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Origin and maintenance of mechanosensory feather ornaments

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Mechanosensory use is a seldom-mentioned function for feather ornaments, yet recent experimental evidence showed that the elaborate facial plumes of crevice-dwelling whiskered auklets, *Aethia pygmaea*, have just such a sensory role. Here we explored the evolutionary patterns of mechanosensory function of similar facial feather ornaments in related species. In an experimental chamber (maze) devoid of visible light, crested auklets, *A. cristatella*, a close relative of the whiskered auklet, showed an increase in head bumps (262%) after trial flattening of their forehead crest. The frequency of head bumps in the absence of the crest was positively correlated with the natural crest length of the crested auklet. There was no correlation between crest length and head bumps when we added an artificial crest to least auklets, *A. pusilla*, which do not have a natural crest. Thus, only the ornamented *Aethia* species that breed in deep-crevice appear to have detectable mechanosensory ability. A pairwise analysis across all nonpasserine bird families further revealed a greater frequency of elongated facial plumes in birds that live in complex habitats and are active during low light conditions. We suggest that selective pressure enforced by complex habitats may trigger facial feather exaggeration for mechanosensory use. Once the primordial sensory structures evolved, sexual and other social selection processes could act on these traits and lead towards further exaggeration.

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Across the many examples of gaudy and bizarre traits expressed by animals, some of the most extreme are the elaborate and colourful feathers of birds, yet controversy continues about the evolutionary origins of these ornamental structures (Darwin 1871; Andersson 1994). Bird feathers are complex integumentary derivatives specialized primarily for flight, thermoregulation and maintenance of streamlined body shape (Lucas & Stettenheim 1972). However, feathers have many secondary functions, including crypsis (Baker & Parker 1979), visual signalling for mate attraction (Andersson 1994), information about age, sex or individual identity (Whitfield 1987; Dale 2000), mechanical protection (Conover & Miller 1980), pursuit-deterrent (Murphy 2006) and mechanosensory use for navigation (Seneviratne & Jones 2008). Whiskered auklets, *Aethia pygmaea*, nocturnal, crevice-dwelling seabirds of the North Pacific, use their long ornamental forward-curving forehead crests and facial plumes as tactile devices to navigate in underground rock crevices (Seneviratne & Jones 2008). These elaborate feather traits of whiskered auklets were generally believed to be products of sexual selection driven by mating preferences (Jones

1999). Therefore, the recent finding of mechanosensory use for auklet feather ornaments (Seneviratne & Jones 2008) raises the question: how widespread is mechanosensory use in elongated feathers that appear to be visual display traits in birds?

Multiple selective forces, including natural and sexual selection, can act on ornamental traits (Murphy 2007), leading to change in the original function (Brooks & Endler 2001; Wiens 2001; Takahashi et al. 2008) or to functions other than mate attraction (e.g. barn swallow, *Hirundo rustica*: Møller 1991; Kleven et al. 2006; Bro-Jørgensen et al. 2007). Natural selection for mechanosensory function could thus explain the enigmatic feather structures of a wide range of birds, not just the whiskered auklet crest (Küster 1905; Seneviratne & Jones 2008). Complex habitats that are composed of many solid surfaces such as tree branches and leaves (e.g. canopy of a rainforest, rock crevices) could pose significant challenges to birds, where vision is the primary navigational aid (Gibson 1998). This imposed selection pressure could lead to development of novel traits (e.g. in bats: Neuweiler 1989; Harvey & Krebs 1990; Safi & Dechmann 2005); however, such information is scarce for birds (see Swaddle & Witter 1998; Martin et al. 2004; Price et al. 2004). A comparative approach examining the occurrence of facial feather appendages in birds and their co-occurrence with habitat preferences, characteristics of the nest and daily activity pattern provides an opportunity to test this suggestion.

Auklets (family Alcidae, tribe Aethiini) are a group of seabirds with characteristic facial ornamentation (Gaston & Jones 1998)

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including conspicuous white facial plumes and curved forehead crests. Experimental evidence supports a role for sexual selection in the maintenance of the crest in the crested auklet, *A. cristatella*, and natural selection in the maintenance of the crest in the whiskered auklet (Jones & Hunter 1993, 1999; Jones 1999; Seneviratne & Jones 2008). Least auklets, *A. pusilla*, which do not have a crest, showed a preference for mates that had an artificial crest added (Jones & Hunter 1998). Although the social environments of auklet species are similar, colony attendance behaviour and characteristics of nesting cavity differ between species. Cassin's auklets, *Ptychoramphus aleuticus*, and whiskered auklets visit the colony only at night, and the remaining auklet species are diurnal (Jones 1999); Cassin's auklets breed exclusively in self-dug burrows in soft soil (Thoresen 1964; Manuwal & Thoresen 1993), and the other auklet species breed mainly in natural rock crevices (Jones 1993a, b; Zubakin & Konyukhov 1999; Jones et al. 2001). Of the two crest-bearing auklet species, one species is a nocturnal, shallow-crevice nester and the other is a diurnal, deep-crevice nester (Jones 1999).

