

Heterospecific mating preferences for a feather ornament in least auklets

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Auklets (Alcidae, Aethiini) include five species of small, socially monogamous, sexually monomorphic seabirds that display a variety of feather and bare-part ornaments during the breeding season. Previous experimental work on two auklet species has demonstrated that some ornaments are likely to be favored by sexual selection because mutual male and female mating preferences benefit individuals with the most elaborate expression of these traits. In this study we experimentally investigated whether naturally crestless least auklets *Aethia pusilla* have a mating preference for forehead crests similar to the most prominent ornament of two other species, crested *A. cristatella* and whiskered auklets *A. pygmaea*. Our objective was to investigate the function of this ornament as a species-recognition mechanism or as a product of one or more of three proposed sexual selection models that address the origin of elaborate traits and preferences. During the experiment, least auklets reacted to realistic models equipped with artificial forehead crests with approximately an order of magnitude more frequent sexual displays and greater interest, consistent with the idea that they have a mating preference for crests, even though they do not naturally express this ornament. This heterospecific preference also favored large crest size. These results refute the possibility that least auklet forehead ornamentation alone determines species recognition at present. Among models of sexual selection considered, the results are consistent with the sensory exploitation model, although this could not be established unequivocally because a viability indicator or Fisherian mechanism could have been involved if least auklets had an ancestor with a forehead crest. **Key words:** *Aethia pusilla*, Alcinae, auklet, feather ornament, Fisherian runaway, mate choice, sensory exploitation, sexual selection, species recognition, viability indicator. [*Behav Ecol* 9:187–192 (1998)]

There is considerable evidence that the elaborate ornamental traits of many animals have evolved through intersexual selection resulting from mating preferences that benefit ornamented individuals (Andersson, 1994). However, determining the origin of mating preferences for these ornamental traits has been fraught with difficulty because of problems with discriminating among a variety of possible mechanisms (Balmford and Read, 1991; Johnstone, 1995; Lotem, 1995). However, recent observations that some animals have mating preferences for display traits of other species, which are not expressed naturally in their own species, have had a profound impact on development of sexual selection theory (Johnstone, 1995; Shaw, 1995).

A debate continues to focus on three evolutionary mechanisms that address the origin of elaborate display traits: (1) a Fisherian runaway process driven by a genetic linkage between an ornamental trait (usually of males) and a mating preference for the ornament (usually by females; Fisher, 1930; Kirkpatrick, 1982; Lande, 1980, 1981); (2) a viability indicator (also commonly known as a "good genes," or "handicap" process) driven by direct or indirect selection on mating preferences (e.g., Andersson, 1986; Kirkpatrick and Ryan, 1991; Pomiankowski, 1988); and (3) sexual selection for sensory exploitation (Ryan, 1990; Ryan and Rand, 1993), in which a mating preference arises due to natural selection for sensory biases unrelated to mate choice; then later, mutation results in a display trait that can "exploit" the preexisting sensory biases, and subsequently, the trait is favored by intersexual selection driven by the mating preference that results from the sensory biases. Additional explanations related to sexual selection are also often considered, as in some cases the requirement for individual or species recognition signals could

lead to the evolution of elaborate signals or displays through intersexual selection.

Testing mechanisms of sexual selection with intraspecific studies has been difficult because each mechanism can accommodate many of the predictions of the others, and several may have operated at once or in sequence to produce the ornaments we see expressed. Furthermore, the degree to which the mechanisms address historical origin versus present-day maintenance of display traits and preferences is controversial. Table 1 summarizes some predictions of the different mechanisms in the case of a hypothetical species with a conspicuous ornamental trait that has no use outside of social signal function.

