



## ARTICLES

# Experimental evidence for mutual inter- and intrasexual selection favouring a crested auklet ornament

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During the breeding season, female and male crested auklets, *Aethia cristatella* (Alcidae), display similar conspicuous crest ornaments composed of elongated forward-curving feathers on their foreheads. Based on quantifications of brief agonistic interactions at a large breeding colony, we found that crest length was strongly correlated with dominance within both sexes. Across the full range of crest length, individuals with longer crests were dominant over shorter-crested individuals in agonistic interactions involving same-sex adults. Within subadults (2-year-olds of unknown sex), there was a similar trend towards longer-crested individuals being dominant. In agonistic interactions involving individuals of different sex and age, adult males were dominant over adult females and adults were dominant over subadults, regardless of crest length. In an experiment in which we manipulated crest length using life-size realistic models, male auklets that responded were less aggressive to male models with longer crests than to models with normal or shorter crests, confirming that crest length by itself signals dominance status. In a related experiment in which we controlled intrasexual competition, both males and females responded to opposite-sex models with more frequent sexual displays when the models had long crests compared with those having short crests, suggesting that crested auklets also have mating preferences that favour long crest ornaments. Taken together, these results support the idea that the crest ornament is favoured by both intra- and intersexual selection.

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There is now abundant evidence that elaborate ornamental traits such as feather ornaments displayed by some bird species are the product of sexual selection driven by mating preferences (Andersson 1994). Examples of intersexual selection concern strikingly sexually dimorphic species with showy polygynous males, including fish such as green swordtails, *Xiphophorus helleri* (Basolo 1990), and birds such as peacocks, *Pavo cristatus* (Petrie et al. 1991), and Jackson's widowbirds, *Euplectes jacksoni* (Andersson 1992; for a detailed review see Andersson 1994). In some cases, ornamental traits or badges (again usually of males) may relate to intrasexual selection because they signal dominance status. Examples include the bib patch of male house sparrows, *Passer domesticus*

(Møller 1987b), the breast plumage stripe of male great tits, *Parus major* (Järvi & Bakken 1984), male and female least auklet, *Aethia pusilla*, plumage coloration (Jones 1990), and pectoral plumage tufts of male scarlet-tufted malachite sunbirds, *Nectarinia johnstoni* (Evans & Hatchwell 1992). Two patterns have emerged in the literature (Andersson 1994): (1) ornaments have usually been inferred to be the product of either inter- or intrasexual selection and less frequently both (Berglund et al. 1996); and (2) studies relating morphological ornaments to either inter- or intrasexual selection have usually concentrated on male characteristics (even if the trait is expressed in both sexes). Nevertheless, similar ornaments are often displayed by both males and females of the same species. For example, among birds, female and male grebes (Podicipedidae; facial plumes and crests), tropicbirds (Phaethontidae; tail streamers), herons (Ardeidae; plumes and bright bare skin), jaegers (Stercoraridae; tail streamers), auks (Alcidae; facial plumes, crests, brightly

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coloured bills and feet), parrots (Pssitacidae; bright plumage), jays (Corvidae; crests and bright plumage), motmots (Momotidae; tail ornaments and bright plumage), toucans (Rhamphastidae; bright bills and plumage), and flycatchers (Tyrannidae; crests, tail streamers and bright plumage) display similar adornments. Despite the attention to showy polygynous male birds, and in some cases, a virtual equating of sexual dimorphism with sexual selection (e.g. Lande 1980), there are many monomorphic species with male and female adornments similar to the extravagant male ornaments of polygynous species.