Here we tested for mechanosensory ability of crest ornaments in two closely related auklets, crested auklets and least auklets, in a lightproof maze that structurally resembled natural breeding crevices of these two species. We hypothesized that if the mechanosensory ability of facial plumes in the whiskered auklet was shaped by environmental factors, then the closely related crested auklet, which shares similar breeding habitat, should use the crest similarly. We also tested whether the position of forward-curving crest alone facilitates navigation through crevices (i.e. by preventing the head from hitting the maze wall), or whether the crest has a putative mechanosensory function (Seneviratne & Jones 2008). We tested the hypothesis that, when given an artificial crest, naturally crestless least auklets would not show similar tactile use as a result of the absence of innervations. We then compared the relationships of habitat complexity, daily activity pattern and nest type to facial ornaments in nonpasserine bird families to look for a correlation between ecological factors and facial ornamentation. We hypothesized that across all bird species, the elongated facial plumes would be more likely to evolve in species that inhabit complex habitats.

METHODS

Comparison of the Mechanosensory Use of Elongated Plumes in Aethia

Field experiments were undertaken at Buldir Island in the Aleutian Islands, Alaska, U.S.A. (52°22′N, 175°54′E) during May–July 2007 (the incubation phase of auklets' breeding season). Crested and least auklets were captured using 0.3×0.3 m noose carpets placed on selected locations at the main auklet colony similar to the methods of Jones (1990) and Jones et al. (2000). The colony consisted of large numbers of auklets of both species, and this trapping method appears to capture birds more or less randomly (Jones et al. 2004). Captured birds were held separately in cloth bags before being introduced into the experimental chamber.

We used the same three-chambered maze design of Seneviratne & Jones (2008) to quantify birds' ability to avoid obstacles in the absence of visual clues. The internal dimensions of the mazes differed, however, to accommodate differences in the body size of crested and least auklets: lightproof test chambers were 9 (height) $\times\ 30 \times 35$ cm for least auklets and $13 \times 40 \times 46$ cm for crested auklets. Two $2 \times 8 \times 8$ cm wooden panels were attached to the roof as barriers for least auklets; dimensions of the barrier were $2 \times 14 \times 14$ cm for crested auklets. The entranceway ($10 \times 10 \times 10$ cm) connected the $20 \times 20 \times 20$ cm holding pen to the test chamber in both set-ups. A Sony DCR-DVD308 camcorder

with built-in infrared light-emitting diode (peak wavelength 850 nm) recorded the subjects' behaviour through a front window of the test chamber. We used the camcorder's 'Niteshot Plus' mode, which allowed recording under near-infrared illumination with greater sensitivity to longer wavelengths (peak spectral sensitivity 800 nm). Specific information on auklet visual perception is lacking; however, the spectral sensitivity of both phylogenetically and ecologically closely related bird groups falls between 350 and 600 nm (Liebman 1972; Bowmaker & Martin 1985; Bowmaker et al. 1997; Hart 2001). Therefore, we assumed that the auklets' vision was insensitive to infrared wavelengths emitted by the camcorder (see Seneviratne & Jones 2008).

Treatment Exposure

Both species ($N = 70$ of each species) were exposed (or introduced) to three treatments: ornament manipulation, sham and unmanipulated treatment, in a balanced random order. The experimental design for the crested auklet was similar to that for whiskered auklets (Seneviratne & Jones 2008). In the ornament manipulation treatment (flattening of the elongated plumes), three pieces of 15×2 mm black one-sided tape were used to tape down the forward-curving crest to the back of the head. Auklets cannot move their crests actively, and in the wild these crest feathers are sufficiently flexible to be bent and lie flat on the crown feathers in flight and underwater diving (Jones 1993a). Therefore, experimentally bending these flexible feathers was unlikely to cause undue mechanical stress or to cause pain or irritation (Seneviratne & Jones 2008). In the unmanipulated treatment, test birds were exposed to the maze with no experimental manipulation to crest. In sham treatment, pieces of tape were attached as in the manipulative treatment but the ornament was left unaltered. The sham treatment was used to test for the effect of stress caused by handling and irritation as a result of the attached tape.