Mating preferences often focus on the expression of ornamental traits that correlate with health or viability (summarized by Andersson, 1994), consistent with viability indicator mechanism, in which mating preferences are initially favored because they confer benefits to choosers. In contrast, under the Fisherian runaway mechanism, mating preferences may also spread for arbitrary or even deleterious traits that confer no benefits to choosers outside of sexual selection (Kirkpatrick, 1982). Nevertheless, intraspecific field experiments and comparative approaches have been largely unsuccessful in discriminating between these two models because they have similar outcomes (Balmford and Read, 1991; Johnstone, 1995; Jones, 1992; Kirkpatrick and Ryan, 1991; Read, 1990; but see Balmford et al., 1993). Both Fisherian runaway and viability indicator processes may lead to the evolution of elaborate and costly ornaments that will thus be best expressed in the healthiest or highest quality individuals in a population. Furthermore, costly traits that have become elaborated by sexual selection for sensory exploitation (Ryan, 1985), or as species or individual recognition signals, could also correlate with viability (Table 1). Thus, although a correlation between health or viability and a preferred ornament suggests that the orna-

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Table 1

Some predictions of sexual selection mechanisms for the origin of mating preferences for elaborate ornamental social signal traits, with the simplifying assumption that reduction or disappearance of ornaments has not occurred subsequent to their original evolution

Observation	Consistent with				
	Fisherian runaway?	Viability indicator?	Sensory bias?	Species recognition?	Individual recognition?
Elaborate ornaments correlate with health and viability	Yes	Yes	Yes	Yes	Yes
Arbitrary ornaments with no apparent benefit outside of recognition	Yes	No	Yes	Yes	Yes
Greater response to ornaments of own species than to ornaments of other species	Yes	Yes	Yes	Yes	Yes
Mating preferences for ornamental traits of other species not expressed by own species	No	No	Yes	No	No

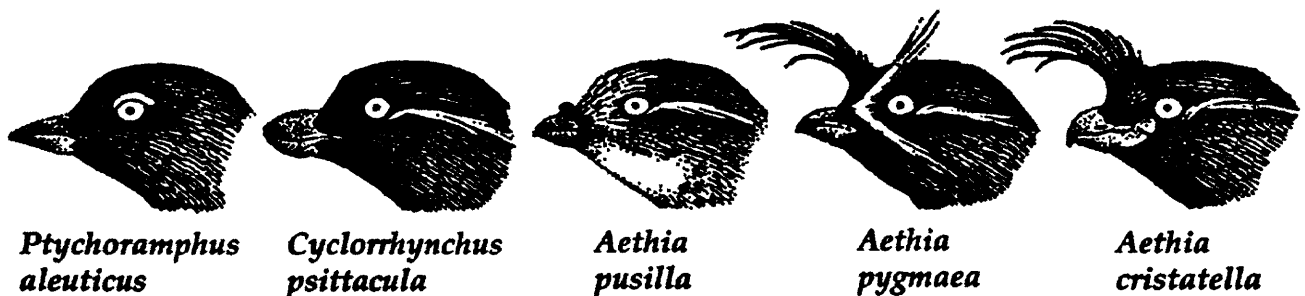
ments may serve as a viability indicator at present, this correlation reveals little about the original evolution of the ornament and the preference. Mating preferences for arbitrary ornaments that are cheap to produce and maintain and that do not reflect individual quality would also be compatible with all mechanisms, with the exception of the viability indicator model (Table 1b, but see below). The observation that individuals' mating preferences favor ornaments of their own species is compatible with all models, but is the main theme of the species recognition hypothesis (Table 1).

