

Mechanosensory function for facial ornamentation in the whiskered auklet, a crevice-dwelling seabird

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Sexual selection has been the prevalent explanation for the evolution of birds' elaborate feather ornaments. An overlooked possibility is that feather appendages arose due to a naturally selected sensory function involving sensitivity to pressure or touch to facilitate obstacle avoidance either in flight or on land. Here, we show experimentally that elongated facial feather adornments of whiskered auklets (*Aethia pygmaea*), a sexually monomorphic crevice-dwelling seabird, have a mechanosensory use for orientation in darkness underground. While navigating inside a lightproof maze simulating the structure and conditions of breeding crevices, whiskered auklets ($n = 99$) showed a 275% increase in frequency of head bumps in the absence of their protruding feather crest and facial plumes. A weak positive relationship ($R = 0.36$, $P = 0.04$) between natural crest length and the frequency of head bumps in the absence of the crest suggested that individuals with longer ornaments depend more on these traits for navigation in the wild. We hypothesize that protruding feathers evolved through a combination of natural selection for sensory function and sexual selection as known for other auklets. More widely, birds inhabiting cluttered environments would benefit from elongated facial plumage that mechanically detects obstacles. *Key words:* *Aethia*, feather ornaments, mechanosensory function, sexual selection, whiskered auklet. [*Behav Ecol* 19:784–790 (2008)]

Sexual selection driven by mating preferences has been a frequent explanation for the evolution of elaborate feather adornments including showy tails, bright plumage coloration, and crests in birds (Darwin 1871; Andersson 1994). Such elaborate ornamental traits may be favored during mate choice because of an arbitrary genetic linkage between trait and preference (Fisher 1958; Kirkpatrick 1982; Kirkpatrick and Ryan 1991), because they indicated health or viability (Hamilton and Zuk 1982; Andersson 1986), or because they exploited sensory biases of the chooser (Basolo 1990; Ryan 1990). In some cases, empirical evidence has not supported a sexually selected function for such feather ornaments. Some of the explanations for this include involvement of composite traits and hence inability to detect the weak preference (Johnstone 1996; Hagelin and Ligon 2001), secondary transformation of the original function (Ligon and Zwartjes 1995; Wiens 2001; Parker et al. 2005), and development and/or maintenance of the traits involved by selection pressures other than the sexual selection. However, other functions for elaborate feather traits are sometimes mentioned (e.g., camouflage and predator evasion: Baker and Parker 1979; individual identity: Whitfield 1987, Dale 2000; fertilization success: Birkhead and Møller 1992; aerodynamic performance: Rowe et al. 2001, Bro-Jørgensen et al. 2007; feeding apparatus: Jackson 2003; protective guard: Conover and Miller 1980). An additional, neglected, possibility is that elaborate feather appendages could serve a naturally selected sensory function either in flight (to aid in optimizing aerodynamic performance) or on the ground to facilitate obstacle avoidance in a complex environment.

Bird feathers are complex integument derivatives that perform a variety of functions (Lucas and Stettenheim 1972;

Spearman and Hardy 1985; Clark 2004). Filoplumes are hair-like feathers with a fine shaft and sparse barbules, which together transmit vibrations and pressure changes to sensory corpuscles (Stettenheim 1972; Gottschaldt 1985). These serve as mechanoreceptors within the plumage for aiding flight and general plumage maintenance (Lucas and Stettenheim 1972; Spearman and Hardy 1985; Brown and Fedde 1993; Clark 2004). Some filoplumes in Pelecaniformes (Childress and Bennun 2002), Procellariiformes (James 1986), and Passeriformes (Clark and Cruz 1989) visibly project beyond the surrounding contour feathers. Such elongated filoplumes in some passerines (oscines) may have a role in feather self-maintenance in parts of the plumage, which are not visible to the bird (Clark and Cruz 1989). Some filoplumes form ornate external structures that might have a role in display. For example, the elongated filoplume crest of the great cormorant (*Phalacrocorax carbo*) serves as a condition-dependent signal used in mate assessment (Childress and Bennun 2002) with untested sensory use. However, most feather ornaments are modified contour feathers, flight feathers, or rectrices (Andersson 1994). Bristles are another feather type, primarily found on the head, with numerous sensory receptors (Küster 1905; Schildmacher 1931; Lucas and Stettenheim 1972). Members of several unrelated avian families that are either nocturnal or crepuscular, breed in tree cavities, or feed on flying insects (e.g., Caprimulgidae, Mimidae, Capitonidae, and Tyrannidae) have facial bristles. Küster (1905) and Lucas and Stettenheim (1972) suggested that these feather structures could be used as tactile organs analogous to mammalian vibrissae to negotiate cluttered or low-light situations. However, this hypothesis has not been empirically tested (Lederer 1972; Conover and Miller 1980; Jackson 2003).