We treated least auklets similarly to crested auklets except that, for the plumage manipulation, we glued an artificial crest to the forehead of least auklets (two crested auklet crest feathers) to resemble the crest of a whiskered auklet. Attached crest length varied from 12.8 to 42.1 mm (mean 28.6 mm). The bases of the two feathers were dipped in a small amount of cyanoacrylate (superglue) and placed on the forehead with forceps (glued to the bases of surrounding dense contour feathers but not to the underlying skin). The glue dried instantly; therefore, the bird was available immediately for the exposure. In the sham treatment, only the feather bases with the glue base were attached to the forehead.

For both species, each bird was subjected to all treatments (M = manipulation, U = unmanipulated, S = sham) once, in a sequential (constrained random) order in all possible combinations (MUS, MSU, UMS, USM, SMU, SUM; e.g. bird n_1 was exposed to MUS, n_2 to MSU, etc.), to reduce the carryover effect due to repeated exposures (Nater et al. 1996). Birds were kept in the holding pen for acclimation prior to each exposure, and allowed to walk from the pen to the test chamber. When the bird entered the test chamber its exploratory behaviour was videorecorded for about 2 min. After each exposure, the subject was removed from the maze, switched to the next treatment and immediately reintroduced to the holding pen for the next exposure. Digital video recordings were uploaded to a computer and later S.S. reviewed the recordings and counted the frequency of head bumps (number of head touches on the roof and the walls per minute), crest contacts and beak contacts (similar to the above counts). The definitions of unambiguous 'head bump', 'crest contact' and 'beak contact' were established prior to the counts (rationale for the scoring is given in Seneviratne & Jones 2008). A naïve observer obtained similar scores (sign test:

$P = 0.062$) for a part of the data set (recordings of all three exposures of 14 crested and 14 least auklets).

Birds were colour-banded with plastic leg bands prior to release to avoid retesting them in the event of recapture. The length of crest plumes (including the artificially placed crest in least auklets) was measured with dial calipers (to ± 0.02 mm; Jones et al. 2000). Crest size of crested auklet, and white forehead plumes, bill knob and belly colour of least auklet are ornaments with similar ornamental function suggested for those of whiskered auklet (Jones & Montgomerie 1992; Jones & Hunter 1993, 1999). Hence we recorded the number of long crest feathers, the extent of the area of white forehead plumes (the length of the anterior most part of the patch of feathers to the tip of the longest plume), height of the bill knob, belly colour and age. Sex of crested auklets was determined using plumage and morphological characters (Jones 1993a).

Phylogenetic Comparison for the Expression of Long Facial Plumes

A phylogenetic comparison across all nonpasserine birds was undertaken to determine the relationship of elongated facial feathers to complex habitat and nocturnality. Illustrations from Del Hoyo et al. (1992–2002) were used as reference material. We defined 'facial area' (Fig. 1) to describe presence or absence of long facial plumes. Feathers longer than the rest of the facial feathers and/or longer than the beak (only in birds with beak length shorter than the head length) were classified as 'long feathers'. A subjective judgment was made to define 'facial region' for species groups with eyes situated either close to the base of the bill, or towards the back of the head. We adjusted these regions for owls (Strigiformes), which usually were shown in frontal aspect. All 27 nonpasserine orders (Clements 2007) were considered and in those orders, families that had at least a single species with long facial plumes were included to the analysis. Habitat type (4 categories; open forest, dense forest, open ground and dense ground), type of nest (2 categories; open and cavity) and daily activity (2 categories; diurnal and nocturnal) were noted for all species in those families using data from Del Hoyo et al. (1992–2002) blind to the level of facial
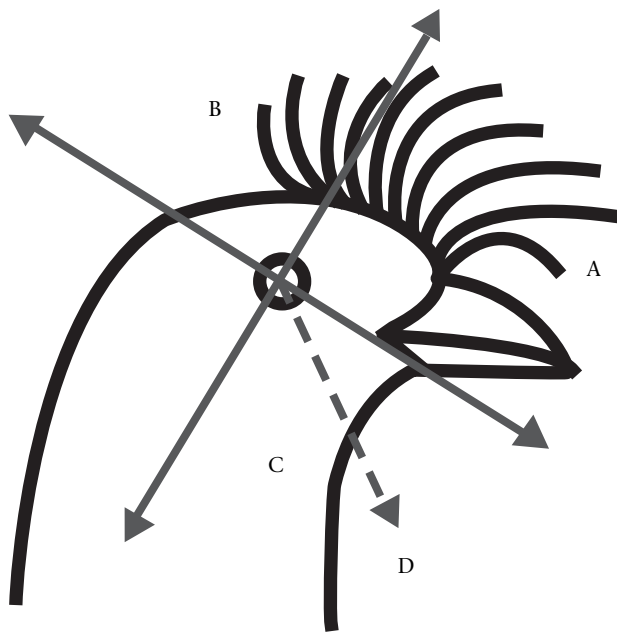
ornamentation. We scored the level of facial feather expression blind to the above variables for each species.

