (auricular = 0.06, superorbital = 0.11, suborbital = 0.06) than the mean for males reported by Møller and Höglund (1991). Indeed, relative asymmetry of Whiskered Auklet superorbital plumes was 24% higher than the maximum reported among Møller and Höglund's (1991) 32 species (range 0.001–0.089).

Asymmetry and environmental stress

The bilateral facial plumes of Whiskered Auklets bear three of the hallmarks of fluctuating asymmetry (Palmer & Strobeck 1986). Thus, the distribution of left- and right-side biases (Fig. 2) was close to normal (Gaussian), with no evidence of directional asymmetry and no evidence of side biases within individuals. Thus, there was no evidence within individuals that a side bias in one ornament was related to a side bias in one of the other ornaments in a given year. Curiously, however, the year-to-year changes in side biases was not random, contrary to expectations.

Mean fluctuating asymmetry at the population level is expected to respond to stresses during development (Palmer & Strobeck 1986). As previously reported for ornament size (Jones *et al.* 2022a), we did find moderate evidence for correlations between the mean absolute asymmetries of auricular and suborbital plumes and two measures of ocean climate in the preceding year (Fig. 6). These two plume asymmetries were negatively correlated with the previous year's North Pacific Index (reflecting area-weighted sea level pressure over the region 30°–65°N, 160°E–140°W, Trenberth & Hurrell 1994). Auricular plume asymmetry was also positively correlated with the previous year's Aleutian Low Pressure Index (reflecting the relative intensity of the Aleutian Low pressure system of the North Pacific during December through March; Surry & King 2015).

These three correlations are consistent with colder and stormier ocean conditions causing physiological stress, presumably via effects on food availability, which manifested during feather growth. Previously, we found that Whiskered Auklet annual adult survival correlated negatively with the Aleutian Low Pressure Index (Jones *et al.* 2007). In the present study, the asymmetries of super- and suborbital plumes were negatively correlated with survival in a given year. Taken together, the results indicate that Whiskered Auklets both experienced greater mortality and grew less symmetrical feather ornaments when the Aleutian Low was most intense, consistent with the notion that ocean climate is an important stressor. However, we treat these results cautiously, and further exploration with new and emerging oceanographic covariates (cf. Litzow *et al.* 2020) would be helpful.

Conclusion

Møller and Höglund (1991) noted that sexual ornaments are exaggerated traits, likely costly in expression and close to the limits of production, potentially showing intricacy in structure prone to a variety of factors disrupting production. Some traits measured in that study, our study and in others of sexually selected feather ornaments are not obviously costly to produce (others are, e.g. Dakin & Montgomerie 2011). Nonetheless, facial feather ornaments of Whiskered Auklets are among the most elaborate ornaments of any seabird, and ornament size correlates with age, breeding status, body condition and favourable ocean climate (Jones *et al.* 2022a). This suggests that size of these traits is somehow constrained in a way mediated by both a cost and the influence of sexual selection. In species studied by Møller and Höglund (1991), size and asymmetries of feather ornaments were also sexually dimorphic, with traits and asymmetries larger for males than females, again as expected for sexually selected male traits influenced by female choice. Whiskered Auklet ornaments are sexually monomorphic (Jones *et al.* 2022a) but there is strong evidence that these traits are influenced by mutual mate choice in the closely related Crested Auklet (Jones & Hunter 1993, 1999) and by sexual selection in all species in this genus (Jones 1999). Nevertheless, links between Whiskered Auklet ornaments and production costs and

developmental mechanisms are unknown and will require careful experiments in the field to elucidate them.

In relation to our original hypotheses regarding the function of asymmetries in Whiskered Auklet feather ornaments, we found that smaller ornaments were more asymmetrical, as predicted by some sexual selection models (i.e. high quality individuals would display ornaments both large and more symmetrical). We also found some evidence that average population-level fluctuating asymmetry correlated on an annual basis with environmental stress during moult (Palmer & Strobeck 1986). However, we found little evidence that subadults were more asymmetrical than adults, no relationship between asymmetry and age in years, no correlation between asymmetry and body condition, and no evidence that non-breeding birds were more asymmetrical than breeders (assuming that non-breeders were of lower quality and less preferred as mates). Thus, our results for Whiskered Auklets showed two of the correlations predicted for fluctuating asymmetry, but the small magnitude of the asymmetries in most individuals may indicate that those asymmetries do not per se have a display function.

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AUTHOR CONTRIBUTIONS

Ian L. Jones: Conceptualization (lead); data curation (lead); formal analysis (supporting); funding acquisition (lead); investigation (lead); methodology (lead); project administration (lead); resources (lead); supervision (lead); writing – original draft (lead); writing – review and editing (lead). **Fiona M. Hunter:** Conceptualization (lead); data curation (equal); formal analysis (supporting); funding acquisition (equal); investigation (lead); methodology (lead); project administration (supporting); resources (equal); supervision (equal); writing – original draft (supporting); writing – review and editing (supporting). **Sampath S. Seneviratne:** Conceptualization (supporting); investigation (equal); methodology (equal); writing – original draft (supporting); writing – review and editing (supporting). **Jeffrey C. Williams:** Funding acquisition (supporting); investigation (supporting); methodology (supporting); project administration (supporting); resources (supporting). **Robert Montgomerie:** Formal analysis (lead); investigation (supporting); methodology (supporting); writing – original draft (equal); writing – review and editing (equal).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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Data Availability Statement

Data and all code used for statistical analyses are available via figshare (<https://doi.org/10.6084/m9.figshare.20301798>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1 Frequency distributions of the lengths of bilateral ornamental plumes that we measured, including multiple measurements from some individuals.

Figure S2 Predicted relative asymmetries for birds of known age.

Figure S3 Results of checking assumptions of the model in Table 1 of the main text to predict the relative asymmetry of superorbital plumes with outliers included.

Figure S4 Results of checking assumptions of a model to predict the relative asymmetry of super-orbital plumes with outliers excluded.

Figure S5 Relationships between absolute asymmetries and ornament sizes for each of the bilateral plumes.

Figure S6 Cross-correlation plots for adjusted mean population absolute asymmetries and indices of ocean climate.

Figure S7 Cross-correlation plots for adjusted mean population absolute symmetries and indices of Whiskered Auklet demographics.

Table S1 Descriptive statistics from a dataset that excludes 8 apparently broken plumes (length < 5mm) and, for each plume, only birds that had both sides measured.

Table S2 Correlations between differences in ornament sizes measured on the same individuals within a 1-week period and the mean size of that ornament $((L+R)/2)$.

Table S3 AIC values for different LMMs with different transformations of relative asymmetry and ornament size for superorbital plumes.

Table S4 Relationships between relative asymmetries of pairs of ornamental plumes.

Table S5 Relationships between relative asymmetries of ornamental plumes and crest size.

Table S6 LLMs to predict relative asymmetry that include year as a factor (Fyr) showing no evidence for year as an effect.

Table S7 Summary of results from LMMs to predict the magnitude of relative asymmetries for each of the ornamental plumes of Whiskered Auklets for which we had their actual age in years.

Table S8 Summary of results from LMMs to predict the magnitude of absolute asymmetries for each of the ornamental plumes of Whiskered Auklets.

