

THE FREQUENCY AND FUNCTION OF AQUATIC COURTSHIP AND COPULATION IN LEAST, CRESTED, WHISKERED, AND PARAKEET AUKLETS¹

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Abstract. Least (*Aethia pusilla*), Crested (*A. cristatella*), Whiskered (*A. pygmaea*), and Parakeet Auklets (*Cyclorhynchus psittacula*) all engage in aquatic courtship and copulation behavior. We quantified auklet sexual behavior at sea to obtain comparative information related to sexual selection and to evaluate why auklets choose this unusual location for mating. Auklet courtship involved a variety of stereotyped displays. Although similar courtship displays occurred both at the colony on land and at sea, copulation took place only on the sea. Courtship and copulation was frequently disrupted by extrapair males. Extrapair copulation attempts occurred in all species and apparently successful unforced extrapair copulations were observed in Least, Crested, and Whiskered Auklets, suggesting that sperm competition is a feature of their mating systems. Male birds risk water damage to their sperm if they mount their female partners at sea and cause their cloacas to become submerged during insemination. Male auklets, lacking an intromittent organ, achieved cloacal contact without mounting the female so that their cloacas remained unsubmerged. Males positioned themselves behind their partners and rapidly flapped their wings, creating lift to bring their cloacas up against their partner's cloacas, pushing upwards and ensuring insemination occurred away from the sea surface. Possible hypotheses to account for exclusively aquatic copulation include predation and sexual harassment avoidance, and female testing of males, but a definitive explanation for this phenomenon remains elusive.

Key words: *Alcidae*, auklet, courtship, copulation, sexual selection, sperm competition.

INTRODUCTION

Darwin (1871) suggested that sexual selection would give rise to variation in both ornamental traits and courtship behaviors among closely related species. In the majority of seabird species in which courtship and copulation have been described, copulation and associated behavior occur at or near the breeding site on land (Hatchwell 1988, Wagner 1991, Hunter et al. 1992). For seabirds that copulate at sea, very little is known about patterns of courtship and the behaviors involved in copulation, due to the difficulties of observing complex behavior at sea. In a study of Black-legged Kittiwake (*Rissa tridactyla*) behavior in offshore flocks, Daniels et al. (1994) found that courtship displays normally seen on land were modified at sea and that one previously unrecorded courtship display occurred exclusively on the water. This suggests that to fully evaluate seabird courtship behavior,

detailed observation of pairs at sea as well as on land is essential.

Observations of sexual behavior at sea also would reveal how species that copulate on water overcome the resulting problem of sperm transfer. When a male bird mounts a female on the water, her cloaca is likely to become submerged (Burns et al. 1980). If sperm are inseminated by cloacal contact, the usual avian method, they are likely to be washed away, diluted, or damaged by the surrounding water, resulting in reduced likelihood of fertilization. Male waterfowl (Anseriformes), which copulate on water, have an intromittent organ which allows direct placement of sperm into the female's reproductive tract (McKinney et al. 1983). Lake (1981) suggested that internal sperm transfer by way of an intromittent organ overcomes the problem of water damage. In a review of birds that regularly spend periods of time on water during the breeding period, Briskie and Montgomerie (1997) found that bird species that have an intromittent organ tended to copulate on water, whereas those that lack an intromittent organ copulate on

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land. This supported the possibility that the intromittent organ is an important adaptation for birds that copulate on or in water. However, Briskie and Montgomerie (1997) found a number of important exceptions to the water damage hypothesis, in particular, phalaropes, pelicans, and alcids, species that lack intromittent organs but copulate on water.

Among the alcids, eight species copulate at sea (Gaston and Jones 1998), including four species of auklets (Least *Aethia pusilla*, Crested *A. cristatella*, Whiskered *A. pygmaea*, and Parakeet Auklet *Cyclorhynchus psittacula*), three species of puffins (Tufted *Fratercula cirrhata*, Horned *F. corniculata*, and Atlantic Puffin *F. arctica*), and the Marbled Murrelet (*Brachyramphus marmoratus*). Auklets (Alcidae, tribe Aethiini) are small socially monogamous seabirds of the North Pacific, Bering and Okhotsk Seas (Gaston and Jones 1998). Least and Crested Auklets are diurnal and highly colonial. These two species occur together at many colonies, but Crested Auklets are larger, more sexually dimorphic and aggressive than Least Auklets. Whiskered Auklets are mainly nocturnal on land, and nest in both dense and dispersed colonies, whereas Parakeet Auklets are diurnal but nest in small dispersed colonies. These four species show varying levels of ornamentation. Whiskered Auklets are highly ornamented, with a spectacular forehead crest and three pairs of long white facial plumes; Crested Auklets have a large crest, one pair of white facial plumes and a bright orange bill; Least Auklets have one pair of small white facial plumes and a red bill with a knob-like ornament; whereas Parakeet Auklets have a red bill and a single pair of white facial plumes. Various studies have described courtship displays of Least and Crested Auklets that occur on land (Jones and Montgomerie 1992, Jones and Hunter 1993). However, courtship and copulation behavior at sea has not been quantified for any auklet species and more specifically it is not known how male auklets avoid water damage during mating at sea.