Sometimes individuals exhibit mating preferences for ornamental or display traits of other species that are lacking in their own species (heterospecific mating preferences; e.g., Basolo, 1990; Ryan and Wagner, 1987; Ryan et al., 1990), or exhibit preferences for completely novel traits (Burley, 1986). The sensory exploitation or sensory bias mechanism may be most consistent with some of these observations because it predicts preexisting mating preferences that pre-date the evolution of the ornament (Table 1; Basolo, 1990; Ryan, 1990; Ryan and Rand, 1993). The sensory exploitation mechanism thus predicts mating preferences for signal traits expressed by some species in a clade even in some other species that have ancestrally lacked the signal trait. However, conclusive tests of sensory exploitation may require unambiguous phylogenetic data, which may be difficult to obtain (e.g., Meyer et al., 1994; Shaw, 1995). Furthermore, Lotem (1995) has suggested that tests of sensory exploitation based on parsimony arguments for reconstructed ancestral character states of ornaments and preferences may be equivocal. Heterospecific mating preferences could be accommodated by the viability indicator mechanism if the preference and ornament originally evolved together by one or both of these mechanisms but subsequently the ornament was lost due to high natural selection costs, for

example, while the preference remains as a historical artifact (Hill, 1994; Lotem, 1995). Similarly, currently arbitrary ornamental traits could be phenotypic relics previously evolved by the viability indicator mechanism but subsequently reduced in expression.

In summary, intraspecific tests provide limited opportunities to discriminate among sexual selection mechanisms, but two possibilities are provided by the suggestions that (1) mating preferences for arbitrary ornamental traits rule out the possibility that preferences are currently maintained because they serve as viability indicators, and (2) mating preferences for ornaments of other species are inconsistent with the ornament serving for individual or species recognition but are consistent with sexual selection for sensory exploitation. Nevertheless, few studies have investigated heterospecific ornamental preferences, particularly among birds.

Auklets (subfamily Alcinae, tribe Aethiini) include five small, socially monogamous, sexually monomorphic seabird species. Male and female auklets display identical (i.e., sexually monomorphic) ornaments during the breeding season only. Least auklets (*Aethia pusilla*) display red bills, white facial plumes, and a knoblike bill ornament (Figure 1; Jones, 1993b; Jones and Montgomerie, 1992). Two closely related species, whiskered (*A. pygmaea*) and crested auklets (*A. cristatella*), have similar conspicuous sexually monomorphic forehead crests composed of black, forward-curving feathers (Figure 1), a distinctive ornamental trait unlike any expressed by other auklet species. Because of the great similarity of this ornament between these two species and because of its unique and distinctive structure, we assume that whiskered and crested auklet crests are homologous and similar by descent. Despite a number of attempts using different approaches (Friesen et al., 1996; Moum et al., 1994; Strauch, 1985), the phy-

**Figure 1**

Facial ornaments displayed by auklets (Aethiini, Alcinae) during the breeding season. Among the Alcidae, only crested and whiskered auklets display the distinctive forehead crest ornament, which is composed of stiff, forward-curving feathers.

logeny of the auklets has not been completely resolved. However, the Aethiini are a monophyletic group (Friesen et al., 1996; Moum et al., 1994; Strauch, 1985). Based on molecular data (Stanley H and Friesen V, unpublished data), and because they share three unique morphological traits (citrus plumage odor, pure tone vocalizations, and similar overall dark plumage, Jones IL, personal observation) in addition to their crests, whiskered and crested auklets are likely the most closely related sister species (based on parsimony; Maddison et al., 1984) and lack of a forehead crest ornament is the most probable ancestral character state for their ancestors throughout the Aethiini and Alcinae.

Auklet courtship and mate choice take place on the rocky surface of colony sites before laying (by pairs breeding in the same year) and throughout the remainder of the breeding season (pair and extrapair courtship for breeding in subsequent years; Jones, 1993b; Jones and Montgomerie, 1991). The ornaments are displayed during courtship encounters, and mate choice follows from the performance of sexual displays by both members of courting pairs (Jones, 1993b). Because both male and female auklets invest heavily in offspring, there is intense competition within each sex for qualified partners. Both male and female auklets approach unknown individuals of their own species, perform sexual displays, and exercise mate choice behavior, providing the opportunity for mutual sexual selection (Jones and Hunter, 1993). Previous experiments have confirmed that the facial plumes and bill coloration of the least auklet and the forehead crest of the crested auklet are favored by mating preferences (Jones and Hunter, 1993; Jones and Montgomerie, 1992). However, Jones and Montgomerie (1992) found little evidence that least auklet ornaments correlate with measures of individual quality, casting doubt on the possibility that a viability indicator mechanism is currently maintaining their ornaments.