Supplementary Information

In this supplement we provide additional details about statistical analyses reported in Jones *et al.* 2023 Limited evidence that the asymmetries of Whiskered Auklet (*Aethia pygmaea*) feather ornaments could serve a display function. Ibis, submitted. In this supplement we provide additional figures, tables and information about other analyses in support of statements made in the main text.

1 Statistical Analyses

In linear mixed models (LMMs), we square-root-transformed measures of asymmetry to normalize residuals and satisfy the statistical assumptions more closely than was evident when using the untransformed data. We used the *check_model* function in the *performance* package in R (v4.2.2) to evaluate the fits to model assumptions and we present the output from some of those model checks here.

2 Descriptive Statistics

We excluded plumes ≤ 5 mm long from all analyses based on the clear distinction between those plumes and the distributions of all of the other plumes of each type (Figure S1). Descriptive statistics for each of the variables, excluding those 8 plumes are shown in Table S1.

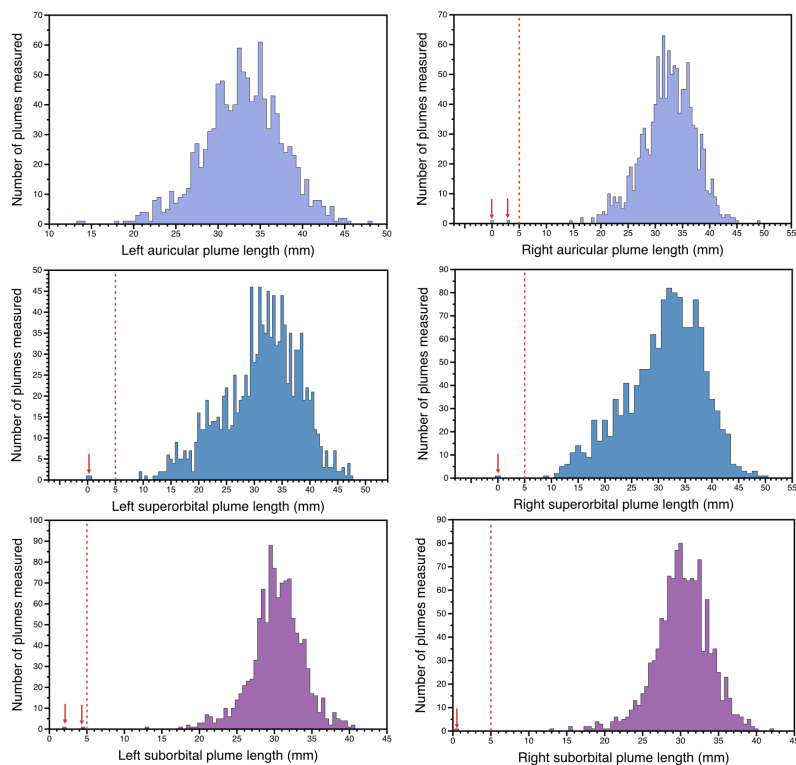


Figure S1 Frequency distributions of the lengths of bilateral ornamental plumes that we measured, including multiple measurements from some individuals. Dotted line at 5 mm indicates our cutoff for categorizing plumes as broken (red arrows)

Table S1 Descriptive statistics from a dataset that excludes 8 apparently broken plumes (length <5mm) and, for each plume, only birds that had both sides measured .

	n	mean	sd	median	min	max	range	skew	kurtosis	se
DOY	1626	158.33	13.39	155.00	139.00	224.00	85.00	1.74	3.14	0.33
age (years)	494	2.94	3.05	1.00	1.00	16.00	15.00	1.94	3.41	0.14
mass (g)	1586	116.27	9.12	116.00	90.00	145.00	55.00	0.24	-0.20	0.23
tarsus length (mm)	1380	22.05	0.82	22.10	17.90	24.70	6.80	-0.17	0.56	0.02
wing length (mm)	478	107.66	2.71	108.00	101.00	115.00	14.00	0.08	-0.23	0.12
crest length (mm)	1619	35.36	8.75	37.30	7.50	57.40	49.90	-1.03	0.87	0.22
AuricularLeft length (mm)	1108	32.96	4.66	33.10	13.30	48.20	34.90	-0.26	0.44	0.14
AuricularRight length (mm)	1108	32.54	4.69	32.70	14.40	49.00	34.60	-0.32	0.34	0.14
SuperLeft length (mm)	1205	31.27	6.86	32.00	9.60	47.30	37.70	-0.46	-0.12	0.20
SuperRight length (mm)	1205	31.17	7.10	32.00	9.40	50.40	41.00	-0.48	-0.10	0.20
SubLeft length (mm)	1106	30.35	3.47	30.45	13.20	40.50	27.30	-0.42	1.28	0.10
SubRight length (mm)	1106	30.31	3.59	30.40	13.10	41.80	28.70	-0.50	1.31	0.11

3 Measurement Error

LMMs to predict absolute asymmetry that include ornament size as a predictor are actually controlling for ornament size and are thus estimating relative ornament size. Nonetheless we included ornament size in all models because there was a positive correlation between the error in measurements during any two week period (measured as the difference between the two measurements) and ornament size ($r = 0.17-0.41$; Table S2). Note, however, that only the correlation between the size and difference between measurements is statistically significant only for the left superorbital plumes, after correction for multiple analyses.

Table S2 Correlations between differences in ornament sizes measured on the same individuals within a two-week period and the mean size of that ornament $((L+R)/2)$. AU = auricular, SP = superorbital, SB = suborbital. P-values corrected using Holm's method.

Parameter1	Parameter2	r	95% CI	t	df	p
AUleftdiff	AUsize	0.28	[0.04, 0.50]	2.30	61	0.498
AUrightdiff	AUsize	0.34	[0.10, 0.54]	2.80	61	0.195
SPleftdiff	SPsize	0.17	[-0.07, 0.39]	1.44	69	> .999
SPrightdiff	SPsize	0.41	[0.20, 0.59]	3.75	69	0.013*
SBleftdiff	SBsize	0.20	[-0.04, 0.43]	1.64	62	> .999
SBrightdiff	SBsize	0.27	[0.03, 0.48]	2.21	62	0.579

4 Linear Mixed Models (LMMs)

In each of these models, ornament asymmetries are square-root transformed to help satisfy assumptions in these statistical models.

4.1 Transformations

To satisfy the assumptions of LMMs, we tried different transformations (Table S3) of both the relative asymmetry and ornament size in models that controlled for day of the year, age

category, breeding status, measurer, tarsus length, and body mass, with individual identity as a random effect. Models with untransformed variables were not linear. See also Figures S3, S4.

Table S3 AIC values for different LMMs with different transformations of relative asymmetry and ornament size for superorbital plumes. Best-fitting model has lowest AIC.

Transformed variables		AIC with predictors:	
response	predictor	log ₁₀ -transformed	square root-transformed
Relative asymmetry	Ornament size	1022.02	1041.30
Relative asymmetry		1012.51	-1046.46

4.2 Relationships among ornament asymmetries

To examine the degree of correlation among the relative asymmetries of the different ornaments, we used LMMs to control for possible confounds due to age (adult vs subadult), sex, breeding status, day of the year, and measurer, with bird identity as a random effect to account for repeated measurements of individuals. We did this both to look for relationships between the relative asymmetries of pairs of bilateral plumes (Table S4) and between the relative asymmetries of each of those bilateral plumes and crest size (Table S5).