The aims of our study were to quantify and compare aquatic courtship and copulation behavior of Least, Crested, Whiskered, and Parakeet Auklets, and to address two specific questions: (1) how do male auklets, which lack an intromittent organ, avoid water damage to their sperm? and (2) why do auklets copulate exclusively at sea?

METHODS

We made observations of all species of auklets at their ocean staging area adjacent to Main Talus on Buldir Island, Alaska (52°2'N, 175°5'E). Observations were made from a hide situated 20 m above sea level, directly overlooking the auklet staging flock. Least and Crested Auklets formed a mixed-species aggregation each morning during the breeding season which maintained a distance of between 100 m and 400 m offshore. Parakeet Auklets formed several smaller single species flocks closer inshore (5 to 50 m offshore), as did Whiskered Auklets at an intermediate distance (30 to 200 m offshore). All behaviors were clearly visible at these distances using either a 30× by 80 mm Kowa TSN-4 or 20× by 60 mm Kowa TSN-2 telescope.

We restricted our observations to days with calm sea conditions and good visibility, to allow clear viewing of focal pairs. We made observations on 14 days between 14 May and 17 June 1995, on 6 days between 5 and 13 June 1996, and on 12 days between 12 May and 10 June 1997, during the period of peak pre-laying courtship behavior for auklet species at Buldir. F. M. Hunter made additional observations of Least Auklets and Parakeet Auklets on the staging area offshore from the Antone Lake auklet colony on St. Paul Island, Pribilof Islands, Alaska (57°08'N, 170°17'W) on 12 days during the period 6 to 20 May 1996, from a vehicle positioned on the Antone Lake sea wall 15 m above sea level, overlooking the staging flock.

We observed the birds for 4 to 5 hr each day during their morning activity period, usually starting soon after dawn when there was sufficient light for viewing. Focal pairs were chosen at random and observed for up to 5 min. Pairs that flew from the staging area or were lost among other birds in the flock before 2 min of the observation period had elapsed were not included in the analysis. A pair was identified as two birds maintaining close proximity, within a maximum distance of two to three bird-lengths, usually closer, and characteristically well separated from other auklets at the staging area. We could not usually identify these couples as mated pairs, breeding together at the colony. However, we regularly observed mated pairs, some of which were identifiable individuals from our color-marked populations at Main Talus, departing from our study plot and flying together to

the staging area where they landed on the sea and engaged in identical behavior to our focal pairs. We assumed that conspecific individuals that disrupted our focal pairs represented extra-pair individuals.

We treated each focal pair as an independent data point because we believe that the probability of observing the same pair more than once during our study was very low. This belief is based on the large auklet populations at our study sites (>200,000 pairs at Buldir, >25,000 pairs at St. Paul Island), estimates of which are based on net movement counts of Least and Crested Auklets by Byrd et al. (1983) and observations by us, and on the large number of pairs that were present in the staging flocks on any day. Estimated numbers of birds in the Main Talus staging flock were 21,000 Least Auklet pairs, 43,000 Crested Auklet pairs, 5,000 Whiskered Auklet pairs, and 500 Parakeet Auklet pairs, whereas estimated numbers in the Antone Lake staging flock were 2,000 Least Auklet pairs and 500 Parakeet Auklet pairs.

We recorded all courtship displays and both attempted and successful pair and extrapair copulations (EPCs) that occurred during the observation period of each focal pair. Stereotyped courtship displays were identified early in the study allowing both of us to record comparable information on display frequency. It was not possible for us to identify whether sperm was transferred during cloacal contact nor indeed whether cloacal contact was accurately achieved in every case. The best measure of copulation success that could be attained was apparent cloacal contact or behaviorally successful copulation.

During observations of auklet behavior on land, we looked for evidence of copulation and attempted copulations throughout the 1990–1998 breeding seasons. To evaluate the possibility of copulation within nesting crevices, we measured the greatest vertical height from ceiling to floor of the nesting chambers of 38 Least, 32 Crested, 54 Whiskered, and 11 Parakeet Auklet crevices using a piece of string with a weight attached. The length of the string was then measured to the nearest 1 mm using a ruler. The sample was limited to crevices that had entrances large enough to allow the passage of our hands and with nesting chambers within an arm's length of the entrance.

