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Fitting in with the crowd: the role of prospecting in seabird behavioural trends

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Abstract: Pre-breeding, sub-adult seabirds have been documented prospecting, or visiting multiple sites throughout the breeding season to gather information on colony reproductive success, identify suitable habitat, evaluate prey abundance, and locate potential partners; however, many aspects of prospector biology remain unknown. We explored prospector behaviour as a means of furthering our understanding of post-natal seabird dispersal and colony attendance using least (*Aethia pusilla* Pallas, 1811) and crested (*A. cristatella* Pallas, 1769) auklets breeding at Gareloi Island, Alaska in 2014 and 2015. We recorded age class, length of time spent on the colony, and behaviour for individuals attending a study plot over the course of two breeding seasons. Although prospectors typically spent more time on the colony surface than adults, prospectors rarely socialized with conspecifics during their visits to the colony, possibly due to the absence of a citrus-like feather odour used in olfactory communication. Additionally, we found substantial differences between observed and predicted data between years, demonstrating that other factors (likely prey abundance or quality) influenced behaviour in 2015. Our results suggest that the collective knowledge of seabird prospecting behaviour is not necessarily transferable between taxa and there may be a range of strategies employed by prospectors when assessing colonies.

Key words: *Aethia* auklets, conspecific cues, least auklet *Aethia pusilla*, crested auklet *Aethia cristatella*, post-natal seabird ecology, recruitment and settlement decisions, sociality

Introduction

Individual fitness is influenced, in part, by habitat selection (Danchin and Cam 2002; Pärt and Doligez 2003) and decisions surrounding dispersal and recruitment are important factors closely linked to survival and reproduction (Lebreton et al. 2003). Philopatry to natal or breeding sites (i.e., fidelity) is a common behavioural tendency observed in many organisms (Greenwood and Harvey 1982; Koenig et al. 1996) as dispersal is costly in terms of time and energy (Bonte et al. 2012). Many species will only search for new breeding sites after individual or colony reproductive failure has occurred (Doligez et al. 2003; Danchin et al. 2004). Previous work has explored habitat selection in terms of dispersal and recruitment decisions (e.g., Boulinier and Lemel 1996; Danchin et al. 1998), particularly related to evolutionarily stable strategies (e.g., ideal free and ideal despotic distributions; Fretwell 1972), leading to the discovery that individuals ‘share’ information in social aggregates (Nocera et al. 2009). For example, when assessing habitat quality, individuals often use cues from conspecifics to acquire information about the local area (e.g., prey distributions and habitat availability; Forbes and Kaiser 1994; Nocera et al. 2009; Quaintenne et al. 2011).

Young, pre-breeding individuals have the opportunity to join either natal or other breeding populations as a recruit and many have been documented visiting multiple colonies during the breeding season prior to recruiting (Boulinier et al. 1996; Dittmann et al. 2007). Often, pre-breeding individuals use social cues and information on local reproductive success when choosing breeding habitat (Danchin and Wagner 1997; Boulinier et al. 2008). Conservation strategies tend to incorporate core aspects of behaviour, particularly conspecific attraction, as a way to recruit individuals to suitable habitat (Kress 1997; Parker et al. 2007).

Seabirds are among the bird taxa most threatened with extinction (IUCN 2009; Croxall et al. 2012). Conservation strategies aimed at restoring damaged or extirpated seabird colonies often employ chick translocations in species with strong philopatry (Kress 1997) or focus on attracting pre-breeders through visual or aural cues (Arnold et al. 2011) in species that exhibit strong natal dispersal. However, restoration projects using the latter technique have had mixed success (Jones and Kress 2012). An explanation for this is our limited knowledge of the behaviours of pre-breeding seabirds that often go undocumented due to the logistical limitations of tracking seabirds (Oro 2003) and the propensity of pre-breeding sub-adults to attend colonies during the chick-rearing period only (Cadiou et al. 1994; Boulinier et al. 1996; Dittmann and Becker 2003).

Auklets (*Aethia* spp.) are socially monogamous seabirds that breed in underground rock crevices on the Aleutian Islands and other islands located in the Bering and Okhotsk Seas (Gaston and Jones 1998). Least (*Aethia pusilla* Pallas, 1811) and crested (*A. cristatella* Pallas, 1769) auklets are abundant species with high adult survival that can begin breeding at three years of age (Jones 1992, 1993). They often breed in mixed colonies (Jones 1993; Bond et al. 2013) with colony populations typically in the hundreds of thousands (Byrd et al. 2005). Auklet species are among the most numerous seabird populations in the Pacific Ocean (Jones 1993; Bond et al. 2013) and are among the few seabird species that are not currently in decline (IUCN 2009). Breeding populations of auklets are relatively resilient to disturbance (Fraser et al. 1999), making them ideal model species for studying common behaviours (e.g., prospecting; Reed et al. 1999) among seabird taxa.