The objectives of our study were to (1) experimentally determine whether naturally crestless least auklets have a hetero-specific mating preference for the crest ornament expressed by two other auklet species, (2) determine whether the preference favors larger crests over smaller crests, (3) determine whether the preference focuses on the auklet crest ornament *per se* or on a similar novel ornament, and (4) assess the results of the experiments in relation to possible mechanisms for the evolution of mating preferences and ornaments through intersexual selection.

METHODS

To test whether least auklets possess a mating preference for the auklet crest, we performed a manipulation experiment using seven realistic models made from the skins of adult least auklets of average appearance collected at the colony (Jones and Montgomerie, 1992). The models were constructed to be as similar as possible, but were not identical and differed slightly in natural ornament expression and posture. Least auklets approach this type of model as in natural encounters and perform four types of courtship display (Jones, 1993b; Jones and Montgomerie, 1992). By placing artificial crest ornaments on least auklet models rather than on live birds, we controlled for two factors that could confound a mate choice experiment: intrasexual competition (Savalli, 1989), and behavioral changes in a manipulated live bird (Balmford and Thomas, 1992; Barnard, 1990). Because we measured the response of least auklets to models in controlled situations, we were able to exclude circumstances when intrasexual interactions were likely to affect individuals' responses to the ornaments (i.e., when more than one bird was present within 2 m of the model). Because our ornament manipulations were made on immobile dummies, we were also able to exclude

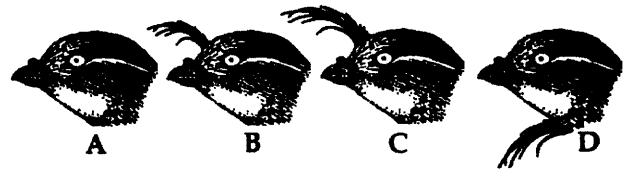


Figure 2

Experimental ornament manipulations: (A) natural appearance, (B) 15-mm forehead crests, (C) 25-mm forehead crest, (D) 25-mm breast crest.

the possibility that the response to the manipulation was due to a change in behavior of the manipulated bird. Like most diving birds, living auklets respond poorly to artificial ornaments attached to their bodies, preening the affected area until the ornament is lost or damaged (Jones IL, personal observation). Our experimental approach was based on the assumption that an increased frequency of sexual displays toward a manipulated model is indicative of a mating preference for that model's phenotype.

To examine whether a mating preference favors larger crest size, we compared the attractiveness of the least auklets' natural crestless appearance to that with 15-mm and 25-mm long artificial crests on the forehead (forehead crests; Figure 2b,c). To examine whether a preference acts specifically on *Aethia* forehead crests, or alternatively on a similar novel ornament, we also presented the same 25 mm artificial crests attached conspicuously to the center of the breast (breast crests; Figure 2d). The breast is a focus of attention because least auklets display to one another face to face with their foreparts clearly visible, and breast plumage color correlates with dominance status (Jones, 1990). We made each of the artificial crests using 12 natural crest shaft feathers obtained from crested auklets, held together at their bases by two 5×5 mm square pieces of fiberglass tape, to simulate as closely as possible the appearance of the natural ornament. We chose 15-mm and 25-mm crests because this approximated the natural range of common proportions of crest size to head length in crested and whiskered auklets. The artificial crests were temporarily attached to the forehead by securing the tape with super glue under the contour feathers at the same location as the base of natural crests. We did not perform sham manipulations because the artificial crests could not affect model "behavior" and because there were no visible artifacts of manipulation.