RESULTS

COURTSHIP DISPLAYS

We described and quantified the behavior of 404 Least, 246 Crested, 43 Whiskered, and 224 Parakeet Auklet pairs at sea. We identified six distinct courtship displays performed by auklets on the sea: hunch, pursuit, ruff-sniff, neck-twist, head-bob, and mutual-court (Fig. 1a–d). The hunch, pursuit, and mutual-court displays were used by all four species, although pursuit behavior was most prevalent in Crested Auklets. The neck-twist display was performed almost exclusively by Crested Auklets, the ruff-sniff display was unique to Crested Auklets, and the head-bob was performed only by Whiskered Auklets (Fig. 2a–e). The hunch display was similar to one performed during Least and Crested Auklet courtship on land (Jones 1993a, 1993b). One or both pair members leaned forward toward the other, with necks stretched outward and held close to the water, bills oriented upwards, and nape and upper back feathers erected (Fig. 1a). Hunch displays often involved one pair member pursuing the other with neck down and head up towards its partner. We referred to this combination of hunched posture and close following as the pursuit display. All four species of auklets engaged in both hunch and pursuit displays (Figs. 2a, b). Hunch displays were most prevalent in Least Auklets with 42.1% (170/404) of focal pairs engaging in this behavior. Pursuit displays were most frequent in Crested Auklets with 73.6% (181/246) of focal pairs displaying this behavior. In Whiskered Auklets, the hunched posture occurred almost exclusively as part of pursuit displays (hunch 2.3%, 1/43; pursuit 20.9%, 9/43).

An exaggerated form of close pursuit behavior was observed in Crested Auklets at sea. One individual would closely follow, with its body alongside but partly behind, its partner, its breast resting on the partner's back and its bill nestling into the neck feathers of its partner (Fig. 1b). This latter behavior appears to be a modified form of the ruff-sniff courtship display which Crested Auklets perform during land-based courtship (Zubakin 1990, Jones 1993a). Both male and female Crested Auklets took the active "nuzzling" role in ruff-sniffing behavior at sea. In Crested Auklets, 8.8% (16/181) of pursuits involved ruff-sniffing.

Another courtship behavior almost entirely

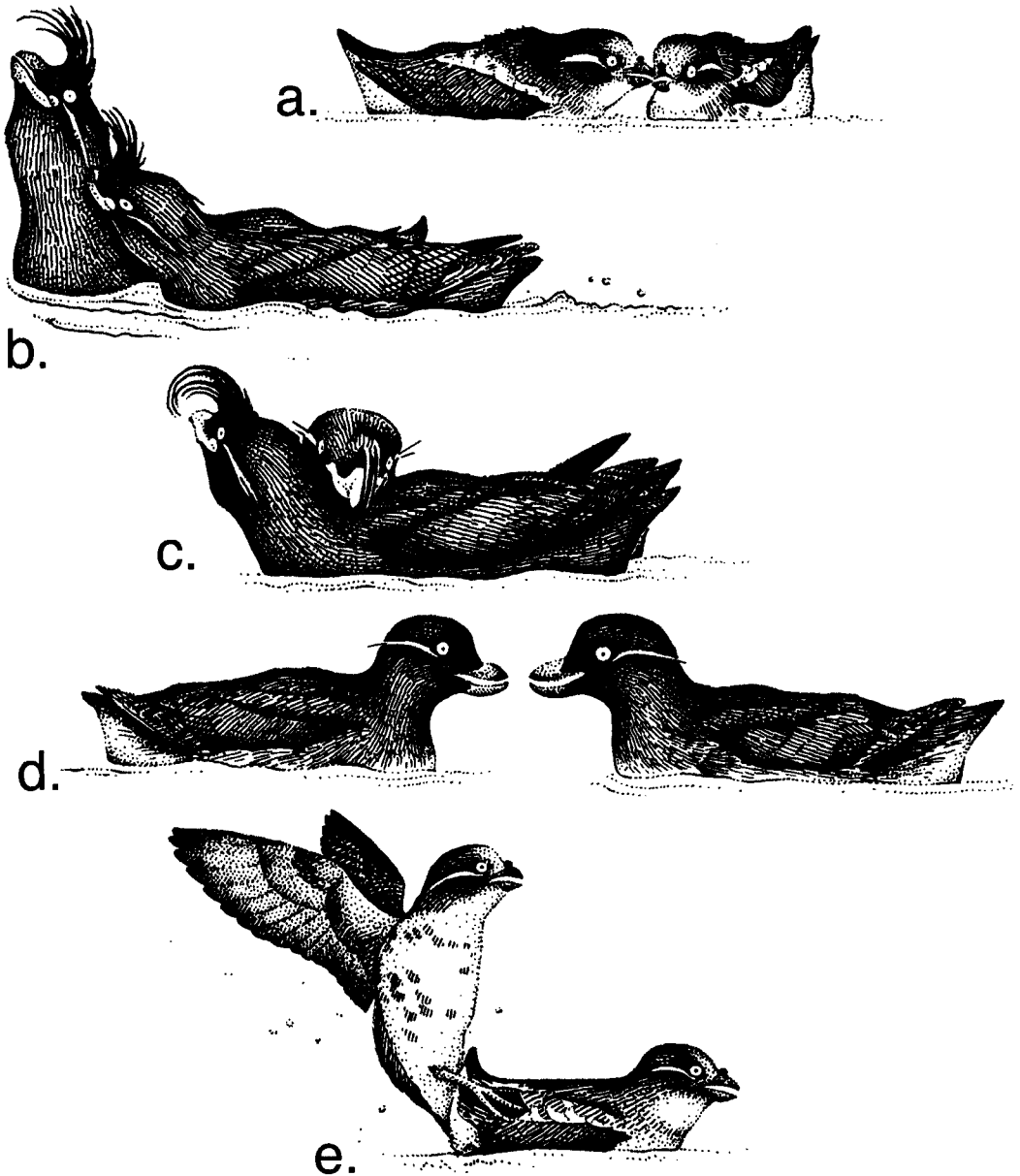


FIGURE 1. Courtship and copulation behavior in auklets. Courtship displays illustrated for the species that engages in that display most frequently. (a) Hunch display in Least Auklets. (b) Pursuit with ruff-sniff behavior in Crested Auklets. (c) Neck-twist display in Crested Auklets. (d) Mutual-court display in Parakeet Auklets. (e) Behaviorally successful copulation involving apparent cloacal contact in Least Auklets.