The use of complex habitats is widespread in birds; hence a detailed phylogenetic comparison to identify the origin of these traits requires a broader phylogeny including all species that live in complex habitats to avoid overrepresentation of long-plumed forms (Höglund 1989; Höglund & Sillén-Tullberg 1994). Since we only considered families with long facial feathers, our data set was not suited for such an analysis. To avoid complex (and often unresolved) phylogenies and to accommodate categorical variables, we used pairwise comparisons (Pagel & Harvey 1988; Møller & Birkhead 1992; Ridley & Grafen 1996), which not only controlled for phylogeny (Møller & Birkhead 1992), but also avoided the pooling fallacy that can potentially arise from common ancestry (Martins & Hansen 1996).

Species pairs were constructed by matching taxa with long facial plumes to their most closely related short-plumed taxa (Whitfield & Tomkovich 1996). Pairs were isolated from the distal and shortest branches of the phylogenetic tree to ensure that they shared relatively similar phylogenetic pasts (Pagel & Harvey 1988; Oakes 1992; Ridley & Grafen 1996), and to minimize errors of incomplete or incorrect phylogenies (Møller & Birkhead 1992). To reduce the phylogenetic dependence of species pairs, a single pair was chosen from each of the distinct clades (Harvey & Pagel 1991; Ridley & Grafen 1996; Maddison 2000). Species pairs were based on the most recent phylogenies available for each family. When that did not provide necessary resolution for a given clade, an older phylogeny was used to revise the recent one, as long as they did not disagree substantially (see Supplementary Material for the complete list of phylogenies used). When more than two candidate species pairs were available for a clade, the first pair in the checklist of Clements (2007) was selected, and when there were multiple species with the same characters, only one representative species was chosen arbitrarily. Groups that lacked a closely related species for comparison or with an ambiguous phylogenetic position (e.g. Hemiprocnidae; tree swifts) were eliminated. Overall, owlet-nightjars (Aegothelidae), hoatzin (Opisthocomidae), frogmouths (Podargidae), todies (Todidae), motmots (Momotidae), and puffbirds (Bucconidae) were excluded. In woodpeckers (Picinae), only typical Asian woodpeckers (Picini) were included as a representative monophyletic group.

Analysis

We used SAS 9.1.3 (SAS Institute, Cary, NC, U.S.A.) and Minitab Release 13.31 (Minitab, State College, PA, U.S.A.) for the analyses. Habituation to the maze and the cumulative effect of stress due to repeated handling and manipulations were collectively tested using the order of exposure in a general linear model (as two-way ANOVA) by keeping both the treatment (M, U, S) and the order of exposure (M−, -M-, −M; U−, -U-, −U; S−, -S-, −S) fixed (Sokal & Rohlf 1995). For crested auklets, there was a reduction of activity from the second to third exposure (two-way ANOVA: $F_{2,204} = 6.92$, $P = 0.001$); hence, the third exposure was excluded from further analysis. As a result, 49, 43 and 46 crested auklets were given crest manipulation, sham and unmanipulated treatments, respectively. The order of exposure of the frequency of head bumps was nonsignificant in least auklet trials ($F_{2,202} = 2.47$, $P = 0.087$). However, we further tested the effect of repeated exposures of birds by assigning all 70 least auklets randomly to the nine possible combinations. Each bird was used once to represent one of the treatments. The order of the exposure of least auklet treatments had no effect on the frequency of head bumps (Supplementary Table S1). Hence the level of stress or habituation caused by repeated exposures was not significant enough to alter the results

Figure 1. For the comparative analysis, the 'facial area' in nonpasserine birds included regions A–D. Region D is the area projecting laterally from either side of regions A–C (on either side of the face).

in the least auklet exposures. We performed the same test to first and second exposures of the crested auklet data set, which also showed no significant change between exposures (Supplementary Table S1).

The frequencies of head bumps, crest contacts and beak contacts under different experimental treatments were compared using two-way ANOVA–randomized blocks as described elsewhere (Seneviratne & Jones 2008). Individual birds were the blocks and were treated as random. Residuals were checked for normality, homogeneity and independent errors. A general linear model (regression; Sokal & Rohlf 1995) was used to test for relationships between contact with the maze and crest length in the manipulative treatment. Chi-square comparisons were performed to determine relationships between presence/absence of long facial plumes to habitat type, daily activity and nest type. We used SAS GENMOD procedure with Poisson distribution and log-link function. Statistical significance of all above tests was reached at $\alpha = 0.05$.

