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Timing of prospecting and the value of information in a colonial breeding bird

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We investigated if one category of birds, prospectors, i.e. those likely to seek future breeding sites, attempt to gather information on the local reproductive success of their conspecifics. If prospecting is an important information-gathering process, it should occur when reliable estimation of the local reproductive success can be made. We tested this prediction in a colonial seabird, the Kittiwake *Rissa tridactyla*, by monitoring the number of prospectors and the value of the information available on local reproductive success in a series of breeding cliffs during two breeding seasons. We found that the bulk of prospecting occurred when the best information on local reproductive success was available. The pattern was very similar in the two study years (1985 and 1992); prospecting occurred late in the season, as reported for most bird species. This result is consistent with the potential use of conspecific reproductive success as a proximate cue for habitat selection.

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Selection of a breeding habitat is of prime importance in the determination of individual fitness, and animals are likely to have evolved complex strategies to choose their breeding habitat (Cody 1985). As underlined recently in the context of mate selection in polygynous species (e.g. Sullivan 1994, Getty 1995), an important element for their choice may be the information they can gather before making their decision. Conspecifics, for instance, can transmit important information on the quality of potential breeding patches in two ways: by their presence or by showing evidence of current reproductive success (Chabrzyk and Coulson 1976, Stamps 1991, Reed and Dobson 1993). Conspecific presence provides indirect information on the quality of potential breeding habitats (Shields et al. 1988, Brown et al. 1990, Stamps 1991, Forbes and Kaiser 1994), and has been recognised as a cue to habitat selection in various animals, such as lizards, mammals and birds (Stamps 1987, 1991, Smith and Peacock 1990, Brown et al. 1990, Reed and Dobson 1993). However, other information based on conspecifics, their current local reproductive success, is likely to be a better gauge of one's chances to breed successfully in a given habitat the following year (Burger 1982, Shields et al. 1988, Boulinier and Danchin in press), particularly in instances of low genotype-environment interaction (Stearns 1992).

In most birds, young prospect breeding places towards the end of the breeding season (Fisher and Fisher 1969, Chabrzyk and Coulson 1976, Smith 1978, Mead and Harrison 1979, Harris 1983, Porter and Coulson 1987, Klomp and Furness 1990, Monnat et al. 1990, Reed and Oring 1992, Zack and Stutchbury 1992, Cadiou et al. 1994, see Danchin et al. 1991 for a review), and failed breeders have been recorded behaving in the same way (Cadiou et al. 1994). The main role of this behaviour has been suggested to be the gathering of information to choose among potential future breeding sites, but little evidence exists on this phenomenon (Mead and Harrison 1979, Monnat et al. 1990, Reed and Oring 1992, Cadiou et al. 1994). In particular, little is known on how the quality of information that is potentially gathered by prospectors varies temporally.

In this paper we investigated in a colonial cliff-breeding seabird, the Kittiwake *Rissa tridactyla*, if one category of birds likely to be seeking breeding sites, namely prospectors, gathered one potentially important component of conspecific-based information: local reproductive success. We predicted that, within a breeding season, the timing of prospecting would correspond to the period when reliable information is available on the local success at breeding cliffs.

Methods

Kittiwakes breed in cliff patches where reproductive success differs locally because of differences in predator pressure and levels of tick ectoparasitism (Danchin and Monnat 1992). At Cap Sizun (Brittany, western France), specific data to address the question of the timing of prospecting were collected in 1985 and 1992.

In these two years, the attendance of prospectors was recorded every three days on intensively monitored cliffs from the end of the nest building period (end of May) until the end of the breeding season (mid August). A prospecting bird is here defined as an individual observed on breeding cliffs where it has not built a nest the current year, i.e. an individual potentially seeking a site for the next year (Cadiou et al. 1994). Individual identification through colour-bands indicated that these birds were mostly individuals that never bred before, but the sample also included failed breeders of the current year and birds that bred in a previous year but which were not currently breeding (Cadiou et al. 1994). The two cliffs monitored for prospector and breeder attendance were different in 1985 and 1992, and held respectively a total of 73 and 124 nests. Our survey provided a quantitative measure of the number of prospectors at the colonies throughout the breeding season.

In parallel, we monitored the reproduction on a large portion of the Cap Sizun breeding cliffs ($n = 6$ in 1985 and $n = 12$ in 1992) in order to calculate an index of the quality of the information available on the local reproductive success at different dates (the number of nests per cliff ranged from 14 to 72). This index was the determination coefficient (r^2) of the relationship between the proportion of currently successful nests (i.e. those containing egg(s) or chick(s) at the time considered) and the actual proportion of nests that produced chicks in each cliff in the same year (see Fig. 2). Thus, it reflected the possibility for a visiting bird to assess the relative quality of the cliffs on a single visit at the different times.