Before chicks hatch, auklets gather on the colony surface and socialize with conspecifics in dense, social scrums (Piatt et al. 1990; Jones 1993) involving specific vocalizations and

carefully executed postures in elaborate behavioural displays (Seneviratne et al. 2009; Zubakin et al. 2010; Bond et al. 2013). These behaviours are thought to maintain dominance status (Zubakin et al. 2010), establish bonds with possible breeding partners (Jones 1993; Bond et al. 2013), and assist the spread of ectoparasite deterrents present in feather odorants through alloanointing (Douglas III 2008). Social activity attracts the attention of other auklets (Jones 1993; Zubakin et al. 2010; Bond et al. 2013), including sub-adult prospectors (i.e., young, pre-breeding individuals that visit breeding colonies to assess the colony as a possible future breeding location), who loiter on the colony surface during the breeding season (Bédard 1969; Roby and Brink 1986) and can be distinguished by plumage colour (Bédard and Sealy 1984). During the chick-rearing period, social activity on the colony surface decreases substantially as breeders begin to spend more time at sea foraging for chick meals (Piatt et al. 1990).

The purpose of our study was to examine how behaviour at a breeding colony differs with age class and relate these differences to age-specific obligations of colony attendance. Given the elaborate behavioural displays of auklets and assumed importance of social behaviours, we hypothesized that sub-adult prospectors attend colonies to initiate social bonds with possible partners of future breeding attempts and locate potential nesting sites and adults attend a colony to ensure their reproductive efforts are successful. Thus, we predicted: (1) that prospecting sub-adults spend more time performing socialization and movement behaviours and adults spend more time performing maintenance (i.e., preening) and resting behaviours, and (2) the length of time spent performing behaviours does not differ between years. Additionally, we hypothesized that the length of time spent performing behaviours is greatest during late incubation and early in the nestling phase (when both sub-adults and adults are present on the colony; Piatt et al. 1990; Jones 1993; Wails 2016) as chicks are either not being provisioned (i.e.,

not hatched) or provisioning rates are minimal. Auklets will spend less time performing social behaviours later in the nesting period because chicks require more care from breeding adults and prospecting sub-adults normally depart colonies for the non-breeding season at this time. Thus, we predict a negative relationship between nesting period (i.e., incubation, hatching, and chick-rearing periods) and the length of time spent performing behaviours for both adults and sub-adults.

Methods

Ethical note

All fieldwork activities were performed under appropriate permits (master banding permit #22181 issued to collaborator Dr. Ian L. Jones [Memorial University of Newfoundland] and University of New Brunswick's Animal Care Committee [CCAC] permits [2014: 2014-1S-12; 2015: 2015-1S-01]).

Field methods

During June and July 2014 and 2015, we observed auklet behaviour (during incubation and the early nestling period of auklet reproduction) at Gareloi Island, Alaska (51°47'N, 178°47'W). Our observations were made at a 10 m × 20 m plot, "Plot D" (51°45'14.4"N, 178°45'31.9"W), delineated by Major et al. (2017), where crested auklet surface abundance (i.e., the number of auklets socializing on the surface of the plot) was ~8 crested auklets per m² during 2009 – 2013 (Major et al. 2017, HLM unpublished data). We do not have a similar estimate of least auklet surface abundance but our observations suggest it is similar to that of crested auklets (authors' personal observation). Two observers (CNW and an assistant), hidden from view of the auklets in a blind and within a distance of 15 m from all areas of the plot, watched adjacent 10 m × 10 m

halves of Plot D using Nikon Monarch 7 binoculars (10×42 , Nikon Vision Co. Ltd., Japan) and a Bushnell Spacemaster II spotting scope ($20 - 45\times$, Bushnell Corp., USA). Observers recorded the behaviour of auklets (see below) during four-hour observation periods (approximately 1100 – 1500 h Hawaii-Aleutian Daylight Time [HADT]), except during harsh weather conditions (high wind and heavy precipitation). In some instances, our watches were shortened and ended early when weather conditions deteriorated.

We made behavioural observations on a focal individual (as described by Altmann 1974) selected haphazardly for observation. Our observations commenced when an individual first became present on the colony surface (either by landing or exiting a crevice and walking onto the colony surface) and ended when the individual left the colony surface (either by flying away or entering a crevice). Because we did not have a timeframe (i.e., a specific length of time focal individuals were followed) for our behavioural watches, once observations of one individual ended, observations on the next individual could begin. For each individual, we recorded age class (i.e., sub-adult or adult), behaviours (Table 1), and interactions with conspecifics as defined by Jones (1993), Zubakin et al. (2010) and Bond et al. (2013). Weather conditions (wind speed, atmospheric pressure, temperature, and precipitation) were recorded every 30 min using a handheld Brunton ADC-PRO Atmospheric Data Center (Brunton, Inc., USA). We recorded all observations using Sony ICD-BX140 digital voice recorders (Sony Corp., Japan), imported sound files into Sound Forge (version 3.0d, Sony Creative Software, Inc., Japan), and transcribed them into Microsoft Excel 2010 (Microsoft, Inc., USA). We recorded the start times of all behaviours and calculated the length of time individuals spent performing each behaviour by calculating the difference between the start time of consecutive behaviours. Thus, for every second an auklet was observed, there is an associated behaviour recorded.