limited to Crested Auklets was the neck-twist display, in which the male and female mutually intertwined their necks, often while facing each other and circling each other on the water (Figs. 1c, 2c). This display also is performed frequently by Crested Auklets courting on land (Jones

1993a). A small number of Least Auklets engaged in this display at sea (2.0%, 8/404 of Least Auklet focal pairs, Fig. 2c) but we never observed it in Whiskered or Parakeet Auklets. The head-bob display was unique to Whiskered Auklets (Fig. 2d; V. Zubakin, unpubl. data).

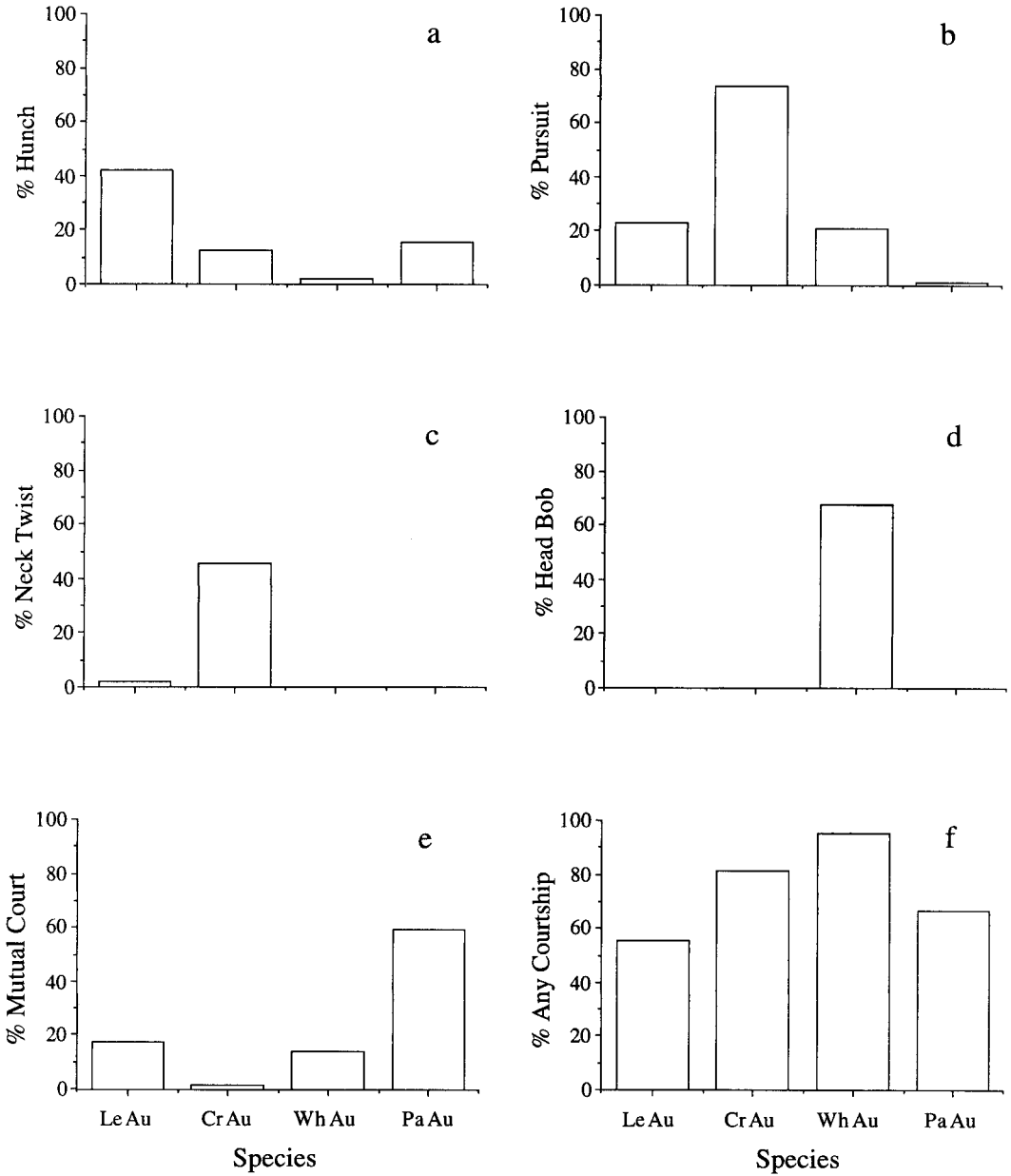


FIGURE 2. Proportion of pairs of Least (LeAu), Crested (CrAu), Whiskered (WhAu), and Parakeet (PaAu) Auklets that exhibited (a) hunch display, (b) pursuit behavior, (c) neck-twist display, (d) head-bob display, (e) mutual-court display, and (f) any courtship display.