Auklets (family Alcidae, tribe Aethiini) include 5 socially monogamous sexually monomorphic seabird species (Gaston and Jones 1998), 4 of which display elaborate facial ornamentation during the breeding season including conspicuous white facial plumes (4 species) and curved forehead crests (2 species;

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Figure 1
Adult whiskered auklet showing the forehead crest and white facial feather ornaments.

Gaston and Jones 1998, Jones 1999). Experimental evidence indicated that crested auklet (*Aethia cristatella*) forehead crests are favored by both intra- and intersexual selection (Jones and Hunter 1993, 1999). Closely related, crestless least auklets (*Aethia pusilla*) have similar mating preferences for their white facial plume (Jones and Montgomerie 1992). Whiskered auklets (*Aethia pygmaea*) are by far the most ornate auklets (Gaston and Jones 1998), possessing a slender black forehead crest and 3 tracts of antenna-like silvery white elongated facial plumes, including superorbital plumes that extend above the eye over the crown from either side of the head, suborbital plumes that extend downward along the neck, and auricular plumes that extend from below the eye toward the neck (Gaston and Jones 1998; Pitocchelli et al. 2003; Figure 1). The white facial plumes are elongated filoplumes, whereas the forehead crest consists of elongated contour feathers (Konyukhov 2001). Whiskered auklets are socially active on land at their breeding colonies only at night, and most displays occur within rock crevices, hampering attempts to experimentally investigate ornament function. However, the display of whiskered auklet's crest and plumes during social activity (Hunter and Jones 1999; Zubakin and Konyukhov 1999) and their structural similarity to least and crested auklet ornaments have suggested that whiskered auklet's ornaments might be a similar product of mutual sexual selection (Jones 1999).

Here, we experimentally measured whiskered auklets' ability to avoid obstacles in the absence of visual clues in a darkened maze, which has similar conditions to their breeding crevices at night where the colony activity takes place, with and without the assistance of elongated facial plumes. Our objective was to test whether the elongated feather ornaments of whiskered auklet are used as a sensory device to avoid obstacles during their nocturnal underground navigation in the absence of visual clues. Exploratory behavior of the subjects was recorded under near-infrared illumination. We predicted that if whiskered auklets' plumage ornaments have a sensory role, the subjects would bump their head against the maze walls and roof more frequently when their crest and superorbital plumes were inactivated.

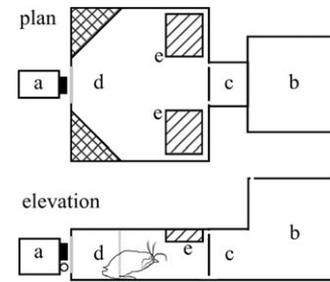


Figure 2
Setup of the whiskered auklet experimental maze with (a) digital camera with the light source, (b) test chamber, (c) entranceway to the test chamber, (d) holding pen, and (e) the barriers attached to the roof of the test chamber.

METHODS

Fieldwork that included capturing auklets, exposing to the test chamber, and taking measurements was undertaken at Buldir Island, western Aleutian Islands, Alaska, United States (52°22' N, 175°54' E), during May–July 2006. The experimental trials were conducted during the incubation phase of the whiskered auklet breeding season as the expression of feather ornaments declines later due to molt (Konyukhov 2001). Birds were captured using two 12 m mist nets at night (0030–0530 h, Aleutian standard time) similar to the method of Jones et al. (2007) from 6 locations in approximately 1 km long beach (north bight, Byrd and Day 1986). We believe that these nets captured birds more or less randomly from the colony (Jones et al. 2007). Captured birds were held temporarily in separate ventilated cloth bags for processing and exposed to a lighttight chamber (maze) to test their exploratory behavior under different treatment conditions.

