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Breeding failure induces large scale prospecting movements in the black-legged kittiwake☆

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ABSTRACT

Before making dispersal decisions, many species are known to gather social information by prospecting potential future breeding sites, especially when they have failed breeding. So far, the role of current breeding performance on the occurrence of prospecting movements has mainly been studied at limited spatial scales, because of difficulties in tracking free-ranging, fast-moving individuals between distant breeding patches. Little information is thus available on individual behaviour and the spatial extent of prospecting movements in response to breeding failure. To address this issue, black-legged kittiwakes which breeding success was manipulated were tracked with GPS at the end of incubation in two Norwegian colonies. Crucially, and as predicted, prospecting visits to other breeding colonies were recorded in 33% of artificially-failed breeders, but never in successful ones. They occurred at large (40 km) as well as local spatial scales (1 km). Time-budgets of successful and failed breeders differed significantly in terms of trip duration, but also foraging, resting and nesting propensities. These results provide important elements to assess trade-offs between prospecting and other activities. They show that a substantial proportion of failed breeders prospect as early as within a week after failure at the egg stage and suggest that these individuals assess their options of future reproduction by prospecting alternative areas, although dispersal decisions may also involve more complex behavioural processes. Because they link breeding colonies situated tens of kilometres apart, prospecting movements may have critical implications for the dynamics of subdivided populations.

1. Introduction

Breeding habitat selection conditions the spatial structure and the dynamics of populations, as well as individual fitness (Arlt and Pärt, 2007; Clobert et al., 2001; Nevoux et al., 2013; Ronce, 2007). In an environment altered by anthropogenic activities and global warming, the ability of individuals to disperse towards alternate breeding habitats underpins the adaptive response of populations to escape degrading local conditions (Kokko and Lopéz-Sepulcre, 2006; Ronce, 2007). However, this strategy may be costly (Bonte et al., 2012) and the decision for an individual to leave or to remain within the same breeding patch is driven by multiple environmental, social, and individual factors (e.g. Berteaux and Boutin, 2000; Danchin et al., 1998; Dugger et al., 2010; Herrera et al., 2011; Trochet et al., 2013).

The breeding performance of individuals is of particular interest in habitat selection processes as it has been found to affect site fidelity in many iteroparous species (Boulinier et al., 2008b; Danchin et al., 1998; Pakanen et al., 2011; Switzer, 1997). In long-lived birds, which are generally faithful to their annual breeding site, individuals facing a breeding failure early in the season can follow two alternative strategies: reinvest immediately in breeding and lay a replacement clutch, or postpone reproductive investment and prepare for the next breeding season (Pakanen et al., 2014). In the first case, they should rapidly attempt to breed again by remaining on the same nest site, with the same mate, investing in the laying of new eggs and increasing resource intake to face the costs of a new incubation and future chick-rearing. Alternatively, if individuals postpone reproductive investment until the next breeding season, they could choose between remaining on the same breeding site or attempting to disperse to a new site to potentially improve their future reproductive performance. Breeding failure can therefore have direct consequences on site fidelity and mate retention

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in the short-term (Boulinier et al., 2008b; Dubois and Cézilly, 2002; Forero et al., 1999; Naves et al., 2006; Robert et al., 2014), which can also have indirect longer-term consequences on population structure and dynamics through dispersal at different spatial scales (Danchin et al., 1998; Matthiopoulos et al., 2005; Ponchon et al., 2015).

In addition to individual breeding performance, numerous studies have recently highlighted the role of social information use in breeding habitat selection (Boulinier et al., 2008a). Information sources reflecting the local quality of habitats are diverse (Dall et al., 2005), but observational (Calabuig et al., 2010; Danchin et al., 1998; Doligez et al., 2004; Kivelä et al., 2014; Pärt and Doligez, 2003; Pärt et al., 2011; Ward, 2005) and experimental studies (Aparicio et al., 2007; Boulinier et al., 2008b; Doligez et al., 2002; Nocera et al., 2006; Parejo et al., 2008) have suggested that individuals can efficiently rely on social information such as conspecific presence and/or performance to assess the local quality of breeding habitats and choose their potential future breeding site. Such information can be gathered during prospecting movements, which are visits to suitable breeding sites where the individual does not currently breed (Reed et al., 1999). These prospecting visits may also be useful to become more familiar with other breeding areas and start the process of acquiring a new breeding site (Bruinzeel and van de Pol, 2004; Cadiou et al., 1994). Prospecting movements, which are mainly displayed by pre-breeders, non-breeders or failed breeders, have been documented in many bird species (Reed et al., 1999), but also in other taxa such as mammals, reptiles, amphibians or insects (see Ponchon et al., 2013 and references therein).