While facing its partner, one or both pair members rhythmically and repeatedly raised and lowered the head, often with the head stretched forward. Of all focal pairs of Whiskered Auklets observed, 67.4% (29/43) were seen to engage in a head-bobbing display. Mutual-courting took

the form of both members of the pair facing and vocalizing towards each other (Fig. 1d). This display was recorded in all four species of auklet although it was particularly prevalent in Parakeet Auklets with 63.7% (121/190) of observed pairs on Buldir and 38.2% (13/34) of pairs on

TABLE 1. Heights of mounted pairs of auklets in relation to space available in the nesting crevice.

Species	Estimated height of copulating pair (mm) ^a	Crevice height (mm)				% crevices smaller than height of copulating pair
		Mean	SD	Range	n	
Least Auklet	120	99.8	37.8	44–192	38	73.7
Crested Auklet	170	153.4	52.3	98–329	32	75.0
Whiskered Auklet	140	112.7	36.3	60–237	54	85.2
Parakeet Auklet	170	175.4	54.6	96–242	11	36.4

^a Conservative estimate of minimum height of copulating pair based on two body thicknesses, using body thickness measurements of Least and Crested Auklets, and estimates of body thicknesses of Whiskered and Parakeet Auklets based on the relative sizes of the four species.

St. Paul Island engaging in this behavior (Fig. 2e). Six pairs of Parakeet Auklets were seen to engage in a sky-pointing display as an addition to the mutual-court display. This took the form of one member of the pair stretching its head and neck up and pointing its bill nearly vertically upwards while vocalizing.

Taking all displays together, the four species differed in the frequency in which they engaged in courtship ($\chi^2_3 = 55.0$, $P < 0.001$; Fig. 2f), with Whiskered Auklets exhibiting the highest courtship frequency (95.3%, 41/43, of observed pairs engaged in courtship), Crested and Parakeet Auklets an intermediate courtship frequency (Crested Auklets: 78.9%, 194/246, of observed pairs engaged in courtship; Parakeet Auklets: 67.0%, 150/224, of observed pairs engaged in courtship), and Least Auklets the lowest courtship frequency (55.4%, 224/404, of observed pairs engaged in courtship). For Least Auklets there was no difference in the frequencies of any of the courtship displays performed by pairs at Buldir and those at St. Paul Island (hunch: $\chi^2_1 = 3.4$, $P = 0.07$; pursuit: $\chi^2_1 = 0.6$, $P = 0.44$; neck-twist: $\chi^2_1 = 0.1$, $P = 0.80$; court: $\chi^2_1 = 0.5$, $P = 0.49$). Similarly, there was no difference in the frequency of hunch or pursuit displays performed by Parakeet Auklet pairs at Buldir and those at St. Paul Island (hunch: $\chi^2_1 = 0.4$, $P = 0.54$; pursuit: $\chi^2_1 = 0.2$, $P = 0.70$). However, Parakeet Auklets at Buldir performed more mutual-court displays than those at St. Paul Island ($\chi^2_1 = 6.7$, $P = 0.01$).

COPULATION BEHAVIOR

All copulations occurred at sea. It is unlikely that pairs copulated in their nesting crevices as the majority of Least, Crested, and Whiskered Auklet crevices were too small to accommodate a pair in the copulation position used by most birds in which the male is positioned over the females back (Table 1).

In all, we observed 394 copulation attempts at sea comprising 166 behaviorally successful and 228 unsuccessful copulations (attempted: Least 176, Crested 157, Whiskered 35, Parakeet 26; successful: Least 71, Crested 69, Whiskered 15, Parakeet 11). Copulation was similar in all four auklet species. The male did not mount the female as in other avian species, but instead positioned himself at the rear of the female, raised himself up with flapping wings, brought his cloaca up under the female's tail and in an upright vertical stance, maintained by vigorous wing flapping and using his feet to steady himself, brought his cloaca up to meet the female's cloaca. The lift generated by rapid beating of the wings appeared to give the male lift to push the female's cloaca up from the water (Fig. 1e). By copulating without mounting, males avoided submerging the female's cloaca under water during insemination. Hence, insemination occurred well clear of the sea surface avoiding water damage to sperm.

Most pairs of auklets engaged in a single copulation attempt during any observation period, but up to five copulation attempts in rapid succession were observed in focal pairs of Least and Crested Auklets, and up to three consecutive attempts were seen in Whiskered and Parakeet Auklets. One Crested Auklet pair engaged in five behaviorally successful copulations and a Least Auklet pair engaged in three behaviorally successful copulations in succession. However, overall there was no difference among the four species in the incidence of single as opposed to multiple copulation attempts or single as opposed to multiple behaviorally successful copulations (attempts: $\chi^2_3 = 4.5$, $P = 0.21$; behaviorally successful $\chi^2_3 = 3.3$, $P = 0.34$).