Table S4 Relationships between relative asymmetries of pairs of ornamental plumes

	Auricular vs Superorbital	Auricular vs Suborbital	Superorbital vs Suborbital
(Intercept)	0.21 [0.178, 0.241] <0.001	0.25 [0.201, 0.304] <0.001	0.21 [0.180, 0.247] <0.001
Asymmetries	0.003 [-0.037, 0.044] 0.87	0.03 [-0.056, 0.120] 0.47	-0.004 [-0.068, 0.060] 0.90
Age (subadult – adult)*	0.06 [0.032, 0.084] <0.001	0.03 [-0.005, 0.0713] 0.09	0.06 [0.033, 0.086] <0.001
Breeding status (breeder – non-breeder)*	0.03 [0.005, 0.048] 0.02	0.02 [-0.011, 0.051] 0.21	0.03 [0.004, 0.048] 0.02
Sex (male – female)*	-0.01 [-0.038, 0.010] 0.26	-0.03 [-0.076, 0.016] 0.20	-0.01 [-0.038, 0.010] 0.25
Sex (unknown – female)*	-0.01 [-0.029, 0.013] 0.45	0.004 [-0.035, 0.043] 0.85	-0.01 [-0.032, 0.010] 0.31
Day of the year	-0.004 [-0.012, 0.003] 0.25	0.003 [-0.007, 0.012] 0.62	-0.005 [-0.012, 0.003] 0.23
Measurer [ILJ – FH]*	-0.01 [-0.027, 0.0054] 0.13	0.001 [-0.019, 0.022] 0.90	-0.01 [-0.028, 0.004] 0.14
Measurer [SS – FH]*	0.01 [-0.058, 0.073] 0.83	0.06 [-0.031, 0.155] 0.19	0.01 [-0.058, 0.074] 0.81
Random Effects			
ICC	0.15	0.52	0.14
Number of individuals / observations	519 / 1025	518 / 1025	521 / 1034
R ² Marginal / Conditional	0.024 / 0.17	0.011 / 0.53	0.025 / 0.16

* estimate is calculated as the difference between the two categories listed

Table S5 Relationships between relative asymmetries of ornamental plumes and crest size

	Auricular	Superorbital	Suborbital
(Intercept)	0.23 [0.178 – 0.285] <0.001	0.29 [0.207 – 0.370] <0.001	0.19 [0.138 – 0.241] <0.001
crest length	-0.0005 [-0.002 – 0.001] 0.37	-0.001 [-0.002 – 0.001] 0.54	0.001 [-0.001 – 0.002] 0.25
Age (subadult – adult)*	0.06 [0.023 – 0.0878] 0.001	0.02 [-0.029 – 0.063] 0.47	0.04 [0.007 – 0.069] 0.02
Sex (male – female)*	-0.01 [-0.037 – 0.012] 0.31	-0.03 [-0.073 – 0.019] 0.26	0.01 [-0.014 – 0.034] 0.41
Sex (unknown – female)*	-0.01 [-0.030 – 0.012] 0.40	0.006 [-0.033 – 0.045] 0.77	0.001 [-0.019 – 0.021] 0.92
Breeding status (breeder – non-breeder)*	0.03 [0.005 – 0.050] 0.02	0.01 [-0.016 – 0.039] 0.43	-0.01 [-0.030 – 0.012] 0.41
Day of the year	-0.004 [-0.012 – 0.003] 0.27	0.0001 [-0.009 – 0.009] 0.98	0.002 [-0.005 – 0.009] 0.60
Measurer [ILJ – FH]*	-0.01 [-0.029 – 0.003] 0.12	-0.001 [-0.021 – 0.020] 0.94	-0.007 [-0.008 – 0.023] 0.35
Measurer [SS – FH]*	0.01 [-0.061 – 0.072] 0.88	0.02 [-0.019 – 0.053] 0.35	0.002 [-0.061 – 0.065] 0.95
Random Effects			
ICC	0.14	0.51	0.18
Number of individuals / observations	522 / 1035	565 / 1127	520 / 1033
Marginal/Conditional	0.03 / 0.17	0.009 / 0.52	0.02 / 0.19

* estimate is calculated as as the difference between the two categories listed

4.2 Predicting Relative Asymmetries

We constructed linear mixed models using as predictors all of the variables that we thought might plausibly influence relative asymmetry based on other studies of asymmetry in birds. Because there was no evidence in support of differences among years (Table S6), we omitted year from LMMs to simplify the presentation and reduce the number of parameters in the models.

Table S6 LLMs to predict relative asymmetry that include year as a factor (Fyr) showing no evidence for year as an effect. Table 1 in the main text does not include year as a predictor.

