

Short communication

Social and self-maintenance behaviour of adult and sub-adult Little Auks *Alle alle* and Least Auklets *Aethia pusilla* at two breeding colonies

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Little Auks *Alle alle* and Least Auklets *Aethia pusilla* are ecologically similar, planktivorous, colonial, crevice-nesting, socially monogamous seabirds of arctic waters of the North Atlantic and North Pacific regions, respectively (Gaston & Jones 1998). Although each is the smallest alcid within its usual range and the two have similar appearance, feeding apparatus, diet preferences and breeding habitat selection, they are phylogenetically rather distantly related. The Little Auk is an unusual outlier within the clade (Alcini) that includes the extinct Great Auk *Pinguinnis impennis*, Razorbill *Alca torda* and Brünnich's Guillemot *Uria lomvia*. The Least Auklet is one of five auklet species produced by an adaptive radiation of the tribe Aethiini (Jones 1999) within the puffin–auklet clade (Strauch 1985, Friesen *et al.* 1996, Gaston & Jones 1998), a separate evolutionary lineage from the Alcini. Ecological similarities between the Little Auk and Least Auklet have been discussed previously by Bédard (1969). The form of Little Auk (Evans 1981, Stempniewicz 1981, summarized in Cramp *et al.* 1985 pp. 219–229) and Least Auklet (Jones 1993) social behaviour has been described anecdotally. Here we quantify the social and self-maintenance behaviour of the two species. We evaluated differences between these two species in the diversity and frequency of social and sexual displays and other activities at breeding colonies. We also assessed the relationship of these behaviours to age (adult vs. sub-adult) within and between species.

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Comparative studies of the behaviours of prebreeding individuals at colonies are thus crucial to any understanding of convergent evolution in social behaviour. Social learning by prebreeding individuals before they obtain a mate and breeding site are crucial to an individual's lifetime reproductive success in long-lived seabirds. An individual's activities upon returning to the colony prior to reaching the 'age at first breeding' include: learning how to manoeuvre in flight and on land at the colony site, to recognize and locate suitable breeding habitat and territories, to interact socially with conspecifics, to avoid predation, and to avoid competition with other species occupying the same habitat. Therefore, prebreeding colony attendance may aid an individual's learning to obtain breeding sites and mates for future breeding. No previous study has quantified the behaviour of immature Little Auks and Least Auklets at colonies.

In summary, the objectives of our study were: (1) to quantify the frequency and outcome of sexual and agonistic displays in relation to age (adult vs. sub-adult) of Little Auks and Least Auklets attending two representative colonies during the breeding season, (2) to quantify the frequency of breeding site prospecting, self-maintenance and other non-social behaviour in this situation, and (3) to evaluate interspecific differences in these behaviours in relation to phylogeny.

METHODS

Study areas

We quantified Little Auk behaviour at Bjørndalen, Isfjorden, Svalbard, Norway (78°14'N, 15°22'E; Isaksen & Bakken 1995), during the incubation period 10–17 July 1999. We quantified Least Auklet behaviour at Main Talus, Buldir Island, Aleutian Islands, Alaska (52°24'N, 175°54'E; Byrd & Day 1984), during the incubation and early chick-rearing periods of 1 June–4 July 2000. For both species, our observations were made only during the part of the breeding season when both adults and sub-adults were present at the colony (Roby *et al.* 1981, Jones 1992, Jones 1993).

Behavioural observations

We recorded the presence or absence of stereotyped behaviours during 2-min watches of focal individuals selected randomly from among birds attending the rocky surface of breeding colonies. Focal individuals that left the colony site before 2 min elapsed were excluded from further analysis (except for Little Auk observations in which a 'butterfly flight' occurred and the individual returned immediately to its display rock). At Bjørndalen, we made observations of Little Auks throughout the colony site including two study plots where 101 individuals had been colour marked previously (Isaksen & Bakken 1995, F. Mehlum *et al.* unpubl. data). Because we made our

