

# Mutual sexual selection in a monogamous seabird

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DARWIN<sup>1</sup> believed that elaborate ornamental traits expressed in both sexes might be favoured by mutual sexual selection driven by both female and male mate choice. Experimental studies on birds<sup>2-5</sup> and fish<sup>6-9</sup> have shown that male ornaments can be favoured by female mating preferences. But the concept of mutual mate choice has remained untested experimentally, although it has been supported by recent modelling<sup>10</sup>. Here we report the results of a study of mate preferences of the crested auklet *Aethia cristatella*, a monogamous seabird in which both sexes are ornamented. In two experiments we recorded the sexual response of male and female auklets to realistic opposite-sex models with crest ornaments experimentally shortened and lengthened within the range of natural variation. Males responded to accentuated female models with more frequent sexual displays, as did females to accentuated male models, confirming the idea that ornaments expressed in both sexes could be favoured by mutual mating preferences.

The crested auklet is a socially monogamous, sexually monomorphic seabird in which both sexes contribute parental care. During the breeding season, adults of both sexes have a spectacular forehead crest consisting of 2-23 (mean, 12) narrow forward-curving feathers, 8.1-58.5 mm in length (Fig. 1). The crest is displayed during courtship encounters at breeding colonies. Courtship occurs throughout the breeding season, as individuals pair before laying for breeding in the same year, or pair later in the season for breeding in the following year. Mate fidelity between breeding seasons is relatively low<sup>11</sup>, so a high proportion of the population re-pair each year. But many individuals fail to pair early enough in the season to breed, and others fail to obtain mates<sup>12</sup>. The resulting variation in mating success in both sexes provides an opportunity for sexual selection to favour ornaments that are displayed during courtship.

To test whether crest size could be favoured by male and female mating preferences, we performed two manipulation experiments using realistic models made from mounted skins of three male and three female crested auklets of average appearance. By manipulating ornaments on models we were able to eliminate two factors that can confound mate choice experiments involving manipulation of living birds: (1) intrasexual competition<sup>13</sup>, and (2) behavioural changes in a live bird resulting directly from manipulation of its ornament<sup>14,15</sup>.

We tested for a mating preference for large crests by comparing the attractiveness of models with short crests to the same models with crest feathers lengthened (Fig. 1), using three

models of each sex to ensure that responses were not biased by unique characteristics of any one specimen. To lengthen the crest, we used cyanoacrylate 'superglue' to attach crest shafts collected from other birds to existing crest feathers on models. Manipulations involved changing the length of 10-12 shafts on each model to alter overall crest length and size while maintaining a natural appearance. Presentations were made on more than 30 different large display rocks (boulders with 2-12 m<sup>2</sup> flat upper surfaces, where auklets congregate to engage in courtship<sup>12,16</sup>) throughout a colony of about 200,000 crested auklets at Buldir Island, Alaska (52° 2' N 175° 5' E)<sup>17</sup>. For each auklet that responded to a model, we identified its sex by bill shape, and recorded the occurrence of sexual displays, 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). Response scoring was identical between two observers because these displays and measurements were simple and unambiguous. Because models were moved frequently from rock to rock throughout an immense colony, we believe no individual's response was scored more than once. This was supported by observations of approaches to models at a study plot where more than 400 colour-marked birds were present; no marked individual approached more than once. To control for intrasexual competition and interference among responding birds, we did not score approaches when more than one auklet was present near the model. Sham-manipulations were not performed because ornament manipulation could not have affected model 'behaviour', and there were no visible artefacts of manipulation. Crested auklets did not respond to natural looking least auklet *Aethia pusilla* models.