Experimental setup—test maze

A 3-chambered wooden box simulating a natural breeding crevice of whiskered auklets was used as a maze (Figure 2) for testing birds' ability to avoid obstacles in the absence of visual clues. The maze consisted of 3 wooden chambers. The lightproof test chamber was 10 (height) × 35 × 30 cm with ventilation holes and 2 sidewalls to avoid birds moving away from the field of view of the camera. Two 2 × 8 × 8 cm wooden panels were attached to the roof as barriers, which the birds were required to avoid. The entranceway (10 × 10 × 10 cm) connected the 20 × 20 × 20 cm holding pen to the test chamber. The floor consisted of rough cardboard to allow birds to walk comfortably as in their natural crevices (Hunter et al. 2002). To avoid light penetration into the maze, both insides and outsides of the boxes were painted flat black, the entire maze was covered with a thick black cloth, and the experiment was carried out in darkness at night. A digital camcorder (Samsung SCD103) with built-in infrared light-emitting diode (peak wavelength = 880 nm, part number 0601-001626) recorded the subjects' behavior through a 7 × 4 cm opening in the front wall of the test chamber (Figure 2). We used the camcorder's "Nite pix" mode (Samsung owner's instructions) that allowed recording under near-infrared illumination with a greater sensitivity to the longer wavelengths (peak spectral sensitivity ~700–800 nm). Peak spectral sensitivity of birds in general falls between 350–600 nm (Hart 2001 and references therein). Even though specific information on auklet visual perception is lacking, the spectral sensitivity of both phylogenetically (gulls; Lieberman 1972) and ecologically (shearwaters and penguins; Bowmaker and Martin 1985; Bowmaker et al. 1997) closely related bird groups is restricted to this range

(Hart 2001 and references therein). Therefore, we assumed that the auklet vision was insensitive to infrared wavelengths emitted by the Samsung SCD103, and our subjects had no visual clues to navigate inside the maze. Due to their flexibility and narrow width (less than 1 mm), whiskered auklet crest and superorbital plumes did not produce enough pressure for us to consistently measure the number of touches using a trial remote detection system using touch or pressure detectors (field trials during June 2005). The alternate camera-based visual scoring system was portable and withstood severe weather conditions in the field. Therefore, we were able to increase our sample size and decrease overall stress for the birds by conducting the experiment in a permanent blind situated close to the breeding colony at night during the times of peak colony activity.

Treatment exposure procedure

Each bird ($n = 99$) was exposed to 3 treatments: ornament manipulation, control, and sham in a balanced random order. In the ornament manipulation treatment, the forehead crest and superorbital plumes were taped to the back of the head using 3 pieces of 8×2 mm black one-sided tape. The tape was attached to the nape of the subject causing these plume tracts to blend smoothly with the rest of the crown feathers. The forward-curving crest and the superorbital plumes are thin, highly flexible feather ornaments (Figure 1) that are bent and lay flat with the crown and facial feathers in flight and during underwater diving in the wild (Byrd and Williams 1993; Gaston and Jones 1998; and Seneviratne SS, Jones IL, personal observations). Because it mimics the natural movement for these feathers, our experimental manipulation (bending these extremely flexible feathers) was unlikely to cause unusual stress to the ornament or cause pain or irritation to the bird other than the distraction caused by the small pieces of tape attached. A sham treatment with tapes attached, as for the feather manipulative treatment, was introduced to the experimental design to test for the effect of stress. In the sham, the three 8×2 mm tape pieces were attached to the nape similar to the manipulative treatment but without altering the crest and superorbital plumes. The test bird was placed into the maze unmodified (no ornament alteration) in the control treatment. Following Zubakin and Konyukhov (1999), we observed birds' behavior in the colony throughout the breeding season using a dim red lithium electrode diode headlamp and the above camcorder with infrared light source. We considered only the crest and superorbital plumes for the manipulation as only those feather tracts extend above and to the sides of the head (Figure 1) and whose contacts with the maze walls and ceiling were clearly detectable (Figure 2). Preparation of the bird for each treatment took less than a minute, and each bird (99) was subjected to all the above treatments once, in a sequential (constrained random) order in all possible combinations, MCS, MSC, CMS, CSM, SMC, and SCM (with M = manipulation, C = control, S = sham), e.g., bird n_1 was exposed to MCS, n_2 to MSC, etc. Hence, 34 birds exposed initially to the control treatment, 33 to the plumage manipulation treatment, and 33 to the sham treatment. The order of the exposure of the subsequent treatments (second and third exposures, see above) was chosen in a constrained random order to reduce the carryover effect due to repeated exposure (Neter et al. 1996).