Relative asymmetry Auriculars				Relative asymmetry Superorbitals				Relative asymmetry Suborbitals			
S Rra AUR				S Rra SUPER				S Rra SUB			
Predictors	Estimates	CI	p	Predictors	Estimates	CI	p	Predictors	Estimates	CI	p
(Intercept)	0.1999	0.1520 – 0.2479	<0.001	(Intercept)	0.2455	0.1801 – 0.3109	<0.001	(Intercept)	0.2150	0.1686 – 0.2613	<0.001
ageCAT [sub]	0.0501	0.0208 – 0.0795	0.001	ageCAT [sub]	-0.0590	-0.0983 – -0.0197	0.003	ageCAT [sub]	0.0184	-0.0089 – 0.0457	0.185
fBreed [1]	0.0353	0.0121 – 0.0585	0.003	fBreed [1]	0.0348	0.0069 – 0.0626	0.014	fBreed [1]	-0.0022	-0.0244 – -0.0201	0.849
Fyr [1993]	0.0194	-0.0224 – 0.0612	0.364	sex2 [m]	0.0114	-0.0312 – 0.0540	0.601	sex2 [m]	0.0216	-0.0031 – 0.0463	0.087
Fyr [1994]	0.0049	-0.0310 – 0.0408	0.789	sex2 [u]	0.0278	-0.0094 – 0.0650	0.142	sex2 [u]	0.0079	-0.0143 – 0.0300	0.486
Fyr [1995]	0.0037	-0.0339 – 0.0414	0.846	Fyr [1993]	0.0434	-0.0093 – 0.0960	0.106	Fyr [1993]	0.0250	-0.0152 – 0.0653	0.223
Fyr [1996]	-0.0013	-0.0391 – 0.0365	0.947	Fyr [1994]	-0.0116	-0.0580 – 0.0348	0.624	Fyr [1994]	-0.0031	-0.0377 – 0.0314	0.860
Fyr [1997]	0.0145	-0.0192 – 0.0481	0.399	Fyr [1995]	-0.0034	-0.0525 – 0.0457	0.892	Fyr [1995]	-0.0077	-0.0440 – 0.0285	0.676
Fyr [1998]	-0.0036	-0.0398 – 0.0326	0.847	Fyr [1996]	-0.0111	-0.0607 – 0.0384	0.659	Fyr [1996]	-0.0030	-0.0395 – 0.0336	0.873
Fyr [2000]	0.0004	-0.0364 – 0.0372	0.984	Fyr [1997]	0.0044	-0.0401 – 0.0488	0.847	Fyr [1997]	0.0085	-0.0239 – 0.0409	0.607
Fyr [2001]	0.0070	-0.0283 – 0.0423	0.699	Fyr [1998]	0.0010	-0.0463 – 0.0484	0.965	Fyr [1998]	-0.0059	-0.0409 – 0.0290	0.740
Fyr [2004]	0.0223	-0.0303 – 0.0749	0.405	Fyr [2000]	0.0010	-0.0474 – 0.0493	0.969	Fyr [2000]	0.0128	-0.0228 – 0.0483	0.481
Fyr [2005]	0.0223	-0.0521 – 0.0967	0.556	Fyr [2001]	0.0150	-0.0316 – 0.0616	0.528	Fyr [2001]	-0.0016	-0.0358 – 0.0325	0.925
Fyr [2006]	-0.0143	-0.0563 – 0.0277	0.505	Fyr [2004]	-0.0168	-0.0869 – 0.0532	0.638	Fyr [2004]	0.0219	-0.0288 – 0.0726	0.398
sex2 [m]	-0.0000	-0.0256 – 0.0255	0.997	Fyr [2005]	0.0043	-0.0924 – 0.1009	0.931	Fyr [2005]	-0.0270	-0.0987 – 0.0446	0.459
sex2 [u]	-0.0010	-0.0239 – 0.0218	0.929	Fyr [2006]	0.0113	-0.0439 – 0.0665	0.687	Fyr [2006]	0.0325	-0.0080 – 0.0729	0.115
DOY	-0.0057	-0.0146 – 0.0031	0.206	Fyr [2007]	0.0410	-0.0946 – 0.1765	0.553	DOY	-0.0032	-0.0118 – 0.0053	0.456
Mass	0.0005	-0.0081 – 0.0091	0.908	DOY	-0.0005	-0.0110 – 0.0099	0.921	Mass	-0.0038	-0.0121 – 0.0046	0.375
tarsus	-0.0030	-0.0113 – 0.0054	0.486	Mass	0.0072	-0.0044 – 0.0187	0.224	tarsus	-0.0046	-0.0127 – 0.0035	0.262
Measurer [ILJ]	-0.0202	-0.0421 – 0.0018	0.072	tarsus	-0.0091	-0.0211 – 0.0028	0.135	SIZEsub	-0.0144	-0.0224 – -0.0064	<0.001
Measurer [SS]	-0.0300	-0.1286 – 0.0687	0.551	SIZEsuper	-0.0740	-0.0871 – -0.0610	<0.001	Measurer [ILJ]	-0.0081	-0.0292 – 0.0130	0.452
SIZEaur	-0.0133	-0.0226 – -0.0041	0.005	Measurer [ILJ]	-0.0161	-0.0439 – 0.0117	0.255	Measurer [SS]	-0.0005	-0.0955 – 0.0945	0.992
Random Effects				Random Effects				Random Effects			
σ^2	0.01			σ^2	0.01			σ^2	0.01		
τ_{00} band	0.00			τ_{00} band	0.01			τ_{00} band	0.00		
ICC	0.16			ICC	0.44			ICC	0.17		
N _{band}	517			N _{band}	559			N _{band}	516		
Observations	1020			Observations	1107			Observations	1019		
Marginal R ² / Conditional R ²	0.043 / 0.197			Marginal R ² / Conditional R ²	0.154 / 0.530			Marginal R ² / Conditional R ²	0.046 / 0.210		

In models in Table 1 of the main text, we categorized the ages of all birds as subadult or adult. We did not include the actual age of birds because we had data on real ages for less than 175 of the birds. There was also no clear pattern of the effects of age on relative asymmetries (Table S7, Figure S2).

Table S7 Summary of results from LMMs to predict the magnitude of relative asymmetries for each of the ornamental plumes of Whiskered Auklets for which we had their actual age in years. Models include actual age as a factor in case the age effect is nonlinear. Coefficients for day of the year, body mass, tarsus and ornament size are standardized and can be compared directly with one another; bold indicates statistical significance in support of a difference from zero. For each ornamental plume, estimates [95%CI] *P* are listed.

Auricular plumes			
Predictors	S Rra AUR		
	Estimates	CI	<i>p</i>
(Intercept)	0.2623	0.2044 – 0.3201	<0.001
Fage [2]	-0.0622	-0.1176 – -0.0068	0.028
Fage [3]	-0.0340	-0.1004 – -0.0325	0.316
Fage [4]	-0.0472	-0.1167 – -0.0223	0.183
Fage [5]	-0.1261	-0.2059 – -0.0463	0.002
Fage [6]	0.0224	-0.0648 – -0.1096	0.613
Fage [7]	-0.0584	-0.1405 – -0.0238	0.163
Fage [8]	-0.1194	-0.2402 – -0.0013	0.052
Fage [9]	-0.1396	-0.2712 – -0.0080	0.038
Fage [10]	-0.0490	-0.2634 – -0.1655	0.653
Fage [11]	-0.0483	-0.2044 – -0.1079	0.543
Fage [12]	-0.0927	-0.2468 – -0.0614	0.237
Fage [15]	0.1264	-0.0953 – -0.3482	0.263
Fage [16]	-0.0091	-0.1528 – -0.1345	0.901
fBreed [1]	0.0355	-0.0125 – -0.0836	0.146
sex2 [m]	-0.0149	-0.0690 – -0.0392	0.588
sex2 [u]	-0.0110	-0.0557 – -0.0337	0.630
DOY	-0.0142	-0.0318 – -0.0034	0.114
Mass	-0.0069	-0.0257 – -0.0119	0.471
tarsus	-0.0077	-0.0236 – -0.0082	0.340
Measurer [ILJ]	-0.0270	-0.0586 – -0.0046	0.093
Measurer [SS]	-0.1109	-0.2725 – -0.0506	0.178
SIZEaur	-0.0098	-0.0272 – -0.0075	0.266
Random Effects			
σ^2	0.01		
τ_{00} band	0.00		
ICC	0.26		
N band	173		
Observations	313		
Marginal R^2 / Conditional R^2	0.128 / 0.350		

Superorbital plumes			
Predictors	S Rra SUPER		
	Estimates	CI	<i>p</i>
(Intercept)	0.1807	0.1043 – 0.2571	<0.001
Fage [2]	0.0236	-0.0465 – -0.0936	0.509
Fage [3]	0.0300	-0.0554 – -0.1153	0.490
Fage [4]	0.0048	-0.0839 – -0.0936	0.915
Fage [5]	-0.0008	-0.1027 – -0.1011	0.988
Fage [6]	-0.0261	-0.1412 – -0.0889	0.655
Fage [7]	0.0235	-0.0778 – -0.1248	0.648
Fage [8]	-0.1138	-0.2484 – -0.0208	0.097
Fage [9]	-0.0428	-0.2152 – -0.1295	0.625
Fage [10]	0.0422	-0.1202 – -0.2045	0.610
Fage [11]	-0.0774	-0.2587 – -0.1040	0.402
Fage [12]	0.0967	-0.0745 – -0.2679	0.267
Fage [13]	0.1062	-0.1157 – -0.3282	0.347
Fage [14]	-0.1062	-0.4069 – -0.1945	0.488
Fage [15]	-0.1477	-0.4371 – -0.1417	0.316
Fage [16]	0.4365	0.2465 – 0.6266	<0.001
fBreed [1]	0.0489	-0.0086 – -0.1064	0.095
sex2 [m]	0.0004	-0.0711 – -0.0720	0.990
sex2 [u]	0.0225	-0.0358 – -0.0809	0.448
DOY	-0.0021	-0.0239 – -0.0198	0.853
Mass	0.0022	-0.0226 – -0.0270	0.861
tarsus	-0.0114	-0.0325 – -0.0097	0.290
Measurer [ILJ]	0.0104	-0.0305 – -0.0513	0.617
Measurer [SS]	0.0916	-0.0009 – -0.1840	0.052
SIZEsuper	-0.0602	-0.0842 – -0.0362	<0.001
Random Effects			
σ^2	0.02		
τ_{00} band	0.01		
ICC	0.27		
N band	174		
Observations	323		
Marginal R^2 / Conditional R^2	0.208 / 0.418		

