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Intense prospecting movements of failed breeders nesting in an unsuccessful breeding subcolony

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Prospecting for a future breeding site may help individuals decide whether to disperse and where to settle. However, little is known about it because of methodological constraints limiting the acquisition of data at fine spatial and temporal resolutions, especially for individuals that have failed breeding. Using recently developed solar-powered GPS-UHF not requiring the recapture of individuals, we tracked failed breeding black-legged kittiwakes, *Rissa tridactyla*, nesting in a failed subcolony of a large Norwegian colony from the end of incubation and across the chick-rearing period. As predicted, their movement patterns differed significantly from those of successfully breeding birds tracked simultaneously in a nearby successful subcolony. After 1 week of tracking, all failed breeders rapidly abandoned their nesting cliff and males and females simultaneously increased prospecting visits to other parts of their nesting colony and to neighbouring kittiwake colonies situated 40–50 km away. Conversely, none of the successful breeders prospected over the same period. Our results provide new insights on prospecting movements linked to potential dispersal decisions after breeding failure. They suggest that males and females have similar temporal but different spatial prospecting patterns, possibly due to different costs associated with prospecting and dispersal decisions. They also highlight the need to track more comprehensively the movements linked with breeding habitat selection and dispersal in contrasting environmental conditions to better understand the complex behavioural responses of individuals to breeding failure and their consequences for the spatial dynamics of populations.

Breeding habitat selection is an essential process in ecology because it affects several components of individual fitness (Arlt & Pärt, 2007; Clobert, Baguette, Benton, & Bullock, 2012; Nevoux, Arlt, Nicoll, Jones, & Norris, 2013). Prospecting, defined as visits of individuals to breeding areas where they do not currently breed but where they might settle to breed in the future (Reed, Boulinier, Danchin, & Oring, 1999), constitutes a common adaptive behavioural strategy that helps individual decide whether and where to disperse when the environment is spatially heterogeneous and temporally autocorrelated (Boulinier & Danchin, 1997; Doligez, Cadet, Danchin, & Boulinier, 2003; Stamps, 2001). It notably allows individuals to gather personal and social information to assess the local quality of breeding areas and make dispersal and settlement decisions (Danchin, Boulinier, & Massot, 1998; Ponchon et al., 2013). It may also provide an opportunity for individuals to get familiar with a potential future breeding area and start the process of acquiring a breeding site and a mate (Boulinier, Danchin, Monnat, Doutrelant, & Cadiou, 1996; Bruinzeel & van de Pol, 2004; Cadiou, Monnat, & Danchin, 1994; Stamps, 2001).

So far, numerous observational (Calabuig, Ortego, Aparicio, & Cordero, 2010; Cam, Oro, Pradel, & Jimenez, 2004; Danchin et al., 1998; Parejo, White, Clobert, Dreiss, & Danchin, 2007; Pärt, Arlt, Doligez, Low, & Qvarnström, 2011; Pärt & Doligez, 2003; Ward, 2005) and experimental studies (Aparicio, Bonal, & Muñoz, 2007; Boulinier, McCoy, Yoccoz, Gasparani, & Tveraa, 2008; Doligez, Danchin, & Clobert, 2002) have suggested that prospecting individuals, mostly composed of pre-, failed or

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nonbreeders (Reed et al., 1999), use social information such as conspecific breeding success or fledging quality to choose the most suitable breeding area.

Prospecting individuals are usually challenging to track directly and continuously in the field because they are more loosely attached to their breeding area than successfully breeding individuals (Boulinier et al., 2008; Calabuig et al., 2010; Chambert et al., 2012). The recent development of miniaturized tracking loggers has alleviated this issue (Ponchon et al., 2013) and prospecting movements have started to be documented in a substantial number of species thanks to these innovative tools (Calabuig et al., 2010; Dittmann, Zinsmeister, & Becker, 2005; Fijn et al., 2014; Ottosson, Bäckman, Smith, & Dickinson, 2001; Péron & Grémillet, 2013; Ponchon, Chambert, et al., 2015; Votier, Grecian, Patrick, & Newton, 2011; Zangmeister, Haussmann, Cerchiara, & Mauck, 2009). However, detailed information on the potential factors influencing the occurrence and patterns of prospecting movements and subsequent behavioural readjustments in failed breeding individuals relative to successful ones is still limited.

In this study, we used recently developed solar-powered GPS-UHF trackers connected to a base station via radio signals to detail for the first time the spatial and temporal movement patterns and nest attendance of male and female black-legged kittiwake, *Rissa tridactyla*, failed breeders nesting in a failed subcolony. We compared them with those of successful breeders nesting in a nearby successful subcolony over the same period, from the end of incubation to the end of chick rearing. Overall, we considered not only individual reproductive success, but also conspecific reproductive success and sex as potential factors influencing individual movement patterns and nest attendance.