Ethical Note

Plumage manipulative field experiments of auklets were conducted in a temporary blind close to the breeding colony. Captured auklets were placed separately in ventilated cloth bags. After exposure to the experimental chamber, the birds were released without any plumage alterations near the capture site within 30–90 min after their initial capture. This study was conducted under the approval of the Animal Care Committee of the Memorial University of Newfoundland (protocol numbers 07-13-IJ and 07-14-IJ). The capturing and banding of auklets were done with the U.S. federal bird marking and salvage permit (permit numbers 22181 and 22181-D). Throughout the study, recommendations of the Canadian Council on Animal Care (CCAC) and the Animal Behavior Society guidelines for the use of animals in research were followed strictly.

RESULTS

Mechanosensory Use of Elongated Plumes Across Aethia Species

Crested auklets showed more head bumps in the plumage manipulation relative to the unmanipulated treatment (262%, $P < 0.0001$; Tables 1, 2, Fig. 2). Unmanipulated and sham treatments did not differ in mean frequency of head bumps and feather ornament contacts (Tables 1, 2). The natural crest length of the crested auklet (mean $\pm$ SD = 35.7 $\pm$ 7.3 mm) correlated positively with the frequency of head bumps in the manipulated treatment (Tables 1, 2, Fig. 3). Crest length was also positively related to the number of crest feathers (Table 2). However, sex was not related to the number of head bumps (two-way ANOVA: $F_{1,132} = 2.66$, $P = 0.105$). In least auklets the artificial crest had no influence on head bumps (Tables 1, 2, Figs 2, 3). Head bumps and beak contacts did not differ between unmanipulated and sham treatments (Tables 2, 3), suggesting that any stress caused by the glue base did not cause a significant change in the behaviour. The exploratory behaviour of least auklets was similar across treatments, and crest length was not correlated with head bumps in the manipulated plumage treatment (Table 2). The frequency of total hits (crest and head, excluding beak contacts) was high in the plumage manipulation (Table 1), however, beak hits were reduced (Tables 1, 2). There was no relationship between the height of the bill knob or the extent of white facial plumes and the frequency of head bumps in the unmanipulated treatment (Table 2).

Phylogenetic Comparative Analysis

Elongated facial feathers occur in 33 of 102 families in 20 of 27 orders of nonpasserine birds. Of 784 species in these 33 families, we identified 42 species pairs that could be used to compare relationships of facial plumage to habitat, nest type and daily activity patterns (Supplementary Table S2). Presence of long facial feathers was not related to habitat ($\chi^2_3 = 1.79$, $P = 0.62$) or daily activity ($\chi^2_1 = 1.10$, $P = 0.29$). When we collapsed the four habitat categories into two (complex habitat and open habitat; Table 3), the presence of elongated plumes was strongly correlated with complex habitat and activity at low light conditions (Table 4). When the number of species with long facial plumes and without long plumes was compared regardless of their daily activity pattern, we observed the following trends. The ratio of long-plumed species in complex versus open habitats was 31:11 (Table 3), but the ratio of non-plumed species in complex versus open habitats was only 23:19. The ratio of long-plumed species to nonplumed species was 11:19 in open habitats but 31:23 in complex habitats. Furthermore, when considering nocturnal species, the ratio of long-plumed species to nonplumed species was 2:3 in open habitats but 7:2 in complex habitats (Table 3). Elimination of homogeneous pairs (both members of the pair had the same habitat category or the same activity pattern) from the analysis resulted in stronger correlations (Table 4). The presence of long plumes was not related to nest type ($\chi^2_1 = 0.16$, $P = 0.69$).

DISCUSSION

We found evidence that complex environments influence the development of mechanosensory feather traits in birds that resemble ornamental plumes. Crested auklets, like the closely related whiskered auklets (Seneviratne & Jones 2008), bumped into surfaces of the maze more often when the expression of their crest was cancelled by the manipulative treatment. When the crest was flattened, the number of head bumps was positively correlated with the natural crest length of individual birds, suggesting that sensory dependence on crests is greater for birds with longer or well-expressed crests, as previously suggested by maze experiments with whiskered auklets (Seneviratne & Jones 2008). The expression of the crest is highly variable among individuals in crested auklets (Jones et al. 2000). Birds that lack well-expressed crests (e.g. immature birds and adults outside the breeding season) neither enter nor navigate in underground crevices. Only the more

Table 1
Crested and least auklets' performance inside the experimental maze under different treatments