Presentations were made at 30 different display rocks (large boulders with 2–12 m² flat upper surfaces, where auklets congregate to engage in courtship) at Main Talus, Buldir Island, Alaska, USA (Byrd and Day, 1984), a large mixed auklet colony of about 100,000 least, 200,000 crested, and 10,000 whiskered and parakeet auklets. Model presentations were made daily (excluding periods of inclement weather) between 11 June and 15 July 1992 (models 1–3) and 24 June and 15 July 1993 (models 1–7). Observer bias was controlled for by selecting unambiguous displays for scoring (Jones, 1993b), by simultaneous observation trials to maximize observer consistency, and by assigning models and treatments randomly between us so that any scoring differences between us could add noise to the data but could not affect the outcome of the experiments. As far as we could tell, response scoring was identical between us. To control for seasonal effects, whenever possible each model was switched from one treatment to the next after each day of observations, except when fewer than 10 approaches were observed, so the mean presentation date was similar for each model and each treatment. For one of the seven models (model 1), we inadvertently did not score any responses to the 15-mm crest treatment.

For each auklet that responded to a model, we identified

its sex by behavior when possible (Jones, 1993b) and recorded the occurrence of sexual displays (arch, hunch, chatter, touch; see Jones, 1993b, for a detailed description of least auklet displays), their closest approach (0 cm, 1–10 cm, 11–20 cm, 21–30 cm, or >30 cm), and response duration (1–5 s, 6–10 s, 11–15 s or >15 s). We also recorded aggressive responses by least auklets to the models (peck, lunge), and the occurrence of crested auklet approaches to the models. Previous work showed that least auklets responded to models as if they were live birds for at least the first 15 s after noticing the model (Jones and Montgomerie, 1992; Jones and Hunter, 1993). To reduce to an insignificant level the chance that an individual's response was scored more than once, models were moved frequently among display rocks throughout the immense colony of about 100,000 auklets at Buldir. We believe that no individual's response was scored more than once, and this was confirmed by model presentations at a study area with more than 100 color-marked individuals where no bird responded more than once.

Least auklets are sexually indistinguishable morphologically, although individual males frequently reveal their gender by performing sex-specific displays (Jones, 1993b, see Burley, 1981, for an explanation of sexual indistinguishability). Female least auklets rarely reveal their gender except in a distinctive crouched submissive display performed toward (usually displaying) males (Jones, 1993b). At the colony, both male and female auklets perform courtship displays to individuals of unknown sex as part of the mate choice process (Jones and Montgomerie, 1992), providing the opportunity for mutual sexual selection by which male and female preferences focus on the same ornamental traits (Johnstone, in press; Johnstone et al., 1996; Jones and Hunter, 1993). We used the skins of male auklets for the models because we wanted to present as standardized a stimulus as possible. However, it should be noted that (1) the sexes are identical in every measurable aspect of appearance except bill depth (mean difference in depth, 0.3 mm; the model's bill depths were in the broad zone of overlap between the sexes), and (2) the construction of dummies from the auklet skins was likely to obscure any subtle, unknown differences in shape, posture, etc., between the sexes. We believe the birds were responding as if to a live least auklet of unknown sex. Based on earlier work at a colony with a large marked population, individually marked least auklet males and females were equally likely to approach and respond to this type of model (Jones and Montgomerie, 1992).

RESULTS

Least auklets were strongly attracted to models with forehead crests and showed less response to models without a crest (Figure 3). Overall, 23% of 1292 approaching adults performed a sexual display. Total responses scored for each model (and to the plain, big crest, small crest, and breast-crest treatments) were: model 1, 274 (113, 96, 0, 65); model 2, 344 (132, 121, 20, 71); model 3, 246 (108, 35, 9, 94); model 4, 94 (21, 27, 30, 16); model 5, 100 (35, 26, 17, 22); model 6, 120 (27, 25, 25, 43); model 7, 114 (41, 17, 20, 36). To simplify the analysis, we collapsed the data into a single frequency datum for each model for each treatment for (1) the performance of one or more sexual displays, (2) approaches closer than 10 cm, (3) approaches for longer than 10 s, and (4) the performance of one or more aggressive behaviors (including pecks, lunges, or outright attacks directed at the model (Figure 3). Least auklets' sexual display response to the models differed significantly among the four treatments (ANOVA, $F_{3,25} = 42.9$, $p < .0001$). Approaching birds responded to models with 15-mm and 25-mm forehead crests with significantly more frequent sexual displays compared to models presented with no crest