Sexual monomorphism of ornaments of monogamous species has been ascribed to: (1) nonadaptive genetic correlation between the sexes, leading to the expression in females of traits selected for in males (Lande 1980); (2) natural selection for sexual indistinguishability (Burley 1981); or (3) weak or absent sexual selection (Andersson 1994). However, monomorphic ornaments could also result from simultaneous sexual selection on both males and females resulting from mate choice in species with similar male and female parental roles (Darwin 1871; Trail 1990; Jones & Hunter 1993; Andersson 1994). In many monogamous animals, the individual characteristics of a male partner of high quality are likely to be the same as a female partner of high quality, because the sexes have similar roles in reproduction (Trivers 1972). Thus intersexual selection could be based on 'mutual' mate choice by both males and females for similar attractive traits. Furthermore, competition within both sexes can be intense in monogamous species, so intrasexual selection within both sexes could focus on display traits that function in competition for access to mates. Few studies have investigated experimentally whether the simultaneous role of both intra- and intersexual selection in favouring an ornament are regular features of monogamous species.

The objectives of our study were: (1) to elucidate the role of the crest ornaments in intrasexual competition by testing for a relationship between crest length and dominance in natural interactions in the crested auklet, *Aethia cristatella*, a monogamous seabird; (2) to investigate experimentally whether crest length itself signals dominance status using manipulations of crest length on realistic auklet models; (3) to test for a prevalence of long-crested birds in natural courtship interactions and for positive assortment according to crest length; (4) to test for mating preferences for longer crests based on experimental ornament manipulations; and (5) to consider possible mechanisms for the origin and maintenance of auklet morphological ornaments.

## METHODS

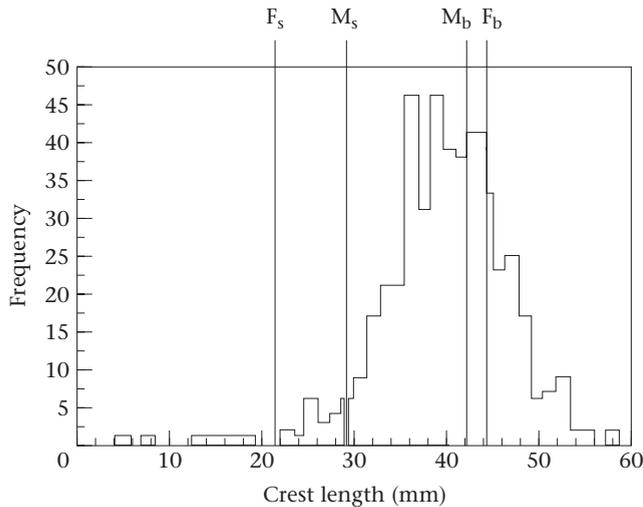
### Study Species

Auklets (family Alcidae) are socially monogamous, sexually monomorphic seabirds in which males and females display ornaments only during the breeding season (Gaston & Jones 1998; I. L. Jones, F. M. Hunter & G. Fraser, unpublished data). Crested auklets have a forehead crest composed of black forward-curving feathers,

less conspicuous white auricular plumes, a brilliant orange bill with curved accessory plates, and a distinctive citrus-like plumage odour (Jones 1993a). Like many sexually selected traits, crested auklet ornaments show extreme variability in expression among individuals (Jones 1993a; I. L. Jones et al., unpublished data). Crested auklet courtship, mate choice, intrasexual conflict over access to mates, and territorial disputes over access to nesting crevices take place at the breeding colony prior to laying (involving individuals and pairs breeding in the same year), and throughout the remainder of the breeding season (see Jones 1993a for breeding in subsequent years). Copulation takes place on the sea near the colony (F. M. Hunter & I. L. Jones, unpublished data), but otherwise auklet social behaviour resembles that of the razor-bill, *Alca torda* (Wagner 1991). Crested auklets have a high divorce rate (ca. 25%; Zubakin & Zubakina 1994), and combined with mortality, this results in more than half of all individuals having to find a new mate each year.