Suborbital plumes			
Predictors	S Rra SUB		
	Estimates	CI	<i>p</i>
(Intercept)	0.2234	0.1767 – 0.2701	<0.001
Fage [2]	-0.0450	-0.0944 – -0.0044	0.074
Fage [3]	-0.0544	-0.1148 – -0.0061	0.078
Fage [4]	-0.0507	-0.1141 – -0.0127	0.116
Fage [5]	-0.0931	-0.1677 – -0.0185	0.015
Fage [6]	-0.0947	-0.1765 – -0.0129	0.023
Fage [7]	-0.0916	-0.1675 – -0.0157	0.018
Fage [8]	-0.1018	-0.2139 – -0.0103	0.075
Fage [9]	0.0166	-0.1108 – -0.1439	0.798
Fage [10]	-0.1111	-0.3186 – -0.0963	0.292
Fage [11]	-0.0095	-0.1615 – -0.1425	0.902
Fage [12]	-0.0409	-0.1902 – -0.1085	0.591
Fage [15]	-0.1004	-0.3140 – -0.1133	0.356
Fage [16]	0.0212	-0.1038 – -0.1462	0.739
fBreed [1]	0.0337	-0.0112 – -0.0786	0.141
sex2 [m]	0.0363	-0.0083 – -0.0808	0.110
sex2 [u]	0.0178	-0.0182 – -0.0538	0.331
DOY	0.0099	-0.0067 – -0.0264	0.242
Mass	0.0026	-0.0144 – -0.0197	0.762
tarsus	-0.0068	-0.0208 – -0.0072	0.340
Measurer [ILJ]	0.0049	-0.0251 – -0.0349	0.748
Measurer [SS]	-0.0544	-0.2037 – -0.0950	0.474
SIZEsub	-0.0148	-0.0294 – -0.0001	0.048
Random Effects			
σ^2	0.01		
τ_{00} band	0.00		
ICC	0.05		
N band	171		
Observations	310		
Marginal R^2 / Conditional R^2	0.086 / 0.135		

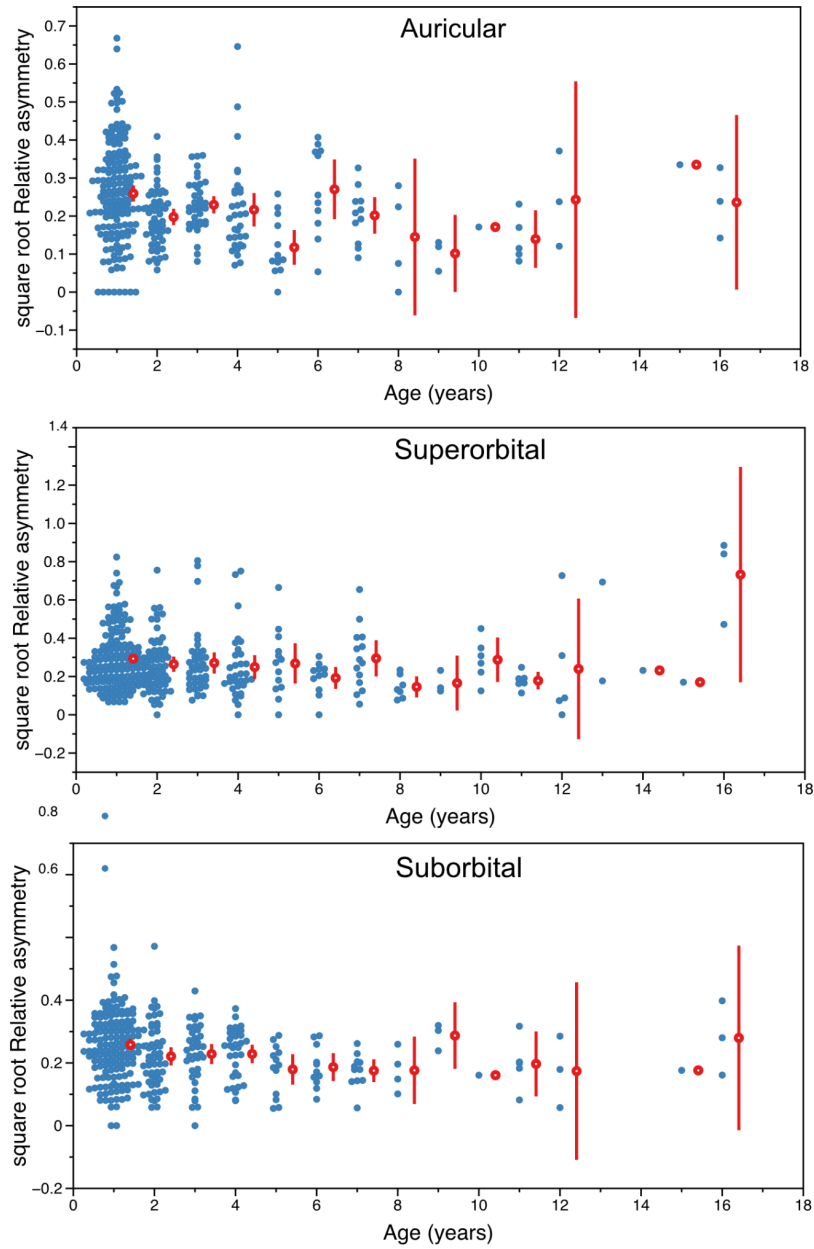


Figure S2 Predicted relative asymmetries for birds of known age. Blue dots are square-root transformed raw data adjusted for predictors in the models, red symbols are means $\pm 95\%$ CL.