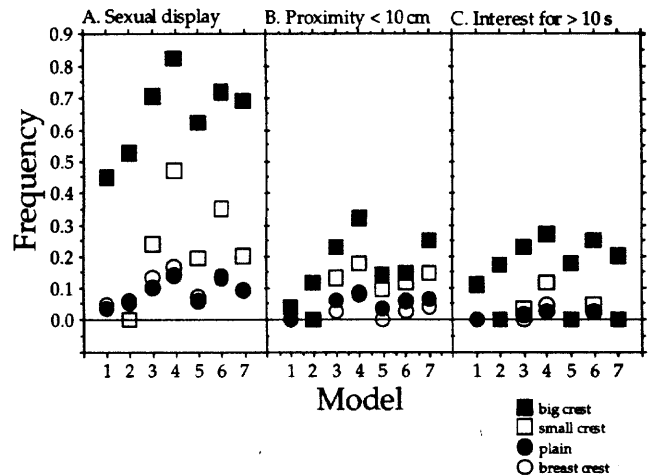


Figure 3

Responses of 1292 least auklets to seven models with manipulated ornaments, as indicated by the frequency of (A) sexual display, (B) approaches closer than 10 cm, and (C) approaches with interest for greater than 10 s. Sample sizes of responses scored: model 1, 274; model 2, 344; model 3, 246; model 4, 94; model 5, 100; model 6, 120; model 7, 114.

(Fisher PLSD post hoc comparisons, $p = .03$ and $p < .0001$ respectively), and sexual displays were significantly more frequent towards the 25-mm crest models compared to the 15-mm crest models (Fisher PLSD, $p < .0001$; Figure 3). These displays are performed only during courtship and thus indicate sexual attraction rather than simple curiosity or aggression (Jones, 1993b). The models with forehead crests were also approached more closely than models without crests and with breast crests ($F_{3,18} = 9.1$, $p = .0003$; for 25-mm versus no crest, Fisher PLSD, $p = .0004$, for 25-mm versus breast crest, Fisher PLSD $p < .0001$). Similarly, approaching individuals' response duration differed significantly among treatments ($F_{3,25} = 43.7$, $p < .0001$; for 25-mm versus no crest, 25-mm versus breast crest, 25-mm versus 15-mm crest, Fisher PLSDs, $p < .0001$). There was no difference in any response between models with breast crests and models without crests (Figure 3; Fisher PLSD, $p > .3$). There was no difference in the frequency of aggressive acts (pecks, lunges, attacks) toward models among the different treatments ($F_{3,24} = 0.3$, $p = .7$), but few such acts were recorded (only 16/1292 responding birds behaved aggressively).

Seventy-nine (6%) of the auklets that responded were of known sex, either because they were color-marked individuals of known sex or because they exhibited sex-specific behavior (usually males) while under observation (Jones, 1993b). Of the birds of known sex that approached the models, 72 were males and 7 were females. In our experiments, males were significantly more likely to perform sexual displays to forehead-crest models compared to crestless models. Female responses were qualitatively similar ($n = 7$), but the small sample of known-sex birds that approached models makes it impossible to quantitatively investigate sexual differences in response to the ornaments. In similar experiments on crested auklets, in which the sexes are easily distinguishable in the field (Jones, 1993c), both sexes showed a preference for longer crests (based on similar sexual displays; Jones and Hunter, 1993).