### Behavioural Observations

We quantified agonistic interactions among crested auklets at a large, mixed-species auklet colony at Buldir Island, Aleutian Islands, Alaska (52°2'N 175°5'E; Byrd & Day 1984), with a breeding population of approximately 450 000 crested and least auklets (Byrd et al. 1983). We observed the behaviour of crested auklets during their morning activity period (see Jones 1993a), from a distance of 2–10 m using binoculars. We defined an agonistic interaction as occurring when two auklets approached one another closely and engaged in a brief conflict. Evidence of a conflict included one or more of the following common forms of behaviour: lunging towards another individual with head and bill lowered or with head and bill outstretched, pecking or biting the opponent, or more rarely, grasping with the bill, or grasping with the bill combined with shoving the opponent over the edge of a display rock (see Jones 1993a for details of crested auklet agonistic behaviour). We scored interactions involving two birds only, where both individuals had a clear and unobstructed view of one another. The winner of an agonistic interaction was defined as the individual that maintained its physical position on the rock; the loser was the individual that voluntarily or involuntarily was displaced (by abruptly departing on foot, by flying away, or being physically pushed off the display rock). We scanned the talus for cases of unusually intense aggression (fighting involving simultaneous grasping with the bill, kicking with the feet, and beating with the leading edge of the wings) and noted the sex of the individuals that initiated these incidents. For each agonistic interaction observed, we noted for the winning and losing individual: age (adult or 2-year-old subadult; see Jones 1993a), sex (of adults only, based on bill shape criteria; Jones 1993b), and crest-length category (if both individuals had crests in the same category, we noted whether either individual had a longer crest or whether crest length was identical, based on the direct comparison of the two birds in close proximity to one another). Although crest length varied continuously (Fig. 1), we



**Figure 1.** Histogram of crest length, based on measurements of 535 adult crested auklets at the Buldir colony (sexual dimorphism in crest length:  $t_{533}=2.0$ , NS), showing the manipulated crest lengths of the female and male models.  $F_s$ : female models short crest;  $F_b$ : female models long crest;  $M_s$ : male models short crest;  $M_b$ : male models long crest.

roughly quantified crest length in the field by assigning each individual we observed to one of five crest length categories (0: no crest; 1: crest length less than or equal to bill depth, which averaged 11 mm on individuals captured; 2: crest length between one and two bill depths; 3: crest length between two and three bill depths; or 4: crest length greater than three bill depths), based on a reference card with illustrations of a typical individual from each category. We determined the overall repeatability (intraclass correlation coefficient; see Zar 1984, page 324) of crest category scoring by comparing repeated scoring (on different days) of individually colour-marked birds:  $r_1=0.70 \pm 0.05$  (SE);  $F_{1,21}=5.67$ ,  $P<0.0001$ ; of 122 birds scored at least twice, 88 (78%) were classified in the same category. To avoid recording the same individuals more than once, we made our observations from more than 40 different locations throughout the 5-ha auklet colony at Main Talus, including a study plot with 373 individually marked crested auklets. Based on our observations of colour-marked and unmarked individuals, we believe that very few, if any, individuals were scored more than once.

To investigate the relationship between the crest ornament and intersexual selection by observation, we scored the crest length categories of all male–female pairs engaged in courtship in the colony during the prelaying period (see Jones 1993a). If inter- and intrasexual selection favours crest length, we expected that courting pairs would tend to have longer than average crests and would show positive assortments for crest length (but see Jones & Montgomerie 1991).

## Model Experiments

To test experimentally whether the crested auklet crest ornament is subject to mating preferences (intersexual