There was no difference among the four species in the likelihood of a pair being behaviorally successful when engaging in one or more

copulation attempts during an observation period ($\chi^2_3 = 1.3$, $P = 0.73$). Failure of copulation attempts prior to apparent cloacal contact occurred for a number of reasons, including male failure to achieve or maintain correct positioning, female avoidance of copulation, and disruption by an extrapair individual. Female cooperation was necessary for a copulation attempt to result in a behaviorally successful copulation. Females had to actively maintain their position in the water and hold their tails in an upright position for the pair to achieve cloacal contact. Females of all four species were observed both avoiding a male's courtship advances and terminating copulation attempts. They did this by flying away, swimming forward, diving, or simply keeping their tails either flattened against the water surface or submerged under water. Female Parakeet Auklets terminated a relatively high proportion of copulation attempts (36.4%, 4/11). Female Crested Auklets caused failure in 27.9% (17/61) of copulation attempts, and female Whiskered Auklets were responsible for failure in 18.8% (3/16). Female Least Auklets caused relatively few failures (8.6%, 6/70).

Intruding conspecifics disturbed pairs at all stages during courtship and copulation. Disruptions varied from individuals swimming towards a courting pair, to individuals flying in and knocking the male from his copulating position, immediately prior to or during apparent cloacal contact. Least Auklets experienced the highest level of courtship disruption, with 54.4% (43/79) of courtship bouts being disrupted by one or more conspecifics. Crested Auklet courtship bouts were disrupted in 32.3% (52/161) of cases, whereas Whiskered and Parakeet Auklets experienced lower levels of courtship disruption (Whiskered: 10.0%; 3/30, Parakeet: 14.1%, 9/64). Disruptions occurring during copulation were less common for all species (Least: 3.4%, 2/59; Crested: 1.1%, 1/87; Whiskered: 4.5%, 1/22; Parakeet: 0%, 0/14). Disruptions were followed by one or both members of the pair driving the intruder away, or one member of the pair driving the other member of the pair away from the intruder.

One copulation attempt involving a pair of Least Auklets was terminated by a Glaucous-winged Gull (*Larus glaucescens*). The female of the pair dived seconds before the attack and the male was caught by the predator and swallowed whole.

Extrapair copulation attempts were observed in all four species of auklet, and unforced behaviorally successful EPCs occurred in Least, Crested, and Whiskered Auklets (members of focal pairs engaging in EPC attempts: Least 33, Crested 12, Whiskered 2, Parakeet 2; members of focal pairs engaging in behaviorally successful EPCs: Least 3, Crested 2, Whiskered 1). EPCs took the form of an extrapair male rapidly swimming up to, or flying in and landing close to a pair, and attempting to copulate with the female. The pair male was usually close by and in most cases he attempted to disrupt the copulating individuals and either chase the extrapair male away or drive his female away from the extrapair male. In every case in which the behavior of the focal individuals was recorded after the EPC attempt, the female remained with her original partner (Least 13, Crested 11, Whiskered 1, Parakeet 1). Pair males often attempted copulations with their partners immediately following extra-pair copulation attempts (Least: 6 of 33 [18%] attempted EPCs followed by a pair copulation attempt; Crested: 5 of 12 [42%]; Whiskered: 1 of 2 [50%]).

DISCUSSION

Auklets are unusual among seabirds in having exclusively aquatic copulation and related courtship behavior at sea. Most of our focal pairs of Least, Crested, Whiskered, and Parakeet Auklets engaged in courtship displays during the morning activity period at their staging areas near the breeding colony. Pairs also bathed and preened while at the staging area at this time, however single individuals appeared just as likely to engage in self-maintenance as paired birds. Thus it appears that the main reason for auklets being present in pairs near the staging flock was to engage in courtship and copulation behavior. Some behaviors displayed during courtship at sea were similar to land-based courtship displays. The hunch display occurs in both Least and Crested Auklets on land, and the neck-twist and ruff-sniff displays occur in Crested Auklets on land (Jones and Montgomerie 1992, Jones and Hunter 1993). Little is known of Whiskered and Parakeet Auklet courtship behavior on land because of the Whiskered Auklet's nocturnal disposition and the Parakeet Auklet's dispersed nesting and crepuscular habits. Consequently, it is not known whether the Whiskered Auklet's

head-bob or the Parakeet Auklet's mutual-court display occur on land.

With the exception of pursuit behavior, all displays focused on the head region of the displaying birds, where the ornaments of all four species are situated. Therefore, it seems probable that the displays function to highlight or draw attention to ornaments and that individuals engaging in courtship displays assess their partner's ornaments. Crested Auklets' ruff-sniff and neck-twist displays were conspicuous in focusing specifically on the back and sides of the neck. Crested Auklets have a distinctive citrus-like plumage odor which is very noticeable on the nape and neck feathers (pers. observ.) Although it was not possible to determine whether the birds were actively smelling their partners' neck feathers during the ruff-sniff or neck-twist displays, it is possible that this odor is a sexually selected trait.