behaviour observations throughout these colonies where many thousands of individuals were present and because we were able to observe individually colour marked birds, we do not believe that any individual's behaviour was scored more than once. For each Little Auk selected for a focal watch, we recorded its colour band combination (if present) and age (adult or sub-adult), and scored the occurrence of the following social behaviours during the focal watches: bow, skypoint, head nod, head wag, stomp, butterfly flight, vocalize, allopreen and billing (Evans 1981, Stempniewicz 1981, Cramp *et al.* 1985). These displays and behaviours occur at the colony from the laying period until late in the chick-rearing period (review by Cramp *et al.* 1985). We also scored aggressive interactions and their outcomes. Aggressive interactions included one or more of the following common forms of behaviour: lunging towards another individual with head and bill lowered or outstretched, pecking or biting the opponent, or, more rarely, grasping with the bill, or grasping with the bill combined with displacement of the opponent. 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. We did not observe copulations because these occurred only during the prelaying period, prior to our focal observations. We also recorded the following self-maintenance and related behaviours during the focal watches: preen self, carry stone, peer into talus and sleep (Evans 1981, Stempniewicz 1981, Cramp *et al.* 1985).

At Buldir Island, we made observations of Least Auklets from 10 different locations on Main Talus including two study plots, one with 426, and another with 59 individuals colour marked previously (I.L. Jones *et al.* unpubl. data). We recorded the colour band combination (if present), age (adult or sub-adult) and we recorded the presence of the following social behaviours: arch, hunch, vocalize, touch another bird, billing, aggressive interaction – win and aggressive interaction – lose (Jones 1990, 1993). These displays and behaviours occur throughout the breeding season with no consistent seasonal trends in frequency (Jones 1992, 1993). We did not observe copulations because these occurred only at sea and during the prelaying period, prior to our focal observations (Hunter & Jones 1999). For Least Auklets, we recorded the presence of the following self-maintenance and related behaviours: preen self, peer into talus and sleep. We observed and recorded Little Auk and Least Auklet behaviour on display rocks (large boulders with 1–5 m² flat upper surfaces, where birds congregated to engage in courtship and other activities; Stempniewicz 1981, Jones 1993).

The focal individuals selected alternated between adults and sub-adults to ensure an equal number of individuals of each age group and to control for any related systematic time of day and seasonal effects. Adult (2 years old and over) and sub-adult (1 year old) Little Auks were distinguished on the presence of lighter coloured, abraded, primaries, secondaries and wing coverts in sub-adults (Roby

et al. 1981, Bradstreet 1982, Bédard 1985). Adult (2 years old and over) and sub-adult (1 year old) Least Auklets were distinguished by the presence of similar light coloured abraded flight feathers, brownish forehead plumage, and spotted throats in sub-adults (Bédard & Sealy 1984, Jones 1990, 1993, Jones & Montgomerie 1992).

Statistical analysis

To quantify the frequency of sexual and agonistic displays and other behaviours we used the proportion of complete 2-min focal samples from each species and age group in which each behaviour occurred. We used G- or Fisher's exact tests to compare the frequency of behaviours between species and age-groups. We used the binomial test (Zar 1984, p. 371) to evaluate whether adults or sub-adults were more likely to win aggressive interactions.

RESULTS

Little Auk adults performed significantly more courtship displays (bow, skypoint, head nod, head wag, stomp, butterfly flight, vocalize and billing) than sub-adults, which rarely engaged in courtship-related activities (Table 1). Sub-adult Little Auks never performed head wag or head nod social displays and rarely bowed, skypointed, stomped or performed the butterfly flight, but did peer into crevices more frequently (Table 1). Adult and sub-adult Little Auks were equally likely to engage in agonistic interactions. When these interactions involved an adult and a sub-adult bird, adults were significantly more likely to win (i.e. displace the sub-adult): of 17 such interactions observed, all were won by the adult (binomial, $P < 0.0001$). Taken together, our results indicated that sub-adult Little Auks engaged in little activity at the breeding colony other than preening and peering into crevices and were socially subordinate to adults. We observed Little Auks conspicuously modifying the shape of their crown, forehead, throat, nape and the white pre-ocular spot by erecting different feather tracts during social displays. Although we were unable to quantify these 'head shape' displays, these were expressed most conspicuously in adults and rarely observed in sub-adults.