selection) and/or signals dominance status (intrasexual selection), we performed manipulation experiments using six realistic models made from the skins of adult crested auklets (three males and three females, minimizing the number of individuals sacrificed) of approximately average appearance that we killed under permit at the colony. These experiments were required to test whether crest length per se and not some correlated aspect of individual phenotype could be responsible for a difference in dominance status between long- and short-crested individuals, or for mating preferences for long-crested individuals. We presented each model with two different crest lengths and compared the response of approaching auklets to each. The models were constructed to be as similar as possible overall, but differed slightly in natural ornament expression (other than the crest) and posture. Crested auklets approach this type of model as in natural encounters, and display both courtship and agonistic behaviour (Jones & Hunter 1993). By placing artificial crest ornaments on auklet models rather than live birds, we controlled for two factors that could confound a mate choice experiment. Because we measured the response of crested auklets to models in controlled situations, we were able to exclude circumstances when intrasexual interactions (e.g. see Savalli 1989) involving several individuals were likely to affect individuals' responses to the ornaments (i.e. when more than one bird was present within 1 m of the model). Furthermore, because we manipulated ornaments on immobile models, we ensured that birds' responses to manipulations were due to a change in the ornament per se rather than a change in behaviour of the manipulated 'subject' (e.g. see Barnard 1990; Balmford & Thomas 1992). Living auklets respond poorly to artificial ornaments attached to their bodies, preening the affected area until the ornament is lost or damaged and potentially suffering reduced survival. Our experimental approach was based on the assumptions that increased sexual displays (see Jones 1993a) and closer approach for a longer duration towards a manipulated model were indicative of a mating preference for an opposite-sex model's phenotype, and that differences in aggressive behaviour and alarm responses to models indicated an effect of dominance status.

We compared the responses of crested auklets to models with crest ornaments greater than (long crests) and less than (short crests) the mean crest length in the population at Buldir (Fig. 1). We manipulated the crests of female models to a greater extent (24 mm) than those of male models (14 mm) because we suspected a priori that male mating preferences could be more difficult to detect; males are less likely to approach and solicit courtship from females than vice versa (Jones 1993a). We believed that a more conspicuous alteration of female crest length would increase the probability of detecting a male response to crest size. We lengthened the natural (short) crests using 10–12 crest shaft feathers obtained from crested auklets at Buldir, temporarily attached with superglue to the ends of the natural crest feathers. We did not perform sham manipulations because the artificial crests could not affect model

'behaviour', and because there were no visible artefacts of manipulation.

We made model presentations at 30 different display rocks (large boulders with 2–12-m<sup>2</sup> flat upper surfaces, where auklets congregated to engage in courtship) at Main Talus. We made model presentations daily (excluding periods of inclement weather) between 7 June and 14 July 1992 and 24 June and 15 July 1993 during the incubation and hatching periods, when both breeding and nonbreeding birds engage in intense courtship behaviour (Jones 1993a). We alternated the presentation of each model approximately every 10 days, beginning with a short crest, then a long crest, then a short crest again. We scored approximately equal numbers of responses in each phase, so the mean presentation date was similar for each model and each treatment, controlling for seasonal effects. Observer bias was controlled for by selecting unambiguous displays for scoring (Jones 1993a) and by using simultaneous observation trials to maximize observer consistency. Our scoring of responses was identical.

For each adult crested auklet that responded to a model (approached within 30 cm and at least visually inspected the model), we identified its sex by bill shape (Jones 1993b), and recorded the occurrence of sexual displays (arch, hunch, ruff sniff and touch), aggressive behaviour (peck, lunge), alarm (flinch and flee) responses to the models (see Jones 1993a, for a detailed description of crested auklet displays), as well as their closest approach (0, 1–10, 11–20, 21–30, or >30 cm) and response duration (1–5, 6–10, 11–15, or >15 s). Auklets respond to models as if they are live birds for at least the first 15 s following presentation (Jones & Montgomerie 1992; Jones & Hunter 1993). We believe no individual's response was scored more than once; no bird responded more than once and colour-marked individuals that did by chance occur near the models a second time appeared to ignore them.