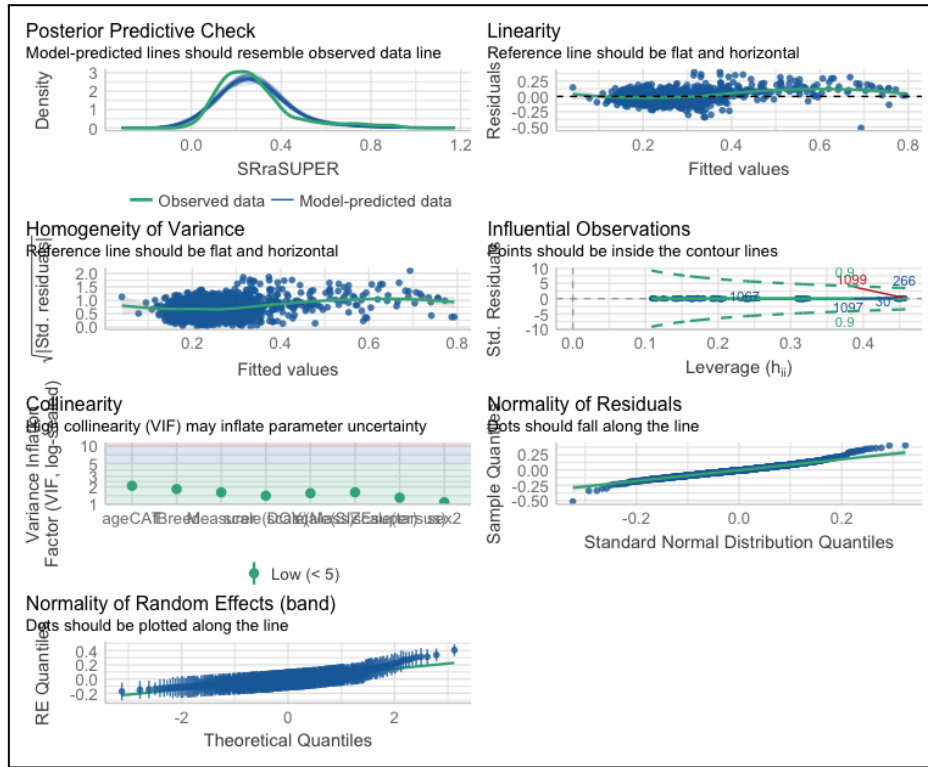


Figure S3 Results of checking assumptions of the model in Table 1 of the main text to predict the relative asymmetry of superorbital plumes with outliers included.

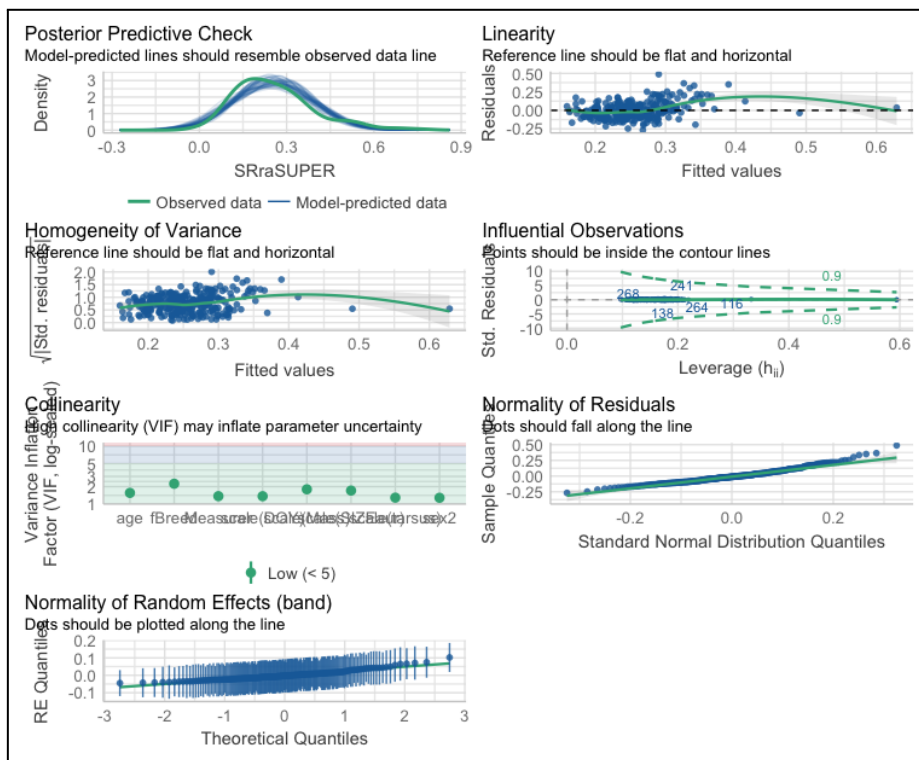


Figure S4 Results of checking assumptions of a model to predict the relative asymmetry of superorbital plumes with outliers excluded.

4.4 Predicting Absolute Asymmetries

In the main paper, we reported the results of linear mixed models to predict relative asymmetries of the three ornamental plumes. Here are the same models to predict absolute asymmetry (Table S8).

Table S8 Summary of results from LMMs to predict the magnitude of absolute asymmetries for each of the ornamental plumes of Whiskered Auklets. Coefficients for day of the year, body mass, tarsus, and ornament size were standardized and can be compared directly with one another. Bird identity was included as a random effect in each model to control for multiple captures of many of the birds. Absolute asymmetries were square-root-transformed to normalize residuals. Bold indicates statistical significance.

Absolute asymmetry Auriculars			
Predictors	S Rabs M Aaur		
	Estimates	CI	p
(Intercept)	1.1334	0.9590 – 1.3078	<0.001
ageCAT [sub]	0.2708	0.1109 – 0.4307	0.001
fBreed [1]	0.1985	0.0691 – 0.3279	0.003
sex2 [m]	-0.0035	-0.1444 – 0.1374	0.962
sex2 [u]	0.0061	-0.1133 – 0.1254	0.921
DOY	-0.0226	-0.0664 – 0.0212	0.311
Mass	0.0058	-0.0417 – 0.0533	0.811
tarsus	-0.0182	-0.0625 – 0.0260	0.419
Measurer [ILJ]	-0.0841	-0.1789 – 0.0107	0.082
Measurer [SS]	-0.0247	-0.4172 – 0.3678	0.902
SIZEaur	0.0211	-0.0290 – 0.0711	0.409
Random Effects			
σ^2	0.31		
τ_{00} band	0.05		
ICC	0.14		
N band	517		
Observations	1020		
Marginal R ² / Conditional R ²	0.020 / 0.156		

Absolute asymmetry Superorbital			
Predictors	S Rabs M Asuper		
	Estimates	CI	p
(Intercept)	1.3001	1.0675 – 1.5328	<0.001
ageCAT [sub]	-0.2955	-0.4977 – -0.0934	0.004
fBreed [1]	0.1980	0.0516 – 0.3445	0.008
sex2 [m]	0.0526	-0.1678 – 0.2731	0.640
sex2 [u]	0.1506	-0.0340 – 0.3352	0.110
DOY	-0.0036	-0.0530 – 0.0457	0.885
Mass	0.0458	-0.0145 – 0.1060	0.136
tarsus	-0.0569	-0.1165 – 0.0026	0.061
SIZEsuper	-0.2267	-0.2939 – -0.1596	<0.001
Measurer [ILJ]	-0.0364	-0.1483 – 0.0756	0.524
Measurer [SS]	0.0764	-0.1136 – 0.2664	0.430
Random Effects			
σ^2	0.39		
τ_{00} band	0.28		
ICC	0.41		
N band	559		
Observations	1107		
Marginal R ² / Conditional R ²	0.071 / 0.456		

Absolute asymmetry Suborbital			
Predictors	S Rabs M Asub		
	Estimates	CI	p
(Intercept)	1.1642	1.0006 – 1.3278	<0.001
ageCAT [sub]	0.0767	-0.0681 – 0.2215	0.299
fBreed [1]	-0.0191	-0.1386 – 0.1004	0.754
sex2 [m]	0.1122	-0.0209 – 0.2452	0.098
sex2 [u]	0.0318	-0.0806 – 0.1442	0.579
DOY	-0.0034	-0.0440 – 0.0373	0.872
Mass	-0.0212	-0.0656 – 0.0233	0.351
tarsus	-0.0232	-0.0650 – 0.0187	0.277
SIZEsub	0.0014	-0.0412 – 0.0441	0.947
Measurer [ILJ]	0.0203	-0.0665 – 0.1071	0.647
Measurer [SS]	-0.1177	-0.4829 – 0.2476	0.527
Random Effects			
σ^2	0.26		
τ_{00} band	0.05		
ICC	0.16		
N band	516		
Observations	1019		
Marginal R ² / Conditional R ²	0.011 / 0.173		