Statistical analyses

We performed all statistical analyses in R version 3.0.3 (R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org/>). Using data from 2014 for both least and crested auklets, in one analysis we compared the length of time spent performing each behaviour (in minutes) in relation to age class (sub-adult or adult), species (least or crested auklet), behaviour category (maintenance, movement, resting, or socialization), and nesting period (incubation, hatching, or chick-rearing) using generalized linear mixed-effects models (GLMMs; R package *lme4*; Bates et al. 2014) with a Gamma distribution and log link (as length of time spent performing a behaviour is a continuous variable > 0 ; pseudo- r^2 of the candidate models from the Gamma distribution were greater than other distributions [results not shown]). To simplify the analysis, we reduced the behaviours performed by auklets to four categories (Table 1). For the majority of our observations, behavioural categories did not overlap; the few instances of overlap occurred when individuals moved to maintain a social interaction, and we classified these instances as ‘socialization’. To account for variability in behaviour related to weather, which has been observed for seabird species (e.g., Schreiber 2001), we included wind speed (knots), temperature (°C), atmospheric pressure (hPa), and precipitation (i.e., none, light, heavy) as random effects after reducing the continuous variables (wind speed, temperature, and atmospheric pressure) into categorical variables (Table 2).

We considered 20 candidate GLMMs, including a null model, using the four independent variables of interest (i.e., age class, species, behaviour categories, and nesting period) and biologically-relevant interactions; the four weather variables were included as random effects in all models, including the null. We compared GLMMs using an information theoretic approach (Burnham and Anderson 2002) using Akaike’s information criterion (Akaike 1974) corrected for

small sample size (AIC_c ; Hurvich and Tsai 1989) to rank top competing models (R package *MuMIn*; Bartoń 2009) and ΔAIC_c and AIC_c weights (ω_i) to evaluate model likelihood (Burnham and Anderson 2002; Johnson and Omland 2004). As our top ranked model weight was < 0.9 , we used model averaging (R package *AICcmodavg*; Mazerolle 2012) to provide averaged parameter estimates using all GLMMs (Johnson and Omland 2004; Lukacs et al. 2010). We then evaluated the predictive ability of the averaged model by standardizing the 2015 behaviour data (i.e., dividing by 2 standard deviations; Gelman 2008) and comparing observed data to model predictions (R package *AICcmodavg*; Mazerolle 2012).

For all summary statistics, means $\pm$ 95% confidence intervals are presented.

Results

During behavioural watches, we found that adults spent less time on the colony surface (2014: 1.2 ± 0.2 min, $n = 430$; 2015: 0.5 ± 0.1 min, $n = 405$) than sub-adults (2014: 1.6 ± 0.7 min, $n = 29$; 2015: 1.3 ± 0.9 min, $n = 41$; Tables 3 and 4), with minor differences related to nesting period, where the most time spent on the colony surface (by adults and sub-adults combined) occurred during the chick-rearing period (2014: 1.3 ± 0.3 min, $n = 137$; 2015: 0.7 ± 0.3 min, $n = 8$) and the least occurred during both the incubation (2014: 1.2 ± 0.2 min, $n = 246$; 2015: 0.5 ± 0.1 min, $n = 334$) and hatching periods (2014: 1.0 ± 0.4 min, $n = 76$; 2015: 0.6 ± 0.1 min, $n = 104$). In 2014, crested auklets spent slightly more time on the colony surface (1.3 ± 0.2 min, $n = 359$) than least auklets (1.0 ± 0.3 min, $n = 100$). However, in 2015 both species spent noticeably less time on the colony surface with least auklets spending slightly more time on the colony surface (0.7 ± 0.2 min, $n = 184$) than crested auklets (0.5 ± 0.1 min, $n = 262$). On average, both adults and sub-adults spent the most amount of time on resting and movement behaviours, and the least amount of time on socialization behaviours (Figure 1).

The top four models in our candidate set investigating the relationship between age class and behaviour received 100% of model weights and each included the terms behaviour category, age class, and an interaction between these two variables (Table 3). Weighted parameter estimates show that sub-adults spent less time overall on the colony than adults and spent more time than adults on resting and movement behaviours (Table 4). Sub-adults spent the most time performing resting behaviours and the least on socialization (Table 4). Although species and nesting period were included in the top four ranked candidate models, neither were strong predictors in our models (Table 4).

When substituting the standardized 2015 data in the averaged model, model predictions differed from observed data by 86.4% ($\pm 7.4\%$) and the averaged model consistently overestimated times spent on behaviours. The percent difference between observed and predicted data were slightly greater for crested auklets than least auklets ($87.5 \pm 9.6\%$ and $84.5 \pm 11.6\%$, respectively), greater for adults than sub-adults ($86.8 \pm 7.7\%$ and $80.6 \pm 27.5\%$, respectively), and differed slightly related to nesting period (incubation: $88.0 \pm 9.7\%$, hatching: $81.8 \pm 13.9\%$, chick-rearing: $86.3 \pm 17.7\%$).