To analyse statistically differences in response between model treatments, we collapsed the data into a single frequency datum for each response type for each model for each treatment. For the badge-of-status experiment, we analysed male responses to male models and female responses to female models using the frequency of: (1) the performance of one or more aggressive behaviours (including pecks, lunges or outright attacks directed at the model); and (2) the occurrence of one or more alarm responses (flinch: an abrupt movement of the head or body away from the model; flee: an abrupt departure from the display rock by flying). For the mating preference experiment, we analysed male responses to female models and female responses to male models using the frequency of: (1) the performance of one or more sexual displays; (2) approaches closer than 10 cm; and (3) approaches for longer than 10 s. We compared responses using paired *t* tests on arcsine transformed display frequency data. We excluded 33 individuals' responses from analysis because of possible ambiguities in some of the response categories. Because theory predicts that larger ornaments should be both more attractive and threatening than small ornaments

(Andersson 1994), we used one-tailed tests to evaluate whether the mean sexual and alarm responses ( $\mu$ ) were greater for larger ornament size (i.e.  $H_0: \mu \leq 0$  and  $H_A: \mu > 0$ ; see Zar 1984).

We also present reanalysed data on mating preferences (see Jones & Hunter 1993) using paired *t* tests to compare these results with those obtained previously (response data were pooled across models and analysed with a contingency table to test the hypothesis that crested auklet males and females have mutual mating preferences for their crest ornaments).

## RESULTS

### Observations of Agonistic Interactions

We scored a total of 608 agonistic interactions: 179 involved two males, 93 involved two females, 188 involved one male and one female, 100 involved an adult (male or female) and a subadult (unsexed), and 48 involved two subadults (unsexed). Assuming an overall 50:50 adult sex ratio (of the birds captured on the colony site and sexed in the hand, 347 were males and 345 were females), males engaged in agonistic behaviour more frequently than females ( $\chi^2_2=20.5$ ,  $P<0.0001$ ). Of the 608 interactions scored, 402 involved birds differing in crest length by at least one crest category (difference in crest length greater than about 9 mm), 87 involved birds scored in the same crest category but still noticeably different in crest length (difference in crest length of about 3–8 mm), and the remaining 119 involved birds without a noticeable difference in crest length. Of 29 instances of extreme aggression (outright fighting), 26 (90%) were initiated by males, indicating that males were significantly more likely to initiate fights ( $\chi^2_1=8.9$ ,  $P<0.003$ ).

Of 153 interactions scored that involved adult males of different crest length, the longer-crested individuals won 133 (87%;  $\chi^2_1=46.5$ ,  $P<0.0001$ ; Table 1). The remaining 26 interactions scored between adult males involved individuals of similar crest length. Of 87 interactions scored that involved adult females of different crest length, the longer-crested individuals won 73 (84%;  $\chi^2_1=21.2$ ,  $P<0.0001$ ). The remaining six interactions scored between adult females involved individuals of similar crest length. Although the repeatability of crest categorization in the field was imperfect (see Methods), the results suggest that the trend for longer-crested individuals being dominant held across the full range of crest length (Table 1).

Taking all crest lengths together, males won 175 of 188 (93%;  $\chi^2_1=83.6$ ,  $P<0.0001$ ; Table 1) interactions involving a male and a female. Among 41 interactions scored involving a male and a female in which the female had a longer crest than the male, the males still won 33 (81%;  $\chi^2_1=7.0$ ,  $P<0.008$ ). Adults were the winners of all 100 interactions involving an adult and a subadult (59 interactions involved an adult male, and 41 involved an adult female, so males and females appeared to be equally likely to engage in agonistic interactions with subadults). Of 39 interactions scored that involved subadults of different

**Table 1.** Interactions involving crested auklets differing by at least one crest-length category

Interactions	Crest-length categories	Total number of interactions	Number of interactions won by longer-crested bird
<b>Among adults:</b>			
Male–male	1 versus 2	16	14 (88%)
	2 versus 3	81	74 (91%)
	3 versus 4	56	43 (77%)
	1 versus 3	3	3 (100%)
	2 versus 4	6	6 (100%)
	Total		
Female–female	1 versus 2	21	16 (76%)
	2 versus 3	50	42 (84%)
	3 versus 4	19	15 (79%)
	1 versus 3	6	6 (100%)
	2 versus 4	1	1 (100%)
	Total		
<b>Among subadults:</b>			
Subadult–subadult	1 versus 2	35	25 (71%)
	2 versus 3	3	3 (100%)
	Total	38	28 (74%)