Variable	Crested auklet		Least auklet	
	Mean$\pm$SE hits/min	N	Mean$\pm$SE hits/min	N
Head bumps				
Manipulated	5.35$\pm$0.44	69	2.72$\pm$0.28	69
Unmanipulated	2.04$\pm$0.26	69	3.00$\pm$0.24	70
Sham	1.74$\pm$0.21	69	2.81$\pm$0.29	70
Crest hits				
Manipulated			6.85$\pm$0.54	69
Unmanipulated	6.63$\pm$0.43	69		
Sham	6.26$\pm$0.54	69		
Total hits				
Manipulated	5.35$\pm$0.44	69	9.57$\pm$0.77	69
Unmanipulated	8.67$\pm$0.62	69	3.00$\pm$0.24	70
Sham	8.01$\pm$0.70	69	2.81$\pm$0.29	70
Beak touches				
Manipulated	5.83$\pm$0.53	69	4.15$\pm$0.66	69
Unmanipulated	3.52$\pm$0.40	69	4.93$\pm$0.68	70
Sham	3.86$\pm$0.51	69	5.67$\pm$0.79	70

Table 2
Effects of treatment exposure on crested and least auklets, and their relationship with the size of some of the ornaments

Variable	Treatment	Crested auklet				Least auklet			
		F	df	P	R^2	F	df	P	R^2
Head bumps	Manipulated	32.24	2, 67	<0.001		1.14	2, 134	0.322	
	Unmanipulated vs Sham	0.13	1, 67	0.715		1.16	1, 67	0.284	
Crest hits	Unmanipulated vs Sham	0.42	1, 67	0.521					
Beak contacts	Manipulated	4.52	2, 132	0.013		5.27	2, 134	0.006	
Correlation with crest length									
Head bumps	Manipulated	4.34	1, 66	0.041	0.06	0.13	1, 66	0.772	0.01
Crest hits	Unmanipulated	9.45	1, 66	0.003	0.13				
	Manipulated					4.15	1, 61	0.046	0.06
Total hits	Unmanipulated	6.36	1, 66	0.14	0.09				
	Manipulated					3.39	1, 58	0.071	0.06
Beak contacts	Manipulated	1.17	1, 66	0.283	0.02	0.01	1, 66	0.929	0.00
	Unmanipulated	0.90	1, 66	0.347	0.01				
Number of crest feathers	Unmanipulated	13.18	1, 66	0.001	0.17				
Correlation with head bumps									
White facial plumes	Unmanipulated					0.00	1, 66	0.968	0.00
Bill knob	Unmanipulated					0.37	1, 66	0.544	0.00

derived species of auklets (whiskered and crested auklets; Pereira & Baker 2008) that breed in deep rock crevices express a forehead crest. Hence, the mechanosensory capacity has apparently been acquired in the crested–whiskered branch in Aethiini (Pereira & Baker 2008). Least auklets, which breed in shallow crevices, did not show a similar use of an attached artificial crest, consistent with the idea of a later development of the trait and its use. The frequency of head bumps did not differ between manipulated and unmanipulated treatments of least auklets, suggesting that least auklets gained no benefit from the artificial appendage. This result implies that mechanosensory function in general might not be due solely to a crest's physical position on the forehead, preventing the auklet's head from hitting the maze in crest-bearing auklets. Nevertheless, our experimental attachment of crest feathers to the forehead of least auklets was crude, and knowledge of neuro-anatomy of feather follicles and pressure receptors is fundamental to determine the function of mechnosensory crest feathers (Lucas & Stettenheim 1972).

The expression of elongated facial plumes is rare but widespread among nonpasserine birds, and is correlated with habitat complexity and low light conditions; therefore, similar long facial plumes are likely to have a mechanosensory use in other species. However, other explanations for such long plumes do exist (e.g. camouflage, Lorek 1992; a warning mechanism to startle predators, Galeotti & Rubolini 2007). Although we were unable to pinpoint the origin of this tactile use, the correlation between the habitat characteristics and daily activity pattern suggests that the selective pressure enforced by the habitat could trigger facial feather elongation. Once protruding feathers evolved, sexual selection could explain further elaboration of traits (Jones & Hunter 1993, 1999; Andersson 1994), while the use of the feathers for sensing obstructions continued where necessary and could partly explain the initial function of now highly embellished ornaments of crested and whiskered auklets.