Birds were initially placed in the holding pen for several minutes to acclimatize and allowed to walk from the pen to the test chamber (Figure 2). When the bird entered the test chamber, its exploratory behavior was video recorded for approximately 2 min. After each exposure, the subject was removed from the maze, switched to the next treatment, and

immediately replaced into the holding pen for the next treatment recording. Digital video recordings were uploaded to a computer. The definitions of unambiguous "head bump," "crest contact," "superorbital plume contact," and "beak contact" were agreed between the authors prior to the counts. We did not count blindly to knowledge about the treatment because to count these effects the observer had to view the recordings, where the treatment manipulations were easily distinguishable. In the laboratory, S.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, superorbital plume contacts, and beak contacts (similar to the other counts) in a dark room using tally counters.

Ornament measurements

After the maze experiment, birds were marked with plastic leg bands to avoid retesting them in the event of recapture, and their crest and superorbital plumes were measured using metric dial calipers (to ± 0.02 mm). Crest was measured from the base of its feathers at the skull to the tip of the longest feather, with the feathers flattened and straightened. Superorbital plume length was measured on both sides of the head from the forwardmost point of origin of white plumes near the base of the bill to the tip of the longest plume, with the plumes straightened and parallel. Only adults were used for the experiment. Subadults were identified by extensive pale brown contour feathering on their forehead, chin, neck, and by similarly worn secondaries and greater coverts (Konyukhov 2001; Pitocchelli et al. 2003). All birds were released near the original capture site within 30–120 min after their initial capture. As part of other work on whiskered auklets at Buldir Island, we measured the feather ornaments (as above) and also mass (to ± 1 g), tarsus length, bill length, and depth (to ± 0.02 mm) from a large sample of birds captured each year during 1992–2006.

Ethical note

This study has been conducted under the approval of the Animal Care Committee of the Memorial University of Newfoundland (protocol number 06-13-IJ and 06-14-IJ). 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 strictly followed.

Analysis

We used Minitab Release 13.31 (Minitab Inc., State College, PA) and Statview (Caldarola et al. 1998). The cumulative effect of stress and the bird's habituation to the maze caused by repeated handling and exposure to different treatments were collectively tested using the order of treatment exposure, which was tested using general linear model as 2-way analysis of variance (ANOVA) by keeping both the treatment (M, C, S) and order of exposure (M-, -M-, -M; C-, -C-, -C; S-, -S-, -S) fixed (Sokal and Rohlf 1995). The order of exposure on the mean number of head bumps to the maze had no significant effect ($F_{2,8} = 3.52$, $P = 0.131$). However, because of the lower probability obtained, further analyses were performed to test the same effect in each of the 3 exposures separately using all 99 birds assigning randomly to the 9 possible combinations. Each bird was used once to represent one of the used treatments. One-way ANOVA (with Bonferroni correction) was used. None of the treatments showed significant effect on order of exposure on the frequency of head bumps. The frequency of head bumps for the manipulation was as follows: first exposure $3.31 (\pm 0.57 \text{ SEM})$, second exposure 3.17

(±1.00), and third exposure 2.17 (±0.58) ($F_{2,35} = 0.46$, $P = 0.634$). The frequencies of head bumps for the first, second, and third exposures of the control were 1.01 (±0.25), 0.86 (±0.25), and 0.76 (±0.19), respectively ($F_{2,31} = 0.29$, $P = 0.748$), and those for the sham were 1.60 (±0.38), 0.77 (±0.24), and 1.05 (±0.26), respectively ($F_{2,24} = 1.71$, $P = 0.202$). Hence, we assumed that the level of stress or habituation caused by repeated exposure and handling was not significant enough to alter the results. The frequency of head bumps, beak contacts, total contacts, crest contacts, and facial plumage contacts under different experimental treatments were compared using 2-way ANOVA—randomized blocks (Sokal and Rohlf 1995). Individual birds ($n = 99$) were the blocks hence treated as random, with the treatment fixed. Residuals were checked for normality, homogeneity, and independent errors. There was not any significant deviation of residuals from normality, and errors were homogenous and independent. Relationships between ornamental traits and contacts with the maze were tested using general linear model (regression, Sokal and Rohlf 1995). Statistical significance of all tests was reached at $\alpha = 0.05$.