**Table 2.** Results of model experiments related to status-signal function for crest ornament

	Overall	Short crest	Long crest	Paired $t_2$	$P$ (one-tailed)
<b>Male responses to male models</b>					
Responses scored	322	222	100	—	—
Frequency of attack	0.12	0.14	0.07	7.6	0.008*
Frequency of alarm response	0.12	0.03	0.33	3.1	0.04
<b>Female responses to female models</b>					
Responses scored	555	379	176	—	—
Frequency of attack	0.05	0.06	0.04	1.5	0.1
Frequency of alarm response	0.06	0.05	0.08	0.8	0.3

\*Significant differences at a tablewide  $P < 0.05$ , using sequential Bonferroni analysis (Rice 1989).

crest length, the longer-crested individuals won 28 (72%;  $\chi^2_1 = 3.1$ ,  $P < 0.08$ ; Table 1). The remaining nine interactions between subadults involved individuals of similar crest lengths. Taken together, these results indicate that dominance was significantly correlated with crest length in adult males and adult females, with a similar trend in subadults, and that regardless of crest length, females were subordinate to males, and subadults were subordinate to adults.

**Observations of Courtship Interactions**

We observed a total of 86 pairs engaging in courtship with the following male–female crest category combinations: 2 versus 2:  $N = 2$ ; 2 versus 3:  $N = 3$ ; 3 versus 2:  $N = 9$ ; 3 versus 3:  $N = 36$ ; 3 versus 4:  $N = 8$ ; 4 versus 3:  $N = 7$ ; 4 versus 2:  $N = 1$ ; and 4 versus 4:  $N = 20$ . Courting individuals tended to have longer crests than the population at large. The frequencies of crest length observed for courting males (2:3:4=6:54:28) and females (2:3:4=12:46:28) differed significantly from those of the overall population for each sex (based on birds captured at the study plot: for males, 2:3:4=10:34:7,  $\chi^2_1 = 8.9$ ,  $P = 0.01$ ; for females,

2:3:4=9:24:4,  $\chi^2_1 = 6.9$ ,  $P = 0.03$ ). The frequency of courting pairs observed in each possible combination of crest-length category differed significantly from that expected under random assortment ( $\chi^2_8 = 31.3$ ,  $P < 0.001$ ), with a significant excess of courting pairs with the same crest length category over courting pairs with differing crest lengths ( $\chi^2_1 = 19.1$ ,  $P < 0.001$ ).

**Model Experiments**

Our experiments on the role of the crest in signalling dominance status (based on male responses to male models and female responses to female models) indicated that male crested auklets were significantly less likely to attack male models with long crests than the same models with short crests (Table 2). Females showed no difference in attack or alarm responses between long- and short-crested models.

Our experiments on mating preferences (based on male responses to female models and female responses to male models) indicated that both sexes were significantly more likely to direct stereotyped sexual displays towards models with longer crests than to the same models

**Table 3.** Results of model experiments related to mating preferences for crest ornament

	Overall	Short crest	Long crest	Paired $t_2$	$P$ (one-tailed)
Male responses to female models					
Responses scored	304	194	110	—	—
Frequency of sexual displays	0.24	0.18	0.36	10.9	0.004*
Frequency of approach <10 cm	0.23	0.16	0.37	3.6	0.04
Frequency of interest >10 s	0.22	0.18	0.29	3.5	0.04
Female responses to male models					
Responses scored	416	265	151	—	—
Frequency of sexual displays	0.22	0.10	0.43	3.2	0.01*
Frequency of approach <10 cm	0.16	0.12	0.24	2.2	0.08
Frequency of interest >10 s	0.15	0.06	0.32	13.7	0.003*

\*Significant differences at a tablewide  $P < 0.05$ , using sequential Bonferroni analysis (Rice 1989).

with shorter crests in a paired experiment (Table 3). Furthermore, females responded to models with long crests for a longer duration (Table 3).