All auklet displays were carried out by both sexes. The neck-twist, head-bob, and mutual-court displays involved simultaneous displaying by both sexes, whereas the pursuit and ruff-sniff displays were performed at different times by male and female. Sexually monomorphic courtship behavior is consistent with similar ornaments being expressed in both sexes and with mutual mate choice. Mutual mate choice has been experimentally demonstrated in Least and Crested Auklets (Jones and Montgomerie 1992, Jones and Hunter 1993), and, on the basis of mutual courtship behavior and mutual expression of ornaments, it is likely to occur in Whiskered and Parakeet Auklets.

Three courtship behaviors, hunch, pursuit and mutual court, were observed in all four species of auklet, whereas other displays such as the ruff-sniff display of the Crested Auklet or the head-bob of the Whiskered Auklet were unique to one species. This partitioning of displays may have been useful, at some time in the past, in facilitating species recognition. Although auklet species are morphologically quite distinct at the present time, it is possible that these displays evolved during speciation events by helping individuals to avoid copulating with species other than their own. This is consistent with the observation that the two most closely related auklet species (Crested and Whiskered) have the most distinct courtship display and elaborate morphological adornments.

In species which have an intromittent organ,

males are able to perform forced copulations (Mineau and Cooke 1979, Burns et al. 1980). Forced copulations were not observed in any of the four species of auklets. Instead, female cooperation was necessary for a behaviorally successful copulation to be achieved.

In this study we defined a pair as two birds maintaining close proximity over a period of at least 2 min. We justified this definition on the basis of observations of known pairs leaving the talus together and engaging in behavior identical to that of our focal pairs. However, in the absence of individual identification of focal birds, we could not be certain that all pairs defined in this way were breeding partners or that extrapair males were not in fact breeding partners of the focal female. Following an EPC attempt, females always returned to the original focal male and these males often engaged in copulation attempts so that females copulated with two different males within minutes of each other. This supports the idea that extrapair males were not the female's breeding partners and that sperm competition is a feature of auklet mating systems. Nevertheless, studies of individually marked birds have shown the occurrence of unforced EPCs between two birds in the temporary absence of the partner of one of them (Hatch 1987, Hatchwell 1988, Hunter et al. 1995). Such unforced EPCs tended to be behaviorally indistinguishable from pair copulations (F. M. Hunter, pers. observ.). If a female and extrapair male consorted in this manner in the present study, they would not have been identified as an extrapair partnership. However, rather than artificially inflating the importance of EPCs, this would tend to result in underestimation of the incidence of extrapair activity.

All copulations that we observed in this study occurred at sea. During over 1,500 hours of observations of Least and Crested Auklets on land at the Main Talus breeding colony on Buldir during both morning and evening activity periods (Jones and Hunter 1993, 1998, in press), no copulation was ever observed either on the surface of the talus or in protected areas below or behind boulders. Furthermore, the majority of Least, Crested, and Whiskered Auklet crevices were too small to accommodate a mounted pair, so it is unlikely that many pairs copulated in their nesting crevices. Hence, it appears that auklet copulations must occur mainly or exclusively at sea.

The weight of a male bird mounting a female in water is likely to cause the female's cloaca to become submerged. If sperm were inseminated by the usual avian method of cloacal contact, the male's sperm would likely be washed away or damaged by the surrounding water. Male waterfowl have an intromittent organ so sperm can be safely inseminated inside the female even if her cloaca becomes submerged when the male is mounted (Lake 1981, Briskie and Montgomerie 1997). Auklets, which copulate at sea but do not have an intromittent organ, have an alternative way of overcoming the potential problem of cloacal submergence and water damage to sperm. Male auklets did not mount females when copulating at sea. By remaining unmounted and instead using rapid flapping of the wings to bring himself into the correct position for cloacal contact, male auklets avoided submerging their partners and running the risk of causing water damage to sperm during insemination. This unorthodox system of copulating may be the only way males can achieve sperm transfer by cloacal contact without submerging the female. The unique alcid shape with the legs set far back on the body and the wings compact and powerful, might facilitate this form of copulation, although similarly shaped alcids such as the murres and penguins copulate by mounting on land.

Within the Alcidae, the practice of copulating at sea appears to be phylogenetically constrained. There are two major groups within the Alcidae, one containing the puffins and Rhinoceros Auklet (*Cerorhinca monocerata*, Fraterculini) and the true auklets (Aethiini), the other containing the murres, Razorbill (*Alca torda*) and Dovekie (*Alle alle*, Alcini), the guillemots (Cepphini), the synthliboramphine murrelets (Synthliboramphini), and the brachyramphine murrelets (Brachyramphini; Friesen et al. 1996). Copulation location has been established for 16 of the 23 extant alcid species. Seven of the eight species known to copulate primarily or exclusively at sea all belong to the first group, whereas the eight remaining species known to copulate primarily or exclusively on land all belong to the second group. The one exception to this pattern is the Marbled Murrelet which phylogenetically belongs to the murre-guillemot-murrelet group but has been recorded copulating most often at sea (Gaston and Jones 1998).