RESULTS

Birds in the maze displayed similar exploratory behavior to what they show in their natural crevices in all 3 treatments. In the test maze, our subjects showed a significantly greater frequency of head bumps in the crest and facial plumes taped-down treatment than in the control and sham-manipulated treatments (2-way ANOVA; Tables 1 and 2) with more than double the frequency of head bumps (275%) in the absence

Table 1
Whiskered auklet’s ability to negotiate the experimental maze under different treatments

Variable	Mean	SEM	<i>n</i>
(a) Head bumps			
Manipulation	2.78	0.22	99
Control	1.01	0.12	99
Sham	0.86	0.08	98
(b) FO hits			
Manipulation ^a	—	—	—
Control	9.34	0.50	99
Sham	9.98	0.46	98
(c) Beak hits			
Manipulation	3.82	0.41	99
Control	2.73	0.32	99
Sham	2.43	0.28	98
(d) Total hits			
Manipulation	6.60	0.58	99
Control	13.07	0.79	99
Sham	13.42	0.63	98
(e) Manipulation			
Head bumps	3.07	0.28	32
(f) Control			
Crest hits	7.74	0.70	33
SOP hits	1.50	0.28	33
Total FO hits	9.24	0.78	33
Beak hits	3.17	0.66	33
Total hits	13.56	1.43	33

(a)–(d): All 3 exposures (first, second, and third) combined; birds’ first exposure to the maze (e) in plumage manipulation treatment and (f) in control treatment (unmanipulated ornaments). SEM, standard error of mean; FO hits, total feather ornament hits with the maze; SOP hits, superorbital plume hits with the maze.

^a The expression of feather ornaments was cancelled in manipulation (see Methods).

Table 2
Comparison of the effect of different treatment exposures and the correlation of feather ornament length with body size

Variable	<i>F</i>	df	<i>p</i>	<i>R</i> ²
Head bumps under plumage manipulation	63.21	2,196	<0.001	
Head bumps between control and sham	1.14	1,98	0.288	
Ornament contacts between control and sham	2.04	1,98	0.156	
Ornament contacts in plumage manipulation	142.14	2,196	<0.0001	
Beak contacts under plumage manipulation	7.62	2,196	0.001	
Correlation with natural crest length				
Head bumps under plumage manipulation	4.45	1,30	0.043	0.13
Natural superorbital plume length	67.35	1,96	0.0000	0.41
Ornament contacts under control exposure	1.12	1,31	0.298	0.04
Superorbital plume contacts	1.63	1,31	0.212	0.05
Beak contacts	0.35	1,31	0.559	0.01
Total contacts	0.81	1,31	0.375	0.03
Correlation with natural superorbital plume length				
Head bumps	3.50	1,30	0.071	0.10
Crest contacts	0.05	1,31	0.824	0.00
Ornament contacts	1.31	1,31	0.261	0.04
Beak contacts	0.05	1,31	0.831	0.00
Total contacts	0.18	1,31	0.677	0.01
Correlation with body size ^{a,b}				
Crest length	27.41	1,309	<0.0001	0.08
Superorbital plume length	27.95	1,300	<0.0001	0.08

Two-way ANOVA-randomized blocks, 1-way ANOVA (with Bonferroni correction), and general linear modal (regression) were used for the analysis (see text).

^a PCI of tarsus length, bill length, and body mass.

^b These birds were not exposed to the maze and were captured at the same location in multiple years (see text).

of the protruding feather traits (Figure 3). The difference in mean frequency of head bumps and feather ornament contacts between control and sham treatments did not significantly differ (Tables 1 and 2; Figure 3) suggesting that stress caused by attached tape did not cause these birds to bump into maze walls more often than unaltered birds. The

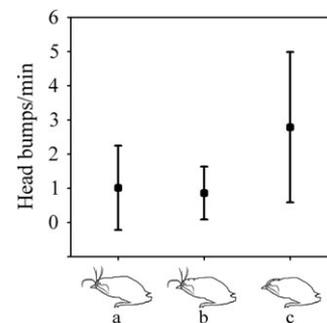


Figure 3
The success of whiskered auklets negotiating the maze ($n = 99$) with (a) unmodified ornaments (control), (b) sham manipulation, and (c) taped-down feather ornaments. The filled center squares indicate the mean frequency of head bumps (±SD).