Crested auklets of both sexes approached the models as in natural courtship encounters, performing four types of stereotyped courtship display (arch, hunch, ruff-sniff and touch<sup>11,12,18,19</sup>) to opposite sex models. In nature, these displays are performed only in courtship, increase in intensity with sexual attraction between courting auklets, and lead to the formation of mated pairs<sup>11,12,16</sup>. In our model experiments, 29% of approaching females and 20% of approaching males performed a sexual display, other individuals merely looked at the model before departing. Models with enlarged crests were extremely attractive to approaching auklets of the opposite sex, compared with the same models with small crests. Females responded to male models with significantly more frequent arch, hunch and touch sexual displays when the models were presented with accentuated crests; males responded to female models with significantly more frequent ruff-sniff and touch displays (Table 1). The models were also approached more closely and for a longer duration when presented with large crests (female responses: for closest approach, log-likelihood ratio  $G = 63.8$ , d.f. = 4,  $P < 0.0001$ ; for duration  $G = 127.3$ , d.f. = 3,  $P < 0.0001$ ; male responses: for closest approach  $G = 28.9$ , d.f. = 4,  $P < 0.0001$ ; for duration  $G = 36.0$ , d.f. = 3,  $P < 0.0001$ ). Overall, these results indicate a strong relationship between sexual attractiveness and crest size in both sexes. Because larger crests are preferred, auklets bearing them are more likely to obtain mates or form pair bonds earlier, a suggestion supported by observations of the marked auklet population.

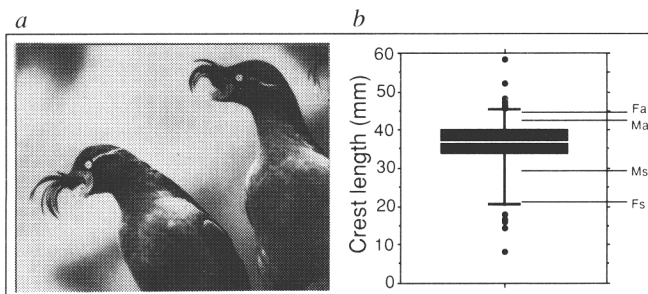


FIG. 1 *a*, Crested auklet courting pair. *b*, Variation in crest length among 253 adult crested auklets measured at Buldir. Box plot indicates 5th percentile (lower bar), 25th percentile (bottom of box), median (white line through box), 75th percentile (top of box) and 95th percentile (upper bar); outliers are represented by points. Crest size did not differ significantly between males and females in this population (based on birds sexed by behaviour or dissection: median male crest, 38.6 mm,  $n = 32$ ; median female crest, 37.3 mm;  $n = 56$ ; Mann-Whitney  $U$ ;  $Z = 0.7$ ,  $P = 0.5$ ; males were about 1.5% larger in measures of body size than females). The mean crest size of the models used in the experiments are indicated by: Fa accentuated female crests; Fs small female crests; Ma accentuated male crests; Ms small male crests (manipulated crest lengths were within 2 mm of the mean for each treatment). Female model crests were manipulated to a greater extent (24 mm) than males' (14 mm) because we suspected *a priori* that male mating preferences could be more difficult to detect.

TABLE 1 Responses to male and female ornament manipulations

Sexual display	Female response to male models					Male response to female models				
	Displays to big crest (151 birds)	Displays to small crest (269 birds)	Relative frequency big/small	G (d.f.=1)	P	Displays to big crest (124 birds)	Displays to small crest (209 birds)	Relative frequency big/small	G (d.f.=1)	P
Arch	28	2	24.9	47.2	<0.0001	6	8	1.3	0.2	NS
Hunch	31	7	7.9	36.3	<0.0001	13	17	1.3	0.6	NS
Ruff sniff	6	5	2.1	1.6	NS	16	11	2.5	5.9	0.01
Touch	24	19	2.3	7.6	0.008	9	3	5.1	7.4	0.006
One or more	76	29	4.7	77.8	<0.0001	45	35	2.2	15.9	<0.0001

Based on responses of 420 females (269 to small-crested male models and 151 to big-crested male models; scored by I.L.J.) and 333 males (209 to small-crested female models and 124 to big-crested female models; scored by F.M.H.) during 165 h of observation between 7 June and 14 July 1992. Each model was presented with a small crest, then with accentuated crest, then with small crest again on about 10 d each; roughly equal numbers of responses were scored in each phase. 'Relative frequency, big/small': relative frequency of display to accentuated versus small crested models (for example, females' arch displays were 24.9 times more frequent to the accentuated model). Sex was determined by bill shape: males have a larger and more strongly hooked bill than females (refs 18, 22, 23). There was no significant difference in response among models (for displays and response measures: female models,  $G=2.0-4.0$ , d.f.=1-8,  $P=0.2-0.4$ ; male models,  $G=0.1-2.4$ , d.f.=1-8,  $P=0.4-0.9$ ), so responses were pooled for all models within each experiment. Female responses to long-crested models were significantly stronger than males' responses for arch ( $G=43.5$ , d.f.=1,  $P<0.0001$ ), hunch ( $G=36.8$ , d.f.=1,  $P<0.0001$ ), and touch displays ( $G=7.9$ , d.f.=1,  $P=0.004$ ). There was a slight seasonal effect of gradually declining response to models, but this could not have biased the results because the response to crest accentuation went in the opposite direction, increasing significantly between early (small crests) presentations and the first accentuated crest presentations. Median presentation dates were the same for small-crested and accentuated-crested models.