Results

In both years, the index of the quality of information available to prospectors on local reproductive success showed an inverted U-shaped curve during the breeding season (Fig. 1(a) and (b)). It first increased slowly from the end of the nest building period until the beginning of the rearing period, then increased sharply and remained high until it dropped at the time when most juveniles fledged and a large portion started deserting the colonies in the third week of July (Fig. 1). Thus, during the end of the rearing period, the quality of the estimate of the actual reproductive success that could be obtained on a single visit was very high (the proportion of successful nests at this period explained 97% of the actual reproductive success on day 195 in 1985 and 93% on day 189 in 1992; $n = 6$, $p < 0.0001$ and $n = 12$, $p < 0.0001$ respectively). At this moment, the slope of the regression of the actual reproductive success on the proportion of successful nests calculated for each day

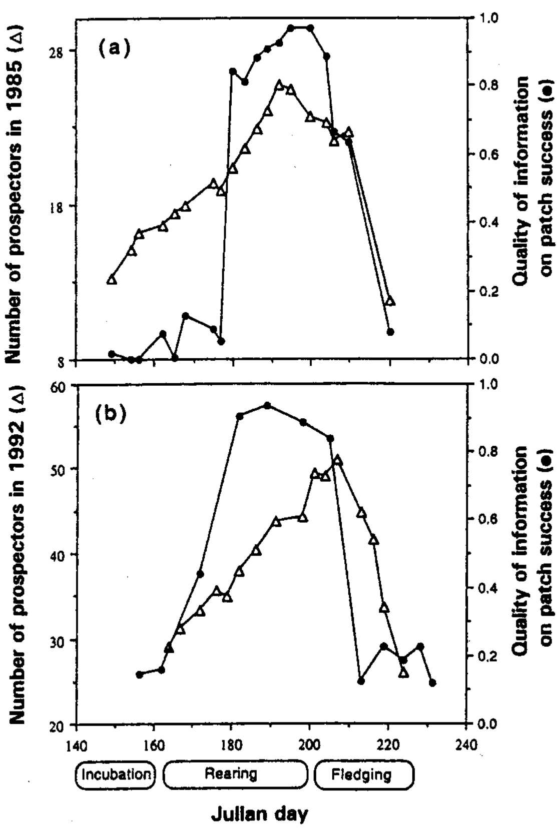

Fig. 1. Number of prospecting birds (Δ) and quality of information on patch reproductive success (●) at different dates along the breeding season in (a) 1985 and (b) 1992. The number of prospecting birds was recorded on two intensively monitored cliffs each year. The index of the quality of information was calculated using a large part of the breeding cliffs used by Kittiwakes in Cap Sizun each given year ($n = 6$ in 1985 and $n = 12$ in 1992).

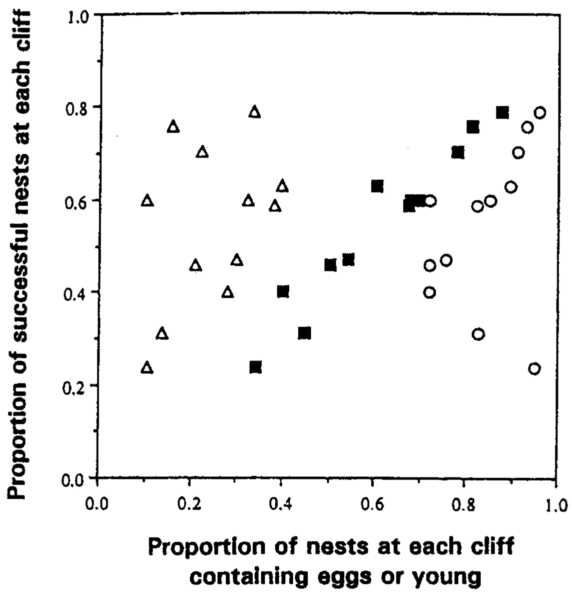

Fig. 2. Proportion of successful nests (i.e. nests fledging young) at each cliff in 1992 in relation to the proportion of nests containing eggs or young at three dates during the course of the breeding season. ○ = Julian date 162, ■ = 189; △ = 213. The determination coefficient of this relationship (r^2) was used as an index of the quality of information available on local reproductive success at each date. On day 162, $r^2 = 0.16$ ($p = 0.20$); on day 189, $r^2 = 0.93$ ($p < 0.001$) and on day 213, $r^2 = 0.13$ ($p = 0.26$).