Discussion

Behavioural differences in colony attendance by breeding adults and pre-breeding sub-adults (i.e., prospectors) can be linked to the role of colony attendance for each age class. Breeding adults are constrained to attend a colony to ensure their current reproductive effort is successful, while pre-breeding sub-adults attend a colony to evaluate the site as a potential future breeding location. Here, we evaluated the hypothesis that sub-adult prospectors attend colonies to initiate social bonds with possible partners of future breeding attempts and locate potential nesting sites and adults attend a colony to ensure their reproductive efforts are successful. Specifically, we

predicted that prospecting auklets spend more time performing socialization and movement behaviours than adults who spend more time performing maintenance and resting behaviours. Our results partially supported our hypothesis and show differences in attendance patterns by breeding adults and sub-adult prospectors (who spent less time overall at the colony) and that behavioural differences related to age class were present. However, in contrast to our prediction, we found that sub-adult prospecting auklets spent the most time on resting and movement behaviours and rarely performed socialization behaviours.

Our samples of prospectors in both years of the study likely included birds from a range of ages (one-year-olds that had been chicks the previous summer up to three-year-olds that will return as breeders in the next summer), but exact ages are unknown as auklet chicks from Aleutian breeding sites are seldom banded, thus we had to consider age categorically (i.e., adult and sub-adult) based on plumage characteristics. It is possible that the youngest prospectors (which are easier to identify based on their small ornaments and plumage colour; Bédard and Sealy 1984; Jones 1993) do not engage in behaviours believed to be beneficial during the pre-breeding period as their first breeding attempt will occur in several years. Older prospectors (two- or three-year-olds who will return as breeders the following summer) have more incentive to participate in these behaviours and use this time to locate their breeding partner for the next year (Jones 1993).

Our averaged model based on the 2014 data should have been able to provide accurate predictions if the included predictor variables, interactions, and random terms were the major contributing factors influencing auklet behaviour. The large differences between predicted and observed data for 2015 demonstrate that additional factors were present. Predator activity is known to result in behavioural changes in seabirds (Watanuki 1986). Because the risk of

predation is usually greater at breeding colonies than at sea (Harfenist and Ydenberg 1995; Hayward et al. 2010) and prospecting sub-adult seabirds have no reproductive obligation to attend a colony, prospectors should only expend energy to visit a breeding colony when individual risks are low. Intense activity and abundance of avian predators at Gareloi Island was noted in 2015 but not in 2014 (authors' personal observation); however, investigators on Buldir Island (52°21'N, 175°55'E, approximately 370 km west of Gareloi), which has a greater avian predator density (Byrd and Day 1986), did not report an increase in predator abundance in 2015 (Mudge and Pietrzak 2015) nor observed changes in auklet behaviour or colony abandonment in relation to predator abundance previously (Jones 1993; Bond et al. 2013). The relatively high density of avian predators and the absence of auklet behavioural differences among other colonies suggest this is not a major factor in the behavioural differences we observed at Gareloi Island. Instead, it seems likely that other factors, such as poor food availability or quality (Cairns 1988; Wanless et al. 2005), were influencing auklet behaviour in 2015.

For other seabird species, it has been assumed that sub-adults attend colonies to locate and evaluate potential nesting habitat, engage in behaviours that will help establish social bonds, and evaluate local food supplies (Dittmann et al. 2007) but these benefits are less apparent to prospecting sub-adult auklets. The timing of colony attendance by prospecting auklets suggests colony productivity has little influence on prospecting behaviour (i.e., assessing potential nesting habitat through colony reproductive success; Wails 2016) but does coincide with the traditional peak in social activity by breeding adults observed at other colonies (Piatt et al. 1990; Jones 1993; Bond et al. 2013). Many of the well-defined social behaviours of crested auklets are related to their citrus-like odour, which is suggested to be important during social interactions and in deterring ectoparasites (Jones et al. 2004; Douglas III 2006). This chemical signal is

present on adult crested auklet feathers during the breeding season and is often gone before the autumn moult (Hagelin et al. 2003), the concentration of this chemical varies among individuals, and may be related to individual quality (Douglas III 2006). Research assessing the presence and concentration of this chemical odorant on prospecting sub-adult crested auklets has not been completed, but given concentrations are highest in high-quality adult individuals (Douglas III 2006), it is likely that most sub-adults would either produce the odorant in low concentrations or not at all. As olfaction appears to be a vital component in most crested auklet socialization behaviours (since many postures involve contact with areas known to produce this odorant; Douglas III 2008), it stands to reason that individuals lacking this olfactory signal, particularly sub-adult auklets, would be ignored during social scrums and possibly pushed out. Indeed, competition among socializing individuals is often observed and aggressive behaviours will lead to the desertion of the social scrum by the antagonized individual (authors' personal observation). We postulate that the observed low frequency of socialization behaviours by sub-adults may serve to reduce conspecific bullying they likely receive due to their lack of the citrus-like odour and these individuals may instead be limited to only watching social behaviours between conspecifics when prospecting. Future research evaluating the presence/absence of the citrus-like odorant on sub-adults is required to test this hypothesis.