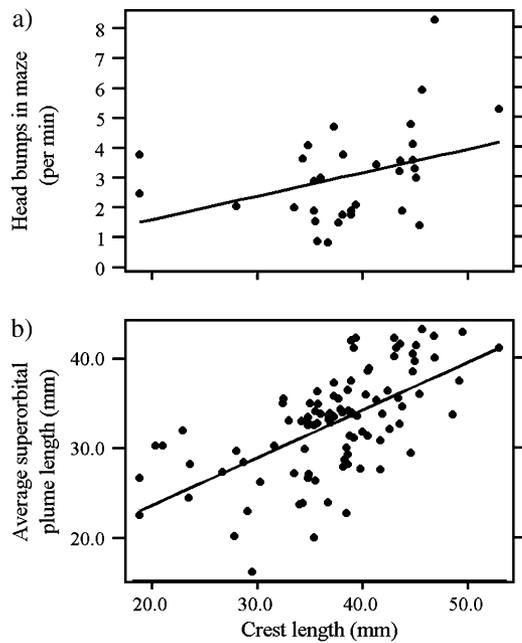


Figure 4
(a) Relationship between individual whiskered auklets' natural forehead crest length and frequency of head bumps within the darkened maze when the crest was taped down ($n = 33$) and (b) the correlation between crest length and mean superorbital plume length ($n = 98$).

frequency of contact of feather ornaments with the ceiling and walls of the maze was high in the control and sham birds (Table 1) and showed a significant reduction in frequency to near zero due to plumage manipulation (Table 2; Figure 3). For birds' first exposure to the maze ($n = 33$); we detected a positive relationship between natural crest length (mean crest length = $38.72 [\pm 7.32 \text{ standard deviation (SD)}]$ mm) and the frequency of head bumps in the manipulative treatment (Tables 1 and 2; Figure 4a), suggesting that birds with longer ornaments had greater difficulty navigating under the plumage manipulation. Birds with longer forehead crests also had longer superorbital plumes (mean average superorbital plume length = $32.75 [\pm 5.85 \text{ SD}]$ mm; Table 2; Figure 4b). However, there were no significant relationships between frequency of feather ornament (crest and superorbital plumes) contacts, superorbital plume contacts considered separately, beak contacts, or total contacts (head bumps, crest and superorbital plume contacts) and crest length (Tables 1 and 2). Similarly head bumps, all feather ornament contacts, crest contacts considered alone, beak contacts, and total contacts showed no significant relationship with superorbital plume length (Tables 1 and 2). A greater number of beak contacts were observed under ornament manipulation (2-way ANOVA, Tables 1 and 2), but it was difficult to differentiate the difference between beak contacts from test subject's occasional deliberate pecking of the maze walls. Among a large sample of birds captured and measured near the experimental study site, crest length (mean crest length = $36.50 [\pm 6.54 \text{ SD}]$ mm) and superorbital plume lengths (mean average superorbital plume length = $31.43 [\pm 6.32 \text{ SD}]$ mm) were both positively correlated with body size (Table 2).

DISCUSSION

Here, we demonstrated that whiskered auklets' crest and superorbital plumes in combination helped individuals detect

obstacles inside an experimental maze simulating their dark, complex, underground breeding crevices. With their protruding facial plumes and crest intact, whiskered auklets were able to navigate in the absence of visible light with fewer head bumps with the maze walls and roof. At their breeding colonies, adult whiskered auklets enter, navigate, and nest in narrow rock crevices in cliffs, lava flows, and talus at night—labyrinthine conditions with sharp irregular obstacles and low or total absence of visible light that were simulated inside the maze. The results of our experiment thus suggest that whiskered auklets use their ornamental facial feathering to aid their underground navigation. Auklet breeding colony sites often include an interlinked network of crevices used by multiple individuals (both conspecifics and other seabird species; Byrd and Williams 1993). Hence, the sensory function of elaborate feathers might further aid in close range detection of these individuals within the confines of their crevices. One interesting finding was that birds with well-expressed (longer) crest and facial plumes may have benefited more from these sensory structures as they showed greater dependence on them in the maze (Figure 4a,b). This may be partly explained by the positive correlation between body size and ornament expression (i.e., large-ornamented birds were simply bigger in overall size so they likely experienced a tighter squeeze in crevices). Nevertheless, it does raise the question of how variability in expression of the elaborate facial plumes and crest might relate to their use for navigation. Compared with adults, juvenile and subadult whiskered auklets have no or shorter protruding ornaments and less frequently enter crevices (Jones 1999; Zubakin and Konyukhov 1999; Pitocchelli et al. 2003; Seneviratne SS, Jones IL, personal observations).