It would appear that for a species that lacks an intromittent organ it would be easier to cop-

ulate on land than at sea. So the crucial question is why do auklets and puffins, which lack intromittent organs, copulate at sea instead of on land like other alcids? We propose several hypotheses to explain auklets' propensity for aquatic mating.

(1) Predation avoidance. At many colonies, auklets suffer frequent attacks by gulls and other avian predators suggesting that birds engaging in copulations on land might be vulnerable to predation. Pairs mating at sea had an excellent view of approaching avian predators and escaped attacks quickly by diving. One pair of Least Auklets in our study suffered predation while copulating at sea but predation pressure on land apparently was greater than that occurring at sea. If copulation on land carries a predation risk, it would be predicted that auklets would copulate at protected sites within the talus where they would be immune from gull predation. We have made many observations of Least and Crested Auklet courtship behavior on the talus (Jones and Hunter 1998, in press) during which protected sites beneath overhanging or jumbled boulders were visible, but we have never seen a pair of auklets copulating on land. Nor does it appear possible for many pairs to copulate in the protection of their nesting crevices as most of these were too small to accommodate a pair of copulating auklets. Furthermore, even if predation pressure on the talus surface was a problem for Least and Crested Auklets, it is not likely to be a problem for the Whiskered Auklet which is active on land only at night, yet this species still copulates at sea. Thus, predation pressure alone does not appear to provide an unequivocal explanation for aquatic copulation.

(2) Harassment and EPC avoidance. Females copulating on land within the colony site might find it more difficult to avoid harassment and forced EPC attempts by extrapair males. Harassment which carries costs of wasted time and potential injury to the female or her unlaidd egg may come in the form of forced extrapair copulation attempts which occur in Pigeon Guillemots (*Cephus columba*), Common Murres (*Uria aalge*), and Razorbills, all of which copulate on land (Drent 1965, Birkhead et al. 1985, Wagner 1991). Behaviorally successful forced EPCs have been reported in Common Murres (Birkhead et al. 1985, Hatchwell 1988). Under normal circumstances it seems unlikely that males in species that lack intromittent organs

can force copulations on females (Fitch and Shugart 1984). Indeed, Wagner (1991) argues convincingly that female Razorbills are in control of copulation success. However, male Common Murres have adopted a strategy to overcome uncooperative females and achieve successful forced EPCs. Males sometimes engage in multiple-male EPC attempts, and when four or more males are involved, the female can be pinned down enabling some males to achieve cloacal contact (Birkhead et al. 1985). By being receptive only at sea, females retain the option of escape by diving at any time and thus can avoid unwanted copulations. Similar avoidance of unwanted copulations is seen in Atlantic Puffins (Creelman and Storey 1991). It would be predicted that if multiple male groups of auklets could force EPCs on females on land, they would do so during those activity periods in which males and females court at the breeding colony on the talus surface, but no copulation was ever observed on land. Female auklets on a flat boulder may always be able to move away from males attempting EPCs, unlike female murres pinned against a cliff face. At sea, female auklets would be able to escape harassment by diving and reduce their susceptibility to disturbance by avoiding areas of high bird density. Mating pairs often frequented the periphery of the staging flock where relatively fewer conspecifics were present. Hence, it appears unlikely that aquatic copulation in auklets is based on a female strategy to avoid forced copulations, but pairs may mate at sea to avoid harassment by conspecifics.

(3) Cleanliness. Individuals spending time in their crevices and under the talus are prone to getting their under-tail coverts, and therefore the area around the cloaca, soiled with feces and mud. During copulation on land, dirt and associated micro-organisms would likely be transferred onto the cloaca of a copulating partner (Sheldon 1993). Aquatic copulation with a partner who has washed on the water surface before copulating would likely reduce the chances of pathogen transmission. Auklet pairs bathed and preened intensely while in the staging flock which supports this idea. However, the question arises as to why birds did not wash and then return to land to copulate. Dirt is likely to pose a similar problem for murres and Razorbills which nest and copulate on feces-covered cliff ledges. Murres at least are constrained to copu-

late at their nest sites because of the need for at least one pair member to be present at all times to defend the nest site from conspecifics. Nevertheless, the question of whether cleanliness plays a role in determining copulation location remains open. A detailed comparative study of cleaning behavior and pathogen transmission in relation to copulation location in alcids would be required to resolve this question.

(4) Female testing of males. If it is hard for a male to achieve a successful copulation at sea, he may be honestly signaling his quality to the female by copulating in this manner. By accepting copulation attempts only at sea, the female may gain by having the opportunity to test the quality of the male.

(5) Nonadaptive. Despite the apparent complications of aquatic copulation, it may not be any more difficult for an auklet pair to copulate at sea than on land. It may be that the ancestor of the auklets and puffins copulated at sea and thus that modern species continue to do so in the absence of any opposing selective force.

In summary, unlike most other bird species, and even unlike most seabird species, auklets court intensely and copulate mainly or exclusively at sea. On the basis of our data, we were unable to unequivocally discriminate among possible explanations which could play a role in favoring aquatic copulation. The question of why these birds copulate at sea remains an enigma that deserves further attention.

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