Given the importance of recruitment to an individual colony in maintaining a viable population and for restoration studies, understanding the behaviour of sub-adult prospectors is of the utmost importance. Here, we have shown that breeding adult and sub-adult auklets differ in the time spent on the colony and the behaviours they perform while there. We found that sub-adult prospectors spend more time resting on the colony surface (possibly watching adults interact) and moving around the colony (possibly searching for unoccupied and suitable nesting

crevices), but less time socializing than adults. Our results suggest that our collective knowledge of seabird prospecting behaviour is not necessarily transferable among taxa and it appears there may be a range of strategies employed by prospectors when assessing potential colonies. Thus, the success of restoration projects using social attraction and conspecific cues will be greatly increased by expanding our knowledge of the behavioural strategies employed by sub-adult prospectors when making settlement decisions.

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References

- Akaike, H. 1974. A new look at the statistical model identification. *IEEE T. Automat. Contr.* **19**: 716–723.
- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**: 227–267.
- Arnold, J.M., Nisbet, I.C.T., and Veit, R. 2011. Assessing aural and visual cueing as tools for seabird management. *J. Wildl. Manage.* **75**: 495–500. doi: 10.1002/jwmg.76

- Bartoń, K. 2009. MuMIn: Multi-model inference. R package version 1.12.1.
- Bates, D., Maechler, M., Bolker, B., and Walker, S. 2014. lme4: linear mixed-effects models using eigen and S4. R package version 1.1-7.
- Bédard, J. 1969. The nesting of the crested, least, and parakeet auklets on St. Lawrence Island, Alaska. *Condor*, **71**: 386–398.
- Bédard, J., and Sealy, S.G. 1984. Moults and feather generations in the least, crested, and parakeet auklets. *J. Zool. (Lond.)* **202**: 461–488. doi: 10.1111/j.1469-7998.1984.tb05047.x
- Bond, A.L., Jones, I.L., Seneviratne, S.S., and Muzaffar, S.B. 2013. Least auklet (*Aethia pusilla*). In *The birds of North America online*. Edited by A. Poole. Cornell Lab of Ornithology, New York. Available from <http://bna.birds.cornell.edu/bna/species/069>.
- Bonte, D., van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., et al. 2012. Costs of dispersal. *Biol. Rev. Camb. Philos. Soc.* **87**: 290–312. doi: 10.1111/j.1469-185X.2011.00201.x
- Boulinier, T., and Lemel, J.Y. 1996. Spatial and temporal variations of factors affecting breeding habitat quality in colonial birds: some consequences for dispersal and habitat selection. *Acta Oecol.* **17**: 531–552.
- Boulinier, T., Danchin, É., Monnat, J.-Y., Doutrelant, C., and Cadiou, B. 1996. Timing of prospecting and the value of information in a colonial breeding bird. *J. Avian Biol.* **27**: 252–256. doi: 10.2307/3677230

- Boulinier, T., McCoy, K.D., Yoccoz, N.G., Gasparini, J., and Tveraa, T. 2008. Public information affects breeding dispersal in a colonial bird: kittiwakes cue on neighbours. *Biol. Lett.* **4**: 538–540. doi: 0.1098/rsbl.2008.0291
- Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference – a practical information-theoretic approach. Springer-Verlag, New York, N.Y.
- Byrd, G.V., and Day, R.H. 1986. The avifauna of Buldir Island, Aleutian Islands, Alaska. *Arctic*, **39**: 109–118.
- Byrd, G.V., Renner, H.M., and Renner, M. 2005. Distribution patterns and population trends of breeding seabirds in the Aleutian Islands. *Fish. Oceanogr.* **14**: 139–159. doi: 10.1111/j.1365-2419.2005.00368.x
- Cadiou, B., Monnat, J.-Y., and Danchin, É. 1994. Prospecting in the kittiwake, *Rissa tridactyla*: different behavioural patterns and the role of squatting in recruitment. *Anim. Behav.* **47**: 847–856. doi: 10.1006/anbe.1994.1116
- Cairns, D.K. 1988. Seabirds as indicators of marine food supplies. *Biol. Oceanogr.* **5**: 261–271.
- Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A., and Taylor, P. 2012. Seabird conservation status, threats and priority actions: a global assessment. *Bird Conserv. Int.* **22**: 1–34. doi: 10.1017/S0959270912000020
- Danchin, É., and Wagner, R.H. 1997. The evolution of coloniality: the emergence of new perspectives. *Trends Ecol. Evol.* **12**: 342–347. doi: 10.1016/S0169-5347(97)01124-5