In our experiment, male responses to accentuated female models were less strong than female responses to male models (although both were significant; Table 1). This initially suggests that female preferences are more important, and raises the question of why female crested auklets have a similar sized crest ornament to males. One possibility is that the sexes have an equal role in mate choice, but our experiment underestimated the expression of male preference because the sexes differ in the way they initiate courtship. Male and female responses to the static models could have differed because crested auklet males tend to wait for females to approach, then aggressively reject unwanted partners, whereas females are more active in seeking out and approaching males (although both sexes show either type of behaviour)<sup>11</sup>. At present we cannot quantify the relative strength of the preference; the solution to this question requires more detailed study of natural pair formation. In our experiment, we controlled for intermale and interfemale competition by excluding responses when more than one bird was near the model, but because crest size is also correlated with dominance in both sexes and aggressive competition for mates is frequent (I.L.J., unpublished data), crest ornament size is likely to be favoured by intrasexual competition as well as by mating preference.

Our experiments indicate that crested auklet ornament size is likely to be favoured by sexual selection involving mutual mate choice by both sexes. For this species, our data refute the hypothesis that female ornaments are functionless but are expressed merely as a result of a genetic correlation between the sexes<sup>20,21</sup>. Our experiments confirm Darwin's<sup>1</sup> suggestion that the evolution of ornaments of monogamous sexually

monomorphic animals could be driven by mutual sexual selection. This has profound implications for our understanding of the evolution of sexually monomorphic ornaments in many other bird species. □

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1. Darwin, C. *The Descent of Man and Selection in Relation to Sex* (Murray, London, 1871).
2. Andersson, M. *Nature* **299**, 818-820 (1982).
3. Møller, A. P. *Nature* **332**, 640-642 (1988).
4. Hill, G. E. *Anim. Behav.* **40**, 563-572 (1990).
5. Andersson, S. *Anim. Behav.* **43**, 379-388 (1992).
6. Bischoff, R. J., Gould, J. L. & Rubenstein, D. I. *Behav. Ecol. Sociobiol.* **17**, 253-256 (1985).
7. Basolo, A. L. *Anim. Behav.* **40**, 332-338 (1990).
8. Milinski, M. & Bakker, T. B. *Nature* **344**, 330-332 (1990).
9. Houde, A. *Science* **248**, 1405-1407 (1990).
10. Kirkpatrick, M., Price, T. & Arnold, S. J. *Evolution* **44**, 180-193 (1990).
11. Zubakin, V. A. in *Study of Colonial Seabirds of the USSR* 9-13 (Academy of Sciences, Magadan, 1990).
12. Jones, I. L. & Montgomerie, R. D. *Behav. Ecol. Sociobiol.* **30**, 43-52 (1992).
13. Savalli, U. M. *Nature* **339**, 432 (1989).
14. Balmford, A. P. & Thomas, A. *Nature* **359**, 487 (1992).
15. Barnard, P. *Anim. Behav.* **39**, 652-656 (1990).
16. Jones, I. L. & Montgomerie, R. D. *Behav. Ecol.* **2**, 249-257 (1991).
17. Byrd, G. V. & Day, R. H. *Arctic* **39**, 109-118 (1984).
18. Flint, V. E. & Golovkin, A. N. *Pititsy SSSR: Chistkovyye [Birds of the USSR: Auks (Alcidae)]* (Nauka, Moscow, 1990).
19. Jones, I. L. in *The Birds of North America* (Academy of Natural Sciences, Philadelphia, in the press).
20. Lande, R. & Arnold, S. J. *J. theor. Biol.* **117**, 651-664 (1985).
21. Lande, R. *Evolution* **34**, 292-305 (1980).
22. Bédard, J. & Sealy, S. J. *J. Zool.* **202**, 461-488 (1984).
23. Jones, I. L. *Wilson Bull.* (in the press).

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