Least Auklet adults performed significantly more frequent courtship displays (arch, hunch, vocalize, and billing) than sub-adults, which rarely engaged in courtship activity or indeed any social behaviour (Table 2). Adult Least Auklets were also significantly more likely to touch other individuals while attending their colony than were sub-adults. However, sub-adults engaged in significantly more frequent preening and peering into crevices (Table 2). Adult and sub-adult Least Auklets were equally likely to engage in agonistic interactions. When these interactions involved an adult and a sub-adult bird, the adults were significantly more likely to win: of 27 such interactions, 26 were won by the adult (binomial, $P < 0.0001$). Our results indicated that like sub-adult Little Auks,

Table 1. Number of 2-min focal individual watches in which displays and other activities of adult ($n = 100$) and sub-adult ($n = 100$) Little Auks occurred at Bjørndalen, Svalbard.

Behaviour	Number (% ^a)			
	Adults	Sub-adults	G_1	P
Display				
Bow	48 (48)	6 (6)	49.4	<0.0001 ^d
Skypoint	12 (12)	3 (3)	6.2	0.01
Head nod	8 (8)	0 (0)	8.3 ^b	0.007 ^{cd}
Head wag	26 (26)	0 (0)	29.9 ^b	<0.0001 ^{cd}
Stomp	36 (36)	2 (2)	44.2	<0.0001 ^d
Butterfly flight	13 (13)	1 (1)	13.0	0.0003 ^d
Vocalize	57 (57)	2 (2)	86.4	<0.0001 ^d
Billing	24 (24)	1 (1)	29.3	<0.0001 ^d
Preen other bird	1 (1)	0 (0)	1.0 ^b	1.0 ^c
Agonistic				
Agonistic interaction	11 (11)	14 (14)	0.4	0.52
Self maintenance				
Preen self	29 (29)	27 (27)	0.1	0.75
Sleep	1 (1)	1 (1)	0.0	1.0
Other behaviour				
Carry stone	1 (1)	0 (0)	1.0 ^b	1.0 ^c
Peer into talus	5 (5)	14 (14)	4.9	0.027

^aPercentage of individuals performing behaviour during 2-min watches. ^{b,c} χ^2 statistic reported and Fisher's exact test used because one cell in two by two table was a zero. ^dSignificant differences at a table wide $P < 0.05$, using sequential Bonferroni analysis.

Table 2. Number of 2-min focal individual watches in which displays and other activities of adult ($n = 63$) and sub-adult ($n = 63$) Least Auklets occurred at Main Talus, Buldir Island, Alaska.

Behaviour	Number (% ^a)			
	Adults	Sub-adults	G_1	P
Display				
Arch	30 (48)	2 (3)	37.9	<0.0001 ^d
Hunch	54 (86)	2 (3)	103.7	<0.0001 ^d
Vocalize	54 (86)	1 (2)	110.7	<0.0001 ^d
Touch	25 (40)	12 (19)	6.6	0.01 ^d
Billing	13 (21)	0 (0)	14.5 ^b	0.0001 ^{cd}
Agonistic				
Agonistic interaction	22 (35)	15 (24)	1.9	0.2
Self maintenance				
Preen self	9 (14)	20 (32)	5.5	0.02
Sleep	0 (0)	1 (2)	1.0 ^b	1.0 ^c
Other behaviour				
Peer into talus	13 (21)	27 (43)	7.3	0.007 ^d

^aPercentage of individuals performing behaviour during 2-min watches. ^{b,c} χ^2 statistic reported and Fisher's exact test used because one cell in two by two table was a zero. ^dSignificant differences at a tablewide $P < 0.05$, using sequential Bonferroni analysis.

sub-adult Least Auklets engaged in little activity at the breeding colony other than preening and peering into crevices and were socially subordinate to adults. Although Least Auklets erected feathers on the upper back during the hunch social display, they did not modify their head shape conspicuously during social displays.

Adult Least Auklets performed vocalizations, engaged in agonistic interactions and peered into rock crevices significantly more frequently than adult Little Auks; Little Auks engaged in more frequent preening (Table 3). Unlike Little Auks, Least Auklets never picked up stones or performed butterfly flights. Least Auklets had only two

Table 3. Number of 2-min focal individual watches in which comparable displays and other activities of adult Little Auks ($n = 100$) and Least Auklets ($n = 63$) occurred.