- Danchin, É., and Cam, E. 2002. Can non-breeding be a cost of breeding dispersal? *Behav. Ecol. Sociobiol.* **51**: 153–163. doi: 10.1007/s00265-001-0423-5
- Danchin, É., Boulinier, T., and Massot, M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology*, **79**: 2415–2428. doi: 10.1890/0012-9658(1998)079[2415:CRSABH]2.0.CO;2
- Danchin, É., Giraldeau, L.A., Valone, T.J., and Wagner, R.H. 2004. Public information: from nosy neighbors to cultural evolution. *Science*, **305**: 487–491. doi: 10.1126/science.1098254
- Dittmann, T., and Becker, P.H. 2003. Sex, age, experience, and condition as factors affecting arrival date in prospecting common terns, *Sterna hirundo*. *Anim. Behav.* **65**: 981–986. doi: 10.1006/anbe.2003.2128
- Dittmann, T., Ezard, T.H.G., and Becker, P.H. 2007. Prospectors' colony attendance is sex-specific and increases future recruitment chances in a seabird. *Behav. Process.* **76**: 198–205. doi: 10.1016/j.beproc.2007.05.002
- Doligez, B., Cadet, C., Danchin, É., and Boulinier, T. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Anim. Behav.* **66**: 973–988. doi: 10.1006/anbe.2002.2270
- Douglas III, H.D. 2006. Measurement of chemical emissions in crested auklets (*Aethia cristatella*). *J. Chem. Ecol.* **32**: 2559–2567. doi: 10.1007/s10886-006-9164-2

- Douglas III, H.D. 2008. Prenuptial perfume: alloanointing in the social rituals of the crested auklet (*Aethia cristatella*) and the transfer of arthropod deterrents. *Naturwissenschaften*, **95**: 45–53. doi: 10.1007/s00114-007-0294-3
- Forbes, L.S., and Kaiser, G.W. 1994. Habitat choice in breeding seabirds: when to cross the information barrier. *Oikos*, **70**: 377–384. doi: 10.2307/3545775
- Fraser, G., Jones, I.L., Williams, J.C., Hunter, F.M., Scharf, L., and Byrd, G.V. 1999. Breeding biology of crested auklets at Buldir and Kasatochi Islands, Alaska. *Auk*, **116**: 690–701. doi: 10.2307/4089330
- Fretwell, S.D. 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton, N.J.
- Gaston, A.J., and Jones, I.L. 1998. The auks, alcidae. *In* *Bird families of the world*. Edited by C.M. Perrins, W.J. Bock, and J. Kikkawa. Oxford University Press, New York.
- Gelman, A. 2008. Scaling regression inputs by dividing by two standard deviations. *Stat. Med.* **27**: 2865–2873.
- Greenwood, P.J., and Harvey, P.H. 1982. The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* **13**: 1–21.
- Hagelin, J.C., Jones, I.L., and Rasmussen, L.E.L. 2003. A tangerine-scented social odour in a monogamous seabird. *Proc. R. Soc. Lond. B Biol. Sci.* **270**: 1323–1329.

- Harfenist, A., and Ydenberg, R.C. 1995. Parental provisioning and predation risk in rhinoceros auklets (*Cerorhinca monocerata*): effects on nestling growth and fledging. *Behav. Ecol.* **6**: 82–86.
- Hayward, J.L., Galusha, J.G., and Henson, S.M. 2010. Foraging-related activity of bald eagles at a Washington seabird colony and seal rookery. *J. Raptor Res.* **44**: 19–29.
- Hurvich, C.M., and Tsai, C.-L. 1989. Regression and time series model selection in small samples. *Biometrika*, **76**: 297–307.
- International Civil Aviation Organization. 1993. Manual of the ICAO standard atmosphere: extended to 80 kilometres (262,500 feet). International Civil Aviation Organization, Montréal, QC.
- International Union for Conservation of Nature. 2009. IUCN red list of threatened species. International Union for Conservation of Nature, Gland, Switzerland.
- Johnson, J.B., and Omland, K.S. 2004. Model selection in ecology and evolution. *Trends Ecol. Evol.* **19**: 101–108.
- Jones, H.P., and Kress, S.W. 2012. A review of the world's active seabird restoration projects. *J. Wildl. Manage.* **76**: 2–9. doi: 10.1002/jwmg.240
- Jones, I.L. 1992. Colony attendance of least auklets at St. Paul Island, Alaska: implications for population monitoring. *Condor*, **94**: 93–100.

- Jones, I.L. 1993. Crested auklet (*Aethia cristatella*). In The birds of North America online. Edited by A. Poole. Cornell Lab of Ornithology, New York. Available from <http://bna.birds.cornell.edu/bna/species/070>.
- Jones, I.L., Hagelin, J.C., Major, H.L., and Rasmussen, L.E.L. 2004. An experimental field study of the function of crested auklet feather odour. *Condor*, **106**: 71–78.
- Koenig, W.D., van Vuren, D., and Hooge, P.N. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. *Trends Ecol. Evol.* **11**: 514–517. doi: 10.1016/S0169-5347(96)20074-6
- Kress, S.W. 1997. Using animal behavior for conservation: case studies in seabird restoration from the Maine coast, USA. *J. Yamashina Inst. Ornithol.* **29**: 1–26. doi: 10.3312/jyio1952.29.1
- Lebreton, J.D., Hines, J.E., Pradel, R., Nichols, J.D., and Spendelov, J.A. 2003. Estimation by capture-recapture of recruitment and dispersal over several sites. *Oikos*, **101**: 253–264. doi: 10.1034/j.1600-0706.2003.11848.x
- Lukacs, P.M., Burnham, K.P., and Anderson, D.R. 2010. Model selection bias and Freedman's paradox. *Ann. Inst. Stat. Math.* **62**: 117–125.
- Major, H.L., Buxton, R.T., Schacter, C.R., Connors, M., and Jones, I.L. 2017. Habitat modification as a means of restoring crested auklet colonies. *J. Wildl. Manage.* **81**. doi: 10.1002/jwmg.21175

- Mather, J.R. 2005. Beaufort wind scale. *In* Encyclopedia of world climatology. *Edited by* J.E. Oliver. Springer, Dordrecht, Netherlands. pp. 156-157.
- Mazerolle, M.J. 2012. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 1.26.
- Mudge, M.L., and Pietrzak, K.W. 2015. Biological monitoring at Buldir Island, Alaska in 2015. Alaska Maritime National Wildlife Refuge, Homer, A.K.
- Nocera, J.J., Forbes, G.J., and Giraldeau, L.A. 2009. Aggregations from using inadvertent social information: a form of ideal habitat selection. *Ecography*, **32**: 143–152. doi: 10.1111/j.1600-0587.2008.05614.x
- Oro, D. 2003. Managing seabird metapopulations in the Mediterranean: constraints and challenges. *Sci. Mar.* **67**: 13–22.
- Parker, M.W., Kress, S.W., Golightly, R.T., Carter, H.R., Parsons, E.B., Schubel, S.E., Boyce, J.A., McChesney, G.J., and Wisely, S.M. 2007. Assessment of social attraction techniques used to restore a common murre colony in central California. *Waterbirds*, **30**: 17–28. doi: 10.1675/1524-4695(2007)030[0017:AOSATU]2.0.CO;2
- Pärt, T., and Doligez, B. 2003. Gathering public information for habitat selection: prospecting birds cue on parental activity. *Proc. R. Soc. Lond. B Biol. Sci.* **270**: 1809–1813. doi: 10.1098/rspb.2003.2419

- Piatt, J.F., Roberts, B.D., and Hatch, S.A. 1990. Colony attendance and population monitoring of least and crested auklets on St. Lawrence Island, Alaska. *Condor*, **92**: 97–106. doi: 10.2307/1368387
- Quaintenne, G., van Gils, J.A., Bocher, P., Dekinga, A., and Piersma, T. 2011. Scaling up ideals to freedom: are densities of red knots across western Europe consistent with ideal free distribution? *Proc. R. Soc. Lond. B Biol. Sci.* **278**: 2728–2736. doi: 10.1098/rspb.2011.0026
- Reed, J.M., Boulinier, T., Danchin, E., and Oring, L.W. 1999. Informed dispersal: prospecting by birds for breeding sites. *Curr. Ornithol.* **15**: 189–259.
- Roby, D.D., and Brink, K.L. 1986. Breeding biology of least auklets on the Pribilof Islands, Alaska. *Condor*, **88**: 336–346.
- Schreiber, E.A. 2001. Climate and weather effects on seabirds. *In* *Biology of marine birds*. Edited by E.A. Schreiber and J. Burger. CRC Press, Boca Raton.
- Seneviratne, S.S., Jones, I.L., and Miller, E.H. 2009. Vocal repertoires of auklets (Alcidae: Aethiini): structural organization and categorization. *Wilson J. Ornithol.* **121**: 568–584. doi: 10.1676/08-008.1
- Wails, C.N. 2016. Movement, colony attendance, and behaviour of prospecting least and crested auklets. M.Sc. thesis, Department of Biological Sciences, University of New Brunswick, Saint John, N.B.

- Wanless, S., Harris, M.P., Redman, P., and Speakman, J.R. 2005. Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea. *Mar. Ecol. Prog. Ser.* **294**: 1–8.
- Watanuki, Y. 1986. Moonlight avoidance behavior in leach's storm-petrels as a defense against slaty-backed gulls. *Auk*, **103**: 14–22.
- Western Region Climate Center. 2009. Historical climate information, western U.S. historical summaries, NCDC 1971-2000 monthly normals - Adak, Alaska. Western Region Climate Center, Reno, N.V. Available from <http://www.wrcc.dri.edu/>.
- Zubakin, V.A., Volodin, I.A., Klenova, A.V., Zubakina, E.V., Volodina, E.V., and Lapshina, E.N. 2010. Behavior of crested auklets (*Aethia cristatella*, Charadriiformes, Alcidae) in the breeding season: visual and acoustic displays. *Biol. Bull. Russ. Acad. Sci.* **37**: 823–835. doi: 10.1134/S106235901008006

Figure caption:

Figure 1. Proportion of time spent and behaviour category (i.e., maintenance [“Maint”], movement [“Move”], resting [“Rest”], and socialization [“Social”]) for breeding adult (dark grey) and prospecting sub-adult (light grey) auklets (both least and crested auklets) observed during the incubation (adult 2014 $n = 228$, 2015 $n = 295$; sub-adult 2014 $n = 23$, 2015 $n = 39$), hatching (adult 2014 $n = 71$, 2015 $n = 102$; sub-adult 2014 $n = 5$, 2015 $n = 2$), and chick-rearing (adult 2014 $n = 131$, 2015 $n = 8$; sub-adult 2014 $n = 6$, 2015 $n = 0$) periods.

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Table 1. Defined behaviours used during observations of auklets in 2014 and 2015 on Gareloi Island, AK and simplified behavioural categories used in statistical analysis.

Maintenance	Movement	Resting	Socialization
Alert posture ^{1,2}	Fluttering/Wing flapping	Lying	Arch display ^{1,2,3}
Preening	Flying	Sitting	Attacks/Fighting/Pecks
Scratching	Running	Sleeping	Billing ^{1,2,3}
Stretching	Walking	Standing	Chatter/Duet chatter display ¹
			Hunch display ¹
			Ruff-sniff ^{2,3}
			Threat postures (crouched, oblique, upright; with or without throat presentation) ²
			Touch display ^{1,2,3}
			Trumpeting display ^{2,3}
			Vocalizations*

¹Least auklet behaviour defined in Bond et al. (2013).

²Crested auklet behaviour defined in Zubakin et al. (2010).

³Crested auklet behaviour defined in Jones (1993).

*For a complete list of vocalizations, see Seneviratne et al. (2009).

Table 2. Categorical weather variables used as random effects in models of behavioural differences between age classes of least (*Aethia pusilla*) and crested auklets (*A. cristatella*) at Gareloi Island, AK in 2014 and 2015.

Variable	Scale	Source
Wind Speed	Beaufort	Mather 2005
	Cool: < 7°C	
Air Temperature*	Average: > 7°C, < 14°C	WRCC 2009
	Warm: > 14°C	
Atmospheric Pressure	Low: < 1013 hPa	ICAO 1993
	High: > 1013 hPa	

*Using seasonal averages from neighbouring Adak Island (51°53'N, 176°38'W, ~146 km east of Gareloi Island).

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Table 3. Generalized linear mixed-effects models (Gamma distribution, log link) ranked by AIC_c for least ($n = 100$, 77 adults, 23 sub-adults) and crested ($n = 359$, 353 adults, 6 sub-adults) auklets observed during the 2014 breeding season (June – July). Independent variables include age class (adult and sub-adult), behaviour category (maintenance, movement, resting, and socialization, see Table 1), and nesting period (incubation, hatching, and chick rearing).

Model	k	Log likelihood	AIC_c	Δ	ω_i
Age+Behaviour+Age:Behaviour	10	-324.01	668.50	0.00	0.42
Age+Behaviour+Nesting+Age:Behaviour	11	-323.45	669.50	0.98	0.26
Age+Behaviour+Species+Age:Behaviour	11	-323.76	670.10	1.60	0.19
Age+Behaviour+Nesting+Species+Age:Behaviour	12	-323.11	670.90	2.40	0.13
Behaviour	8	-334.26	684.80	16.33	0.00

*Number of parameters (k) includes model intercept, the four weather variables included as random terms, slope coefficients for fixed effects of each model, and shape and scale parameters for the Gamma distributed error term.

“:” indicates an interaction.

Table 4. Model averaged parameter estimates for each of the independent variables with their levels shown in brackets. Parameters are ranked by their parameter likelihood (the sum of all Akaike weights for each of the models in which the predictor was included) for the 20 GLMMs including standard errors, confidence intervals, and relative importance of predictors.

Parameter [Level]	Model averaged parameter estimates	SE	Lower 95% CI	Upper 95% CI	Parameter likelihood
Intercept	-0.68	0.28	-1.22	-0.14	1.00
Behaviour [Movement]	-0.32	0.10	-0.52	-0.13	
Behaviour [Resting]	0.39	0.10	0.20	0.59	1.00
Behaviour [Socialization]	-2.55	4.28	-10.93	5.83	
Age [Sub-adult]	-0.90	0.31	-1.50	-0.29	1.00
Age [Sub-adult] : Behaviour [Movement]	1.00	0.37	0.27	1.72	
Age [Sub-adult] : Behaviour [Resting]	1.40	0.36	0.69	2.11	1.00
Age [Sub-adult] : Behaviour [Socialization]	-0.07	0.46	-0.98	0.83	
Species [Least Auklet]	-0.04	0.08	-0.19	0.11	0.39
Nesting [Hatching]	-0.01	0.06	-0.13	0.11	
Nesting [Chick-rearing]	-0.05	0.11	-0.27	0.17	0.32

*Parameter estimates for Age level ‘Adult’, Behaviour level ‘Maintenance’, Species level ‘Crested Auklet’, and Nesting level ‘Incubation’ were set to zero in all models. “:” indicates an interaction between predictors.