Testing for sensory use of feathers in the field was a difficult proposition, but we judged the maze to be the best preliminary approach to answering this question. Further work could address the question of the relative role of the forehead crest versus the white superorbital plumes. We were unable to investigate this here but because the crest is composed of contour feathers whereas the superorbital plumes are filoplumes, one might expect to find a difference in sensitivity (Clark 2004). However, Brown and Fedde (1993) experimentally showed a sensory role for secondary flight feathers that are contour feathers used for flight—indicating that contour feathers can also have a sensory use. Because of the position of whiskered auklets' forehead crest, it seems well placed to take on the most crucial role in detecting low overhead obstructions (Figure 1). Carefully designed studies to investigate extensive innervation or aggregation of mechanoreceptors on or near these feather tracts are urgently required to reveal the anatomical and physiological basis for the observed behavior. Nevertheless, our results suggest to us a broader than recognized role for contour feathers in touch sensing and highlight a sensory use as a plausible explanation for other birds' "ornamental" contour feather appendages. Other types of avian feather traits that deserve attention include swallow tail streamers (e.g., Rowe et al. 2001), quail crests (e.g., Hagelin and Ligon 2001; Parker et al. 2005), and other auklet species' feather ornaments (Gaston and Jones 1998; Jones 1999).

Whiskered auklets are the most nocturnally active crevice-dwelling auklets that display the most elongate antenna-like crest and facial plumes (Jones 1999). Their breeding habitats (mostly piles of small rock and boulder beaches) are unstable due to wave action, soil and wind erosion, and frequent earthquakes; therefore, the internal dimensions of breeding crevices can change unpredictably. Furthermore, whiskered auklets are the only *Aethia* auklet that regularly roost on land at night during the nonbreeding season and coincidentally the only auklet whose elaborate facial ornaments (especially

the crest) are expressed during winter, consistent with a year round sensory function. The mostly diurnal crested auklet also frequents and breeds in deep dark rock crevices and is the only other auklet species possessing a forehead crest (Jones and Hunter 1993, 1999). The other diurnal auklets, least and parakeet (*Aethia psittacula*), nest in shallow well-lit crevices, have no forehead crest, and have short facial plumes (Gaston and Jones 1998; Jones and Hunter 1998; Jones 1999). The remaining auklet species, Cassin's auklet (*Ptychoramphus aleuticus*, no facial plumes) is nocturnal but breeds in relatively stable habitats and uses self-excavated earthen burrows for breeding (Thoresen 1964) that have predictable internal dimensions and are more likely to have smooth internal surfaces of soft earth. Hence, we believe that Cassin's auklets face much less of a challenge to their underground movements and activities compared with the crevice dwellers. These comparative suggestions further favors the notion that mechanosensory function might in part explain the elongated facial feather ornaments of whiskered auklets.

The feather ornaments of both least and crested auklets (homologous to those of whiskered auklets) are favored by mutual mating preferences (Jones and Montgomerie 1992; Jones and Hunter 1993, 1999; Jones 1999). Although experimental evidence is lacking, whiskered auklet ornamentation may be favored by similar mating preferences because this species displays similar ornaments during courtship and social activity (Jones 1999; Hunter and Jones 1999; Zubakin and Konyukhov 1999). Furthermore, these ornaments show the same high variability exhibited by those of other auklet species (Jones and Montgomerie 1992; Byrd and Williams 1993; Jones et al. 2000) and as is known for sexually selected traits in general (Alatalo et al. 1988). Taken together, these indirect evidences point to multiple factors (both sexual and natural selection) having roles in the origin of auklet facial ornamentation, although we cannot conclude which had the greater role in whiskered auklet ornament evolution. However, once protruding feathers evolved, sexual selection could explain the elaboration of traits in species with intense face-to-face courtship displays (Jones and Montgomerie 1992; Jones and Hunter 1993, 1999; Andersson 1994).

To our knowledge, we have described the first empirical evidence for a possibly widespread but overlooked sensory function of elaborate feather ornaments in birds. Similar traits, such as streamers on pin and forked tails, elongated facial plumes, and projecting feathers on the wings and body, that are routinely inferred to function primarily as optical signals during courtship (Darwin 1871; Kirkpatrick and Ryan 1991; Andersson 1994; Amundsen 2000) are all possible candidates for past and present sensory function. Indeed, future comparative and phylogenetic analyses of such trait expressions will likely reveal the role of sensory function as either a precursor for feather ornaments or a selective force that maintains such embellished traits in birds.

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