If the crest provides mechanosensory aid in underground navigation, why has it not evolved in crevice-dwelling least auklets? Some plausible explanations include (1) lack of genetic plasticity to produce the trait (Qvarnstroem et al. 2006; Wright et al. 2008), (2) secondary disappearance due to the cost of bearing the trait, (3) random genetic drift (Borgia 1993; Johnson 1999; Wiens 2001), or (4) absence of sufficient selection pressure to develop long facial plumes (Andersson 1994). The lack of a fully resolved phylogeny for auklets prevents us from determining the origin of the crest, and the genetic makeup of the expression of
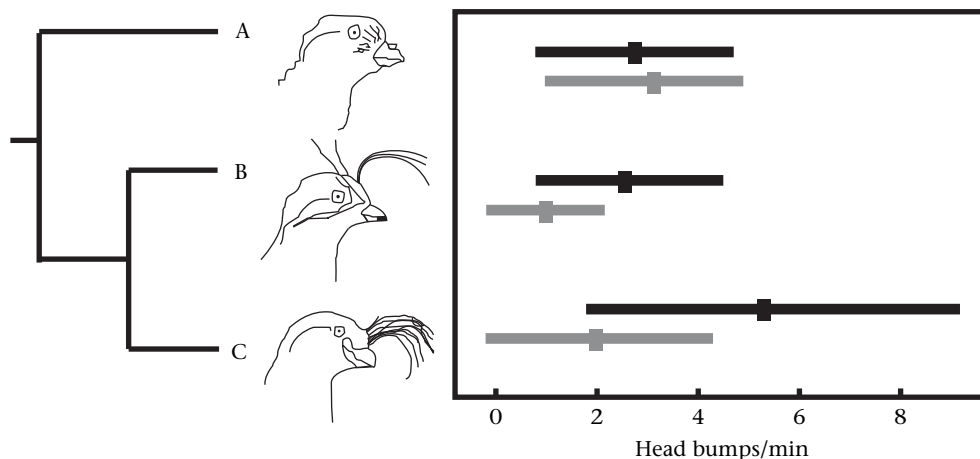

Figure 2. Mean ± SD frequency of head bumps for (a) least auklets ($N = 69$), (b) whiskered auklets ($N = 99$; Seneviratne & Jones 2008) and (c) crested auklets ($N = 69$) in each treatment. black bar: plumage manipulation; grey bar: unmanipulated. In the plumage manipulation treatment, crests of whiskered and crested auklets were flattened, and for naturally crestless least auklets, an artificial crest was added (see text). The phylogenetic tree is adapted from Pereira & Baker (2008).
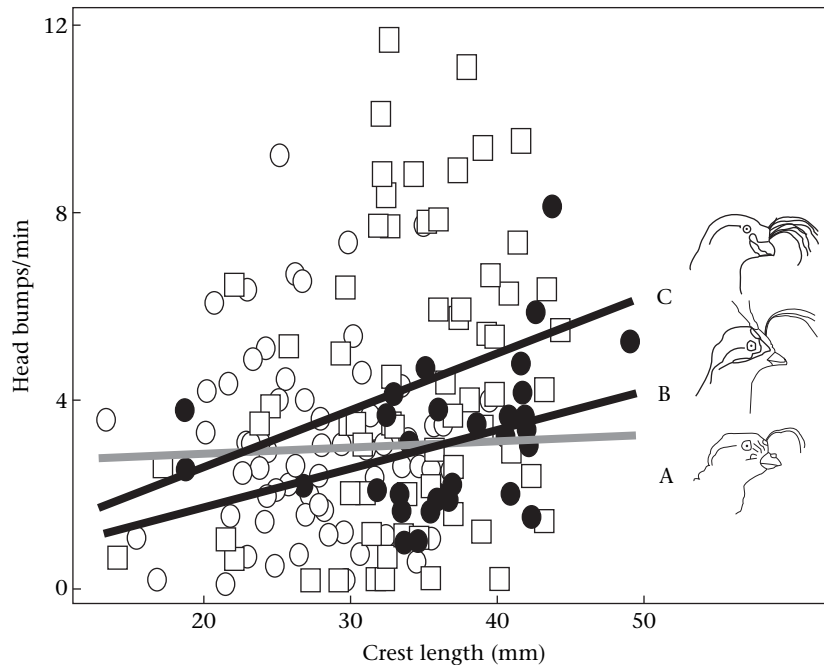
Figure 3. Relationship between natural crest length and frequency of head bumps inside the maze under flattening of the crest. The corresponding trend lines are shown in front of each auklet species (least, A; whiskered, B; crested, C). For least auklets, a crest was attached as shown in the illustration. Open square: crested auklet (*N* = 68); open circle: least auklets (*N* = 68); filled circle: whisked auklet (*N* = 33). Whiskered auklet data was taken from Seneviratne & Jones (2008).