The spatial extent of prospecting movements is particularly important to consider because it can reveal the spatial scale at which environmental factors may act (Boulinier and Lemel, 1996; Ponchon et al., 2013). For example, the detection of large scale prospecting movements could mean that individuals respond to factors affecting habitat quality at large spatial scales (e.g. food availability), whereas fine scale prospecting movements could reflect a response to environmental factors affecting local habitat quality (e.g. predation, parasitism). Yet, little is known about the occurrence of prospecting movements at large spatial scales in response to breeding failure because of the difficulty in tracking free-ranging, fast-moving individuals between distant breeding patches (Fijn et al., 2014; Ponchon et al., 2013). In addition, individuals visiting other breeding sites and gathering information require time and energy (Rieucau and Giraldeau, 2011) and prospecting movements could affect individual behaviour and time-budgets during the breeding season. Despite its importance in a conservation context, and also in terms of potential trade-offs between current and future reproductive events, it is not known how prospecting is traded against other activities such as foraging for food or nest attendance (Ponchon et al., 2013).

Here, the use of GPS loggers was combined with an experimental design to investigate the behavioural responses of birds subjected to breeding failure. In particular, the aim was to track the occurrence and spatial scale of prospecting movements and identify changes in behaviour according to individual breeding performance. One difficulty of working with failed breeders is that those birds are particularly difficult to recapture. Because of this crucial methodological constraint, the study was conducted during the incubation period, when failed birds are expected to continue attending their nest (Boulinier et al., 2008b; Chambert et al., 2012a) and can thus be captured more easily than later in the season. Although incubation is not supposed to be the period during which most prospecting activities occur (Boulinier et al., 1996; Doligez et al., 2004), breeding failure at this stage is expected to strongly impact individual behaviour (Danchin et al., 1998). Indeed, individuals can still choose between reinvesting in a new reproductive attempt or postponing current breeding. The latter could involve visits to different breeding areas to which the individual might disperse in the future (Danchin et al., 1998) and thus, prospecting movements are expected to occur.

In this experimental study, the effect of individual breeding performance on the occurrence of prospecting movements and time-budgets in black-legged kittiwakes *Rissa tridactyla* was tested at two different colonies. Successful breeders were predicted to be constrained by egg incubation. Hence, they were expected to display high nest attendance, regularly interrupted by foraging trips at sea to meet their energy demands and those of their forthcoming offspring (Golet et al., 2000; Weimerskirch et al., 2003). Therefore, no prospecting behaviour was expected in these birds, as most time and energy resources were expected to be allocated to breeding activities. On the contrary, artificially-failed breeders were predicted to prepare for potential future reproductive events, spending additional time at the nest to maintain pair bond and site ownership (Naves et al., 2006) and some were also predicted to display prospecting visits to other breeding colonies during which they may engage in activities related to the potential acquisition of a new breeding site (Reed et al., 1999). These movements were expected to occur at a scale of several tens of kilometres, as indirectly suggested by a previous study estimating gene flow among and within kittiwake colonies and in one of its parasite, the tick *Ixodes Uriae* (McCoy et al., 2005).

2. Material and methods

2.1. Model species and study sites

The black-legged kittiwake is a small colonial gull breeding on coastal cliffs of the northern hemisphere. It lays a clutch of one to three eggs, with an incubation period of 27 days and both members of a pair equally share parental care over the breeding season (Coulson, 2011). The annual survival of breeders has been estimated to *ca*. 0.88 in the study population (Chambert et al., 2012b) and breeding habitat selection has been well studied in this species, notably because the attendance and movements of individually marked birds between nearby breeding cliffs can be easily tracked (Boulinier et al., 2008b; Danchin et al., 1998).

The study was conducted at two kittiwake breeding colonies in Eastern Finnmark (Norway), Hornøya (70°23′N, 31°09′E) and Ekkerøy (70°05′N, 30°07′E), at the incubation stage, defined here as the period when most of individuals nesting in the colony had been incubating for 10–20 days. These two colonies are among the largest in the area and their local productivity is relatively high (Anker-Nilssen et al., 2000; Ponchon et al., 2014).

2.2. Experimental design

The experiment consisted in equipping kittiwakes that had been incubating between 12 and 15 days with GPS devices. The birds were chosen randomly in a highly successful breeding subcolony. Twenty four hours after device deployment, the nest content of the instrumented birds was manipulated following a random block design: within pairs of neighbouring nests, eggs were either moved to foster nests outside the plot or left in the nest to get, for each nest pair, one successful and one artificially-failed nest. We thus obtained two treatment groups during the tracking period: one successful and one artificially-failed group.

Study sites were visited the following year only in Hornøya to resight the birds and estimate the proportion of birds that returned to their breeding site.

2.3. GPS equipment and sample sizes

The birds were colour-ringed and equipped with 12 g MiniGPS-100 (earth&OCEAN Technologies, Germany; ~2.3% of bird body mass). The devices, programmed with an acquisition frequency of 4 min, were attached to the lower back feathers of the birds with TESA® tape. Individual captures were conducted using a noose pole or a noose trap