## DISCUSSION

Crested auklets' ornaments are on permanent display during virtually continuous interactions that occur on the rocky surface of colony sites, where thousands of birds congregate to find mates and nesting crevices. If responses to models are comparable to natural agonistic interactions, our experimental results confirm that crest length signals dominance status among males, with longer-crested individuals dominating shorter-crested individuals. Agonistic behaviour was more frequent among males, which were intolerant of close proximity with other males and used their crests in contests over space, potential nest sites and access to females. Similar behaviour occurred among females jostling for position on a preferred landing rock, and particularly when females accompanying or engaging in courtship behaviour with males drove away other females. Similar female 'mate-guarding' behaviour occurs in razorbills (Wagner 1992). However, the observed dominance of longer-crested females in natural female–female interactions was not confirmed by our experimental results. This suggests that females need a more direct stimulus to provoke aggression because when such a stimulus occurred naturally (e.g. when a rival female approached a courting female's male partner), the length of the crest was apparently important in signalling dominance. We believe the models did not elicit this response from females because they did not provide a moving (direct) stimulus.

Both males and females take part in nest site selection, so the crest could also be used by both sexes to defend nest sites from same-sex rivals. For both sexes, the potential costs of injuries related to fighting are high relative to the benefits of maintaining a nest site or a position on a display rock, favouring the use of a badge of status. Because of the intense competition within both sexes for mates, it seems likely that the crest evolved, or at least is currently maintained, partly by mutual intrasexual selection. Furthermore, because the crest is apparently used for signalling in territorial disputes over nest sites (unrelated

to mating success), this ornament would be favoured by natural selection as well as sexual selection.

Use of a conspicuous status signal is thought to be particularly advantageous in situations of high population densities and the consequent frequent agonistic interactions with unfamiliar individuals (Rohwer 1975; Whitfield 1987). This prediction appears to hold for the auklets. Among five auklet species, crested and least auklets have the highest population densities and the highest rates of agonistic interaction (Gaston & Jones 1998); both have conspicuous badges of status. Previous work demonstrated that least auklet's variable underpart plumage plays a role in status signalling (Jones 1990). Among the remaining three species, the nocturnal Cassin's auklet, *Ptychoramphus aleuticus*, lacks ornaments and plumage variation altogether, the parakeet auklet, *Cyclorhynchus pssitacula*, breeds semicolonally at low densities and lacks elaborate ornaments and plumage variation, while the elaborately ornamented and enigmatic whiskered auklet's, *Aethia pygmaea*, social behaviour remains poorly known because social interactions take place underground at night and at sea by day (Gaston & Jones 1998).

The sexual monomorphism of crested auklet ornaments is paradoxical because the sexes differ in aggressive behaviour: males were more likely to initiate aggressive behaviour and were dominant over females regardless of crest length. Despite these behavioural differences, the balance between sexual and natural selection on males and females maintains the ornaments of each sex at a common level of expression. Disentangling these counterbalancing forces would require careful quantification of the costs of ornament expression to males and females, as well as a relative measure of the strength of sexual selection on either sex. Intrasexual selection on males has apparently produced their strongly hooked bills, which resembles the striking 'kype' of spawning male salmon (Jones 1993b) used in fighting with rival males during the breeding season.