crest feathers is not known. The feather ornaments of auklets are supposed to be cheap to produce (Jones & Montgomerie 1992) and maintain (low aerodynamic and hydrodynamic cost; Jones & Hunter 1998); however, the social cost due to the competition of dominant and aggressive sympatric crested auklets is less clear (Jones & Hunter 1998). Crested auklets have a mating preference associated with the crest (Jones & Hunter 1993, 1999); hence, an agonistic pressure from the sympatric and aggressive crested auklet may hinder the expression of the trait in least auklets. Of the three auklet species considered here, only least auklet uses shallow, comparatively better-lit crevices; therefore, it might not be subject to strong selection pressure for tactile facial feather elongation to cope with complex underground crevices (Seneviratne & Jones 2008). Alternately, the short facial plumes of least auklets might have a sensory function, but our artificial crests simply were attached too crudely to detect mechanosensory function. Taken together, we believe our experimental evidence supports the idea that the deep-crevice nesting habits may have triggered facial feather elongation in auklets.

The greater intraspecific variability and mutual mate preference for the auklet facial plumes indicates a sexually selected ornamental role for these traits (Byrd & Williams 1993; Jones & Hunter 1993, 1999; Jones et al. 2000). In barn swallows, variation in the naturally selected portion of the tail length for optimum flight performance produces the within-species differences in the length of the 'tail ornament' (Bro-Jørgensen et al. 2007). Thus, females might have used this variation as a cue to discriminate between males, and the naturally selected tail length could reflect male quality (Bro-Jørgensen et al. 2007). Similarly, the auklet crest could be a trait favoured through mate choice partly because of its information about individuals' mechanosensory ability in the breeding colony.

Our comparative analysis suggests a possible functional link between habitat complexity and facial feathering. Birds living in complex habitats are likely to encounter a greater density of objects that they have to avoid. Vision is the primary sensory aid in birds; however, acoustic signals, smell and tactile sense are also used occasionally in foraging and exploration (Wenzel 1968; Conover & Miller 1980; Hutchison & Wenzel 1980; Price et al. 2004). Long facial plumes such as semibristles of Caprimulgidae, Mimidae and Tyrannidae could be functioning as sensory whiskers for prey capturing and as a protective guard (Lederer 1972; Stettenheim 1972; Conover & Miller 1980; Jackson 2003). Similarly, protruding filoplumes of some passerines (Passeriformes) are used to sense the disturbance of contour feathers in areas where the bird cannot see, such as on the hind neck and the crown (Clark & Cruz 1989). Therefore, the mechanosensory ability of feathers could be useful

Table 3
Distribution of members of 42 species pairs of nonpasserine birds by habitat, activity pattern and presence/absence of long facial plumes

Habitat	Activity pattern	Long facial plumes	
		Present	Absent
Open	Diurnal	9	16
	Nocturnal[*]	2	3
Complex	Diurnal	24	21
	Nocturnal[*]	7	2

[*] Crepuscular species were lumped with the nocturnal species.

Table 4
Relationships between expression of long facial feathers, habitat and activity pattern for homogeneous and heterogeneous species pairs combined (a–b), and for heterogeneous species pairs separately (c)

	Relationship	χ_1^2	P
a	Between long facial feathers and habitat	6.37	0.0116
	Between long facial feathers and daily activity pattern	2.70	0.1001
	Between habitat and daily activity pattern	0.11	0.7408
b	Between long facial feathers and habitat	11.29	0.0008
	Between long facial feathers and daily activity pattern	4.68	0.0306
c	Between long facial feathers and habitat	13.33	<0.001
	Between long facial feathers and daily activity pattern	6.67	0.01

for birds sensing obstacles at close range (e.g. within a few millimetres of the body), especially in regions of the body near the crown and nape and behind the ear, where vision is less effective, and could partly explain why most long facial plumes appear in these regions. The likelihood of a bird colliding with surrounding objects is high in complex habitats, which could create greater selective pressure to develop additional sensory mechanisms. Therefore, feather elongation in the facial region would benefit birds to navigate through complex habitats that could damage vital organs (e.g. eye, eardrum), bare parts (bill, gape, nostril) or plumage. Low light conditions can cause equal or greater challenges (Hodos 1993; Brooke et al. 1999), and such conditions could force anatomical, physiological and behavioural changes (Fenton 1990; Garamszegi et al. 2001; Mandelik et al. 2003; Safi & Dechmann 2005; Rilov et al. 2007).

Future comparative studies need to test the origin and maintenance of this tactile function in the light of a rigorous phylogenetic background, which we have not attempted here. Furthermore, confirmation of mechanosensory use for long facial plumes requires detailed anatomical and physiological study of representative species to investigate extensive innervation or aggregation of mechanoreceptors on or near these feather tracts, which is expected to be more extensive than in other feather ornaments.

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Supplementary Material

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