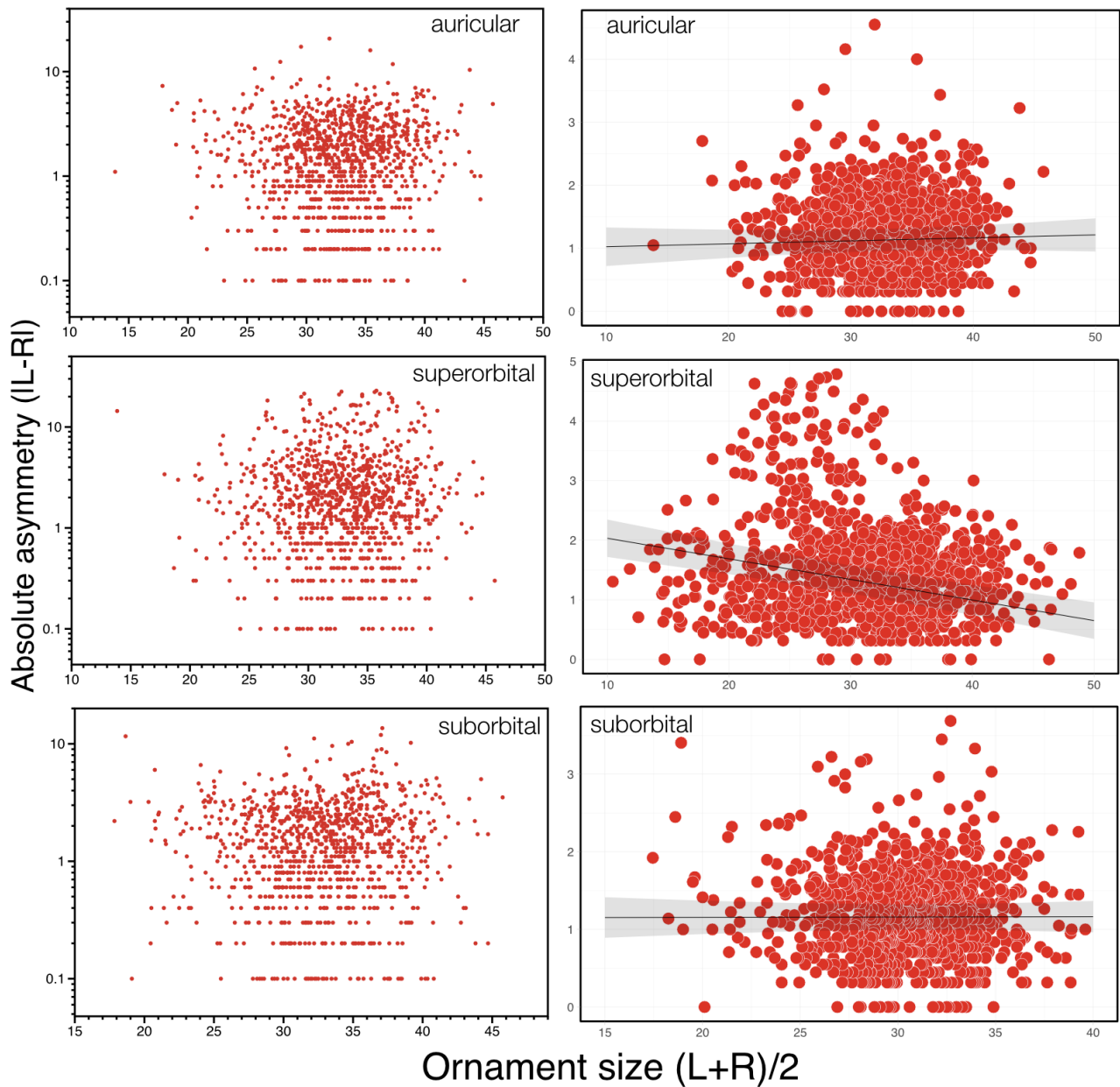


Figure S5 Relationships between absolute asymmetries and ornament sizes for each of the bilateral plumes. Asymmetries are plotted as raw data (left, on log scale), and as predicted (regression and 95%CL) from the models in Table S8 where absolute asymmetry is square-root-transformed on the y-axes.

5 Time Series Analyses

5.1 Ocean Climate

Time series analyses with respect to indices of ocean climate (Figure S6) are relevant only to correlations in the previous 1-4 years (lag = -1 to -4).