Occasionally, crested auklets responded to the least auklet models, although they did not attempt courtship or perform sexual displays. Crested auklets approached the models with forehead crests (47/515, or 9.1%, of approaching auklets were crested auklets) more frequently than models of natural

crestless appearance (12/490, or 2.5%, were crested auklets; $\chi^2 = 20.3$, $df = 1$, $p < .0001$).

DISCUSSION

Our experimental manipulations of least auklet models resulted in a startling increase in the frequency of sexual displays by least auklets toward individuals displaying a crest ornament similar or identical to the most conspicuous ornament of crested and whiskered auklets. We interpret these data as evidence that least auklets have a mating preference that would favor individuals possessing a crest ornament in nature. Similar evidence has been used to infer mating preferences in other studies of birds and other vertebrates (Andersson, 1994). Because a greater frequency of least auklet sexual displays was directed toward the larger crest treatment compared with the smaller crest treatment, this mating preference would likely favor individuals with the largest crests. These experimental results are similar to those for crested auklets which showed preferences for their naturally occurring crests (Jones and Hunter, 1993). Our observation that crested auklets were more likely to inspect least auklet models with crests is consistent with the manipulated ornament eliciting responses in a similar way to a naturally occurring crest ornament. Least auklets showed no response to the artificial ornament placed on the breast of the models, indicating that the mating preference may be specific to the forehead crest. Further experiments would be necessary to determine whether least auklets have mating preferences for a crest ornament located on other parts of the body, or for completely novel ornaments such as investigated by Burley (1986) for zebra finches. Nevertheless, there would appear to be a strong opportunity for intersexual selection to favor a crest ornament in least auklets.

Given that least auklets have a crest preference, it would also be useful to know why this species lacks the ornament. At present, least auklets show no morphological variation in the feathers of their foreheads that in any way resembles the crest ornament of the other species. However, considering hypothetical evolutionary histories for this ornamental trait may be helpful. Two possible histories of this ornament in least auklets are (1) least auklets are descended from a crested ancestor and the crest was lost at some point, before the present day, or (2) no least auklet ancestor ever possessed the crest ornament, the more parsimonious explanation if the crest evolved in the immediate ancestor of the (apparently sister species) crested and whiskered auklets. If least auklet ancestors possessed crests, then its disappearance could be explained by natural selection costs. If least auklets never had crests, then either there has never been suitable genetic variation for sexual selection to operate on to produce an elaborated crest (the evolutionary lag scenario), or the evolution of a crest has been suppressed by natural selection costs of bearing the ornament that are unique to least auklets. Furthermore, if no least auklet ancestor possessed a crest, then the mating preference for crests could not have evolved by the viability indicator or Fisherian runaway mechanisms because these depend on the simultaneous evolution of ornament and preference and cannot explain the existence of a fully developed mating preference in the absence of the related ornament.

Our opportunities for testing these possibilities using the comparative method are limited because of the small number of auk species and the related uncertainty of ancestral character states of the crest ornament. However, we can at least conclude that a viability indicator process is not currently maintaining least auklets' preference for crests that are at present arbitrary with respect to direct or indirect benefits. If such mating preferences for heterospecific or novel ornaments and display traits are common in nature, then this

could cast doubt on the generalization that mating preferences have evolved in response to benefits to choosers. However, there have been relatively few experimental studies looking for heterospecific or novel mating preferences.