Behaviour	Number (% ^a)			
	Little Auks	Least Auklets	G_1	P
Display				
Vocalize	57 (57)	54 (86)	15.8	<0.0001 ^b
Billing	24 (24)	13 (21)	0.3	0.6
Agonistic				
Agonistic interaction	11 (11)	22 (35)	13.4	0.0002 ^b
Self maintenance				
Preen self	29 (29)	9 (14)	4.9	0.03 ^b
Peer into talus	5 (5)	13 (21)	9.4	0.002 ^b

^aPercentage of individuals performing behaviour during 2-min watches. ^bSignificant differences at a tablewide $P < 0.05$, using sequential Bonferroni analysis.

stereotyped postural displays (arch and hunch; Jones 1993), while Little Auks had six (bow, skypoint, head nod, head wag, stomp, butterfly flight; Cramp *et al.* 1985).

DISCUSSION

Consistent with their similarities as ecological counterparts in two oceans, we found striking parallels in the behaviour of Little Auks and Least Auklets at colonies. Both species congregated on display rocks on the surface of their colony sites and engaged in superficially similar activities and social behaviour. In both species, adults performed a conspicuous vocal advertising display. The most obvious difference between the two species was greater diversity of stereotyped postural displays and adjustments of head feathers in the Little Auk. Little Auks had six distinctive visual displays while Least Auklets had only two, and only Little Auks displayed extraordinary modification in head shape by differential feather erection.

We suggest that the apparently smaller behavioural repertoire of Least Auklets may be compensated for by greater and more variable ornamentation (bill colour, bill knob ornament, facial plumes; Jones & Montgomerie 1992) and overall plumage variability (Jones 1990) that function as social signals. Both species performed a conspicuous vocal advertising display, in Little Auks executed by individuals of unknown sex and accompanied by a conspicuous 'butterfly flight' display and in Least Auklets performed only by males from a display rock. Further fieldwork is required to quantify seasonal patterns of Little Auk displays, the complex visual displays of Little Auks, the vocal repertoire of both species, and to establish whether the Little Auk's conspicuous vocal advertising display and associated 'butterfly flight' is performed by both sexes or only by males.

Least Auklets had a higher rate of vocalizing, engaging in agonistic interactions and peering into crevices, than

Little Auks, while Little Auks were more frequently observed preening and sleeping. The Least Auklet's higher activity rate may be related to the need to complete their activities during shorter activity periods (5–6 h per day, Jones 1993) on the colony surface compared to Little Auks (10–12 h or more per day, reviewed by Cramp *et al.* 1985), or to a difference in density between the two colony sites in this study.

Adult Little Auks are the only member of the large auk clade Alcini that performs a conspicuous vocal advertising display, a case of a conspicuous social display diverging from their own clade and converging with the Least Auklet's clade Aethiini. Among the auklets, the vocal advertising display occurs in all species (Jones 1999). The conspicuous vocal advertising display has apparently evolved independently three times in auks: in the auklets Aethiini, in the Little Auk, and in the *Synthliboramphus* murrelets (Jones *et al.* 1989; Gaston & Jones 1998). Convergence of the Little Auk's vocal advertising display with that of other small cavity nesting auk species probably represents a display adaptation related to their concealed nest-sites, which reduce the opportunity for visual display. Otherwise, Little Auks performed behaviour that reflected their phylogenetic relationship with the large auk species. For example, the Little Auk's butterfly flight, bow, allopreening and skypointing displays and head plumage erection strikingly recalled similar displays of the Razorbill (Cramp *et al.* 1985).

The Little Auk's butterfly flight display is considered to be homologous to that performed by Brünnich's Guillemots and Razorbills (Cramp *et al.* 1985). Furthermore, stone carrying, which is not observed in Least Auklets, is a trait shared by Little Auks and large auk species, further reflecting a general similarity of behaviour with the clade Alcini. The form of the Least Auklet's displays was similar to those of other auklet species, all of which perform vocal advertising displays, but showed no similarity to any

display of the Alcini (i.e. no butterfly flight, stone carrying or skypointing). Considered together, apart from the vocal advertising display, our observations showed little evidence of convergence of the form of social displays of the two species.

In contrast to the behaviour of adults, the behaviour of 1-year-old sub-adults of the two species was identical: sub-adults attended colonies and joined flocks of breeding adults, but performed few social displays and did not obtain mates (Gaston & Jones 1998). In both species, the only behaviours frequently recorded during our focal individual watches were preening and peering into rock crevices (neither being a social display). In both species, sub-adults were occasionally observed approaching adults without displaying to them, and being physically driven off by them. More information on demographically related patterns of behavioural traits among auk species is needed for both theoretical and applied purposes.

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