The crests of the crested auklet like the 'badge of status' of great tits (Järvi & Bakken 1984) and house sparrows (Møller 1987b) may mediate minor altercations over resources, but whether they are reliable indicators of status in the face of invasion by potential cheaters

expressing dishonestly large or small badges is unknown (Owens & Hartley 1991; Johnstone & Norris 1993). It has been suggested that badge reliability is maintained by social control of deception (e.g. Møller 1987a), and this appears to be the case for crested auklets, because individuals constantly test one another's strength during their interactions. However, modelling has suggested that even with such social control, invasions by cheaters could still occur unless individuals incur a substantial cost of aggression (e.g. related to androgen levels; Johnstone & Norris 1993). This would imply that individuals must vary in badge expression and dominance in relation to their intrinsic ability to withstand this stress, and thus that badge size should correlate with health or viability in a manner unrelated to the direct costs of producing or bearing the badge itself (Johnstone & Norris 1993). Like some other badges, crests are probably cheap to produce (crest mass <1 g) and cheap to bear (aerodynamic and hydrodynamic drag on the ornament during flight in air or underwater is inconsequential because of its flexibility; A. L. R. Thomas, unpublished data), but are potentially fragile and susceptible to damage during fights. Indeed, the apparent low costs of production of auklet morphological ornaments may make them poor candidates as direct indicators of viability (e.g. Jones & Montgomerie 1992; I. L. Jones et al., unpublished data). Therefore it seems likely that the expression of the auklet crest is limited by a combination of social control and the cost of dominance. Future research on auklets and other species should address the physiological as well as social costs of ornamental traits and badges.

If responses to the models are comparable to natural courtship interactions, our experimental results indicate that in the crested auklet, males and females have mutual mating preferences for each other's ornaments. With intrasexual competition and other forms of sexual interference controlled in our experiments, both sexes responded to longer-crested, opposite-sex models with more frequent stereotypical sexual displays. We believe this is indicative of mutual mating preferences, because increased sexual display and other forms of interest favouring individuals with longer crests would lead to the formation of pair bonds. Our results support Darwin's (1871) mutual sexual selection hypothesis because males and females exercised choice that favoured artificial partners with manipulated long crest ornaments. Few empirical studies have looked for both female and male choice. However, several studies of fish have demonstrated mutual preferences for large body size (Foote 1988, 1989; Foote & Larkin 1988; Côté & Hunte 1989). Among birds, mutual preferences for plumage colour was demonstrated in feral rock doves, *Columba livia* (Burley 1977; Burley & Moran 1979). Further experimental work on other showy but sexually monomorphic species is required to establish whether mutual sexual selection or alternative hypotheses provide the best explanation for the evolution of elaborate monomorphic adornments.

Given the function of the crest ornament as a badge of status, mating preferences favouring crest length are expected because of the benefits of having a socially dominant mate capable of withstanding the related costs

of aggression (Johnstone & Norris 1993; Berglund et al. 1996). This is particularly true in monogamous auklets in which males and females contribute equally to incubation and chick rearing, so both sexes would benefit from mating with a high-quality partner. This combination of intra- and intersexual selection provides an explanation for the widespread occurrence of morphological ornaments that appear to be cheap to produce but are nevertheless correlated with some measures of viability. With evidence for both intra- and intersexual selection currently favouring crests, the question arises as to which mechanism played the initial role during the evolution of the ornament. Berglund et al. (1996) suggested that intrasexual selection takes the initial role in ornament evolution, with mate choice following, but simultaneous roles for intra- and intersexual selection or initiating intersexual selection are also possible. Unfortunately, there are few testable predictions that would discriminate among these possibilities for auklet ornaments. However, the experimental evidence for a heterospecific mating preference for crests by least auklets (Jones & Hunter 1998) may provide a clue. Least auklets have a mating preference for artificial crests similar to crested auklet crests, although least auklets do not possess a crest and avoid contact with larger heterospecifics in nature (Jones & Hunter 1998). The origin of this preference is unclear, but the presence of the crest preference (without any evidence for a badge of status; Jones & Montgomerie 1992) in least auklets is consistent with a primary role for intersexual selection in crest evolution.

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