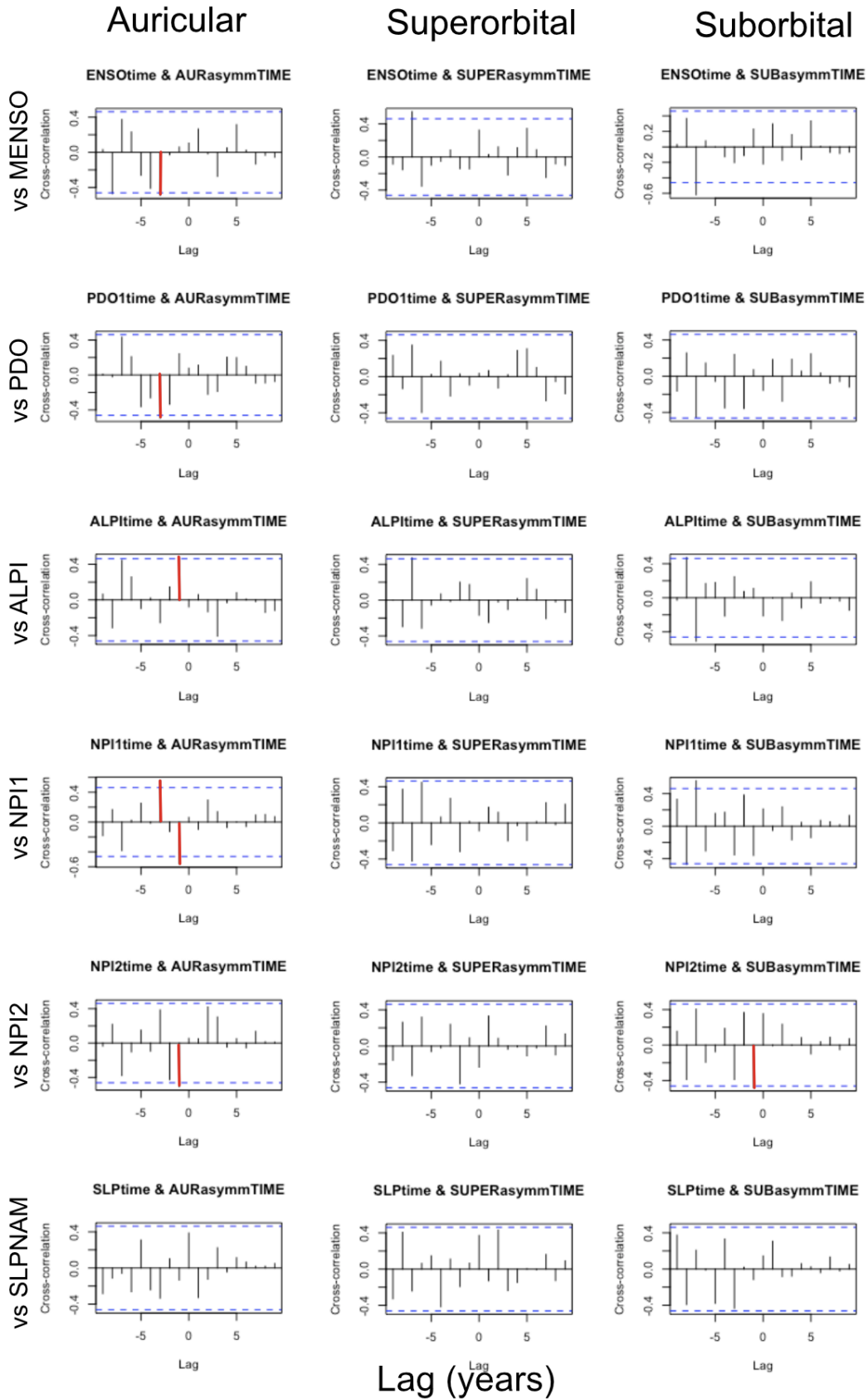


Figure S6 Cross-correlation plots for adjusted mean population absolute asymmetries and indices of ocean climate. Significant cross-correlations for current or previous 4 years are shown in red. The plots with significant cross-correlations in the preceding 2 years are also shown in Figure 6 of the manuscript.

5.2 Whiskered Auklet Demographic Parameters

Time series analyses with respect to indices of Whiskered Auklet productivity (Figure S7) are relevant only to correlations in the same year or the previous year (lag = 0 or -1).

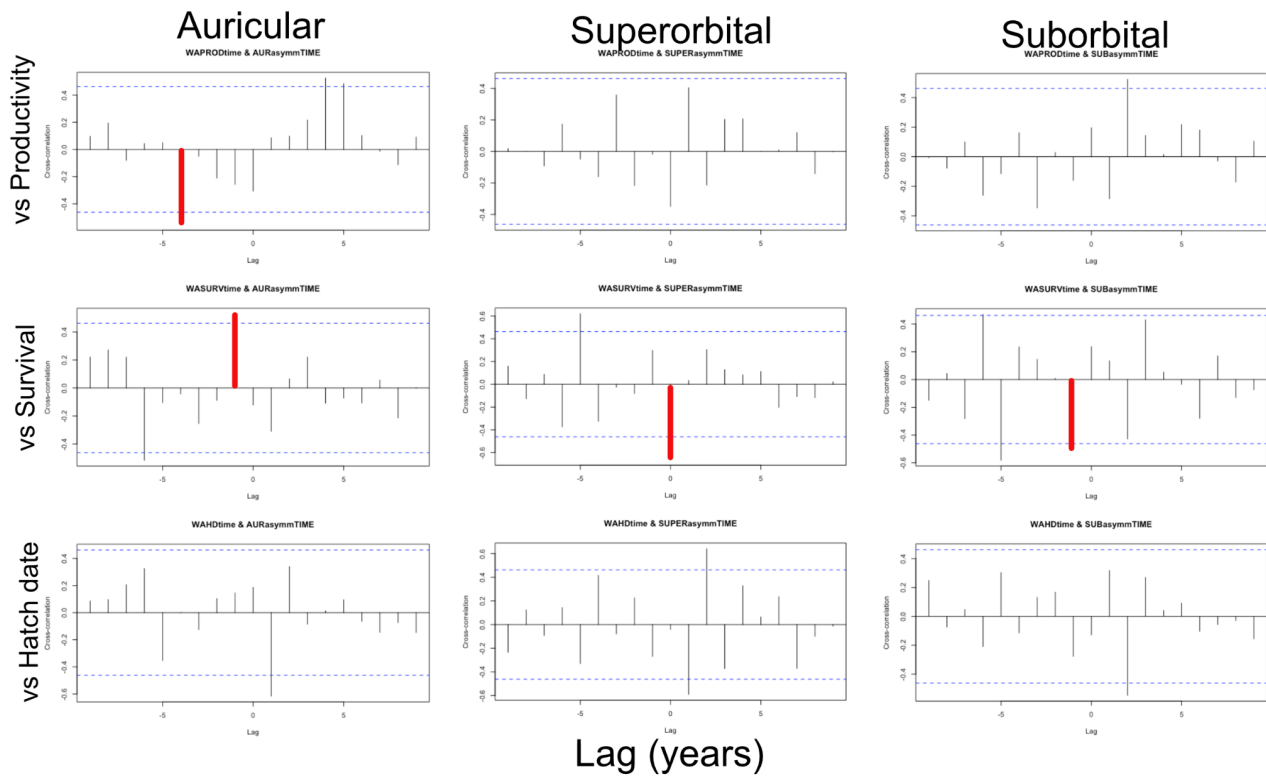


Figure S7 Cross-correlation plots for adjusted mean population absolute symmetries and indices of Whiskered Auklet demographics. The plots for survival are also shown in Figure 6 of the manuscript. Significant cross-correlations for current or previous 4 years are shown in red.

6. Data Sources

6.1 Ocean climate data

We calculated the following ocean climate variables (see data file OceanClimate.csv) from data downloaded from the internet, as follows

PDO = Pacific Decadal Oscillation in preceding 12 months (Mantua et al. 1997)

- downloaded from:

<https://climatedataguide.ucar.edu/climate-data/pacific-decadal-oscillation-pdo-definition-and-indices>

- averaged over preceding 12 months, i.e., May-April of the period preceding the feather measurement

ALPI = Aleutian Low Pressure Index (Surry and King 2015)

- downloaded from: <https://open.canada.ca/data/en/>

dataset/4bb821ce-bef7-46d3-95d2-064065f1bda4

- this index is annual by calendar year, previous years' values (one for each year) used to compare to current feather growth

NPI1 = North Pacific Index in preceding 12 months (Trenberth and Hurrell 1994)

- downloaded from:

<https://climatedataguide.ucar.edu/climate-data/north-pacific-np-index-trenberth-and-hurrell-monthly-and-winter>

- averaged over preceding 12 months, i.e., May-April of the period preceding the feather measurement

NPI2 = North Pacific Index in preceding period from November to March

- same source as NPIp12mths, average value for November, December, January, February, March (to reflect winter conditions)

SLPNAMI = Sea Level Pressure-based Northern Annular Mode index (Trenberth and Hurrell 1994)

- downloaded from:

<https://climatedataguide.ucar.edu/climate-data/hurrell-wintertime-slp-based-northern-annular-mode-nam-index>

- this index is annual by calendar year, previous years' values (one for each year) used to compare to current feather growth

MENSO = Multivariate El Niño Southern Oscillation in preceding 12 months (National Center for Atmospheric Research Staff 2019)

- downloaded from:

<https://climatedataguide.ucar.edu/climate-data/multivariate-enso-index>

- averaged over preceding 12 months, i.e., May-April of the period preceding the feather measurement

6.2 Whiskered Auklet productivity data

We used the following data on the productivity of this population from other studies as follows:

WHAUsurv = annual survival rate since previous year (calculated from mark-recapture data; see Jones et al. 2007)

WHAUprod = proportion of pairs that fledged chicks (left the nest) in current year (measured by Jeff William's team checking active crevices for eggs, incubating adults and chicks at nearby Main Talus; methods described in Hunter et al. 2002)

WHAUhd = mean hatch date in current year

7. References

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