Our experiment has shown that least auklets exhibit a mating preference for a forehead crest specifically as it appears in two other *Aethia* auklet species, casting doubt on one possible explanation for facial ornaments, that they serve for species recognition at the present time (Table 1). Responding least auklets directed sexual displays toward models with forehead ornaments more similar to crested and whiskered auklets than to their own species' ornaments. If least auklets were using the forehead ornaments alone to recognize conspecifics, then we would expect them to have avoided or behaved indifferently toward least auklet models with crests. Auklets breed in mixed colonies where large numbers of least, crested, and parakeet auklets may be present within a few meters of one another at the same time. In this situation, individuals have the opportunity to use body size (there is a threefold size difference between least and both parakeet and crested auklets), vocalizations, overall plumage coloration, bill shape and color, and feather ornaments to discriminate between individuals of their own and other species. In mixed groups, least auklets are subject to considerable harassment and aggression from crested auklets, and not only do not direct sexual displays toward them, but tend to avoid coming into close social contact with the larger species. Thus, possessing a preference for crests apparently does not lead individual least auklets into hazardous encounters with crested auklets.

The available evidence from least auklets fulfills some criteria used in previous studies (Basolo, 1990; Ryan and Rand, 1990; Ryan and Rand, 1993) to make a case for sexual selection for sensory exploitation. The available phylogenetic evidence, although incomplete, suggests that lack of a forehead crest is the primitive state among auklets and the ancestral state for the immediate ancestor of least, crested and whiskered auklets. In addition, mating preferences favor naturally occurring crests in at least one species (Jones, 1993a), and least auklets have a heterospecific mating preference for crests, although they exhibit the ancestral state of lacking a crest. Based on this evidence, the crest preference could have evolved in auklets before the evolution of the crest ornament. This conclusion is based on the logic of parsimony (Maddison et al., 1984) and assumes that least auklets had no crested ancestor. However, the available phylogenetic data (Friesen et al., 1996; Mowm et al., 1994; Strauch, 1985) provide an incomplete picture of the relationships among all members of the auklet tribe Aethiini. Specifically, these data do not indicate which of least or parakeet auklets are more closely related to the whiskered-crested clade.

Further field experiments to investigate whether parakeet and Cassin's auklets possess crest preferences would be helpful because presence of a crest preference in either of these species would support a parsimony argument for sexual selection for sensory exploitation by suggesting the preference evolved first. However, as Lotem (1995) has pointed out, phylogenetic tests of sexual selection for sensory exploitation based on parsimony may be inordinately likely to support an evolutionary lag scenario in which the preference is supposed to have preceded the trait, because the frequency of changes of character state (e.g., no crest to crest) is assumed to be very low (see also Meyer et al. 1994; Schluter et al., 1997). An alternative explanation is that least auklets had a crested ancestor but that the crest was lost, while the preference has been retained. It is unclear what present sources of natural selection would oppose intersexual selection and lead to crest loss. The crest is cheap to produce (low cost of feather production; Jones and Montgomerie, 1992), cheap to bear (ex-

tremely low aerodynamic and hydrodynamic costs; Thomas ALR, unpublished data), but may have a significant social cost of attracting crested auklet aggression. The costs of the forehead crest preference to least auklets are similarly unknown. For the case of auklet crests, the evidence for sexual selection for sensory exploitation is not conclusive. Evolution of currently expressed auklet display traits by sensory exploitation would not preclude that their expression is favored at the present time by other sources of selection, such as the ornaments serving as a viability indicators.

Least auklets' response to the models with crests immediately raises the question, what is it about the forehead crest that elicits sexual displays? In other words, what is the proximate explanation for the bird's sexual response to crests? Our experimental results do not provide an answer to this question. Least auklets may be attracted to crests because they make the bearers more conspicuous, or make them appear larger, or because the shape and movement of the crest feather shafts in the wind is in some way stimulating to their senses. In general, our findings are consistent with emerging evidence that mating preferences can favor supernormal, novel and even heterospecific coloration, ornaments, and displays. As we have found for the auklets, empirical studies face the challenge of several plausible but difficult-to-discriminate alternative explanations for heterospecific preferences. This study provides the first experimental results that we know of for a heterospecific ornament preference in any bird species. We urgently require experimental studies to investigate the existence, costs and benefits, and proximate explanations for similar mating preferences in birds and other animals if we are to fully understand the evolution of elaborate displays and related preferences.

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