Black-legged kittiwakes are especially suitable to study the processes involved in site fidelity, dispersal and recruitment because their behaviour can be readily observed on breeding sites (Boulinier et al., 1996, 2008; Cadiou, 1999; Cadiou & Monnat, 1996; Cadiou et al., 1994; Danchin et al., 1998). Therefore, substantial work on prospecting based on direct observations has already been carried out in this species. It has notably been shown that prospecting is commonly displayed by failed breeders during the chick-rearing period, when public information based on conspecific breeding performance is most available and most valuable (Boulinier et al., 1996; Cadiou, 1999; Cadiou et al., 1994). Prospecting has also been related to dispersal and settlement decisions, since conspecific breeding success is used as a social cue to choose more productive colonies (Boulinier et al., 2008; Danchin et al., 1998). Black-legged kittiwakes generally show high site fidelity when they have bred successfully or when a large proportion of their neighbours are successful. Conversely, they are more likely to rapidly desert their nesting cliff, prospect and disperse to a new breeding site if they have failed breeding in areas where their neighbours have failed as well (Boulinier et al., 2008; Chambert et al., 2012; Danchin et al., 1998). Based on this knowledge, we formulated the following predictions. (1) Many prospecting movements should be recorded in failed breeders nesting among failed conspecifics, in both males and females, but none should be recorded in successful breeders nesting among successful conspecifics. (2) Failed breeders should rapidly desert their nesting subcolony, in concert with an increase in prospecting visits in other breeding areas. In contrast, successful breeders should maintain relatively high nest attendance to ensure reproductive duties linked with chick rearing. (3) The following year, a low proportion of failed breeders should come back to their nest compared to successful individuals breeding among successful conspecifics. More importantly, some failed breeders should be observed breeding in areas they had prospected.

METHODS

Study Site and Species

The study was conducted in the black-legged kittiwake colony of Hornøya (70°23′N, 31°09′E), northern Norway, where approximatively 10 000 breeding pairs nest annually. This colony is composed of several nesting cliffs where breeding success can notably be affected via predation on eggs and chicks by ravens, *Corvus corax*, herring gulls, *Larus argentatus*, and great black-backed gulls, *Larus marinus*, at local spatial scales, and by variability in food resource availability at larger spatial scales (Ponchon et al., 2014). Subcolonies are defined based on the topography and discontinuity of the cliffs within the island of Hornøya. Their spatial resolution is a few tens to hundreds of metres, which corresponds to the average of the length of the cliffs. We assumed that each subcolony has relatively homogeneous local environmental conditions (e.g. same predation or parasitism pressure) and, thus, a homogeneous breeding success.

In our study colony, individuals arrive in March and generally start incubating one to three eggs in early May for 27 days. Chicks hatch in early June and fledge about 35 days later. Both members of a pair equally share parental care over the breeding season (Coulson, 2011) and leave the colony in late July.

Study Design and Individual Tracking

The study design consisted of tracking two groups of kittiwakes: one composed of 11 failed breeders (four females and seven males) nesting in a failed subcolony and a second composed of 16 successful breeders (eight females and eight males) nesting in a successful breeding subcolony.

The failed subcolony was chosen after local evidence of heavy predation on eggs by ravens, suggesting it would remain unsuccessful over the rest of the season. The ‘failed’ group was tracked with 7 g solar-powered GPS-UHF trackers with remote UHF reprogramming and data download link (URIA-68S, Ecotone, Gdynia, Poland; 1.6% of bird weight) from the end of the incubation period (deployments between 31 May and 2 June 2013; see Appendix Fig. A1). The great advantage of the GPS-UHF system is that location data recorded by the loggers are immediately and automatically downloaded by a base station via radio signals when equipped individuals enter the range of the base station. This eliminates the complicated recapture of failed birds to access location data. Moreover, solar panels enable loggers to record high-resolution GPS data over longer periods (a few weeks) than classic ones (a few days).

All equipped failed birds were breeders that had constructed a nest and had eggs assumed to be depredated by ravens within a few days following laying. Five eggs from unequipped birds nesting in the same cliff were also removed and placed in foster nests in another successful subcolony to obtain a completely failed subcolony. At deployment, a total of 26 failed breeding pairs, including the tracked birds, were nesting in the focal subcolony.

The birds from the ‘successful’ group were either tracked with solar-powered GPS-UHF (five individuals: two females, three males) from 29 May to the end of June, or with about 12 g MiniGPS-100 (Earth & Ocean Technologies, Kiel, Germany; 11 individuals: six females, five males; about 2.6% of bird weight) from 5 to 12 June (Appendix Fig. A1). As successful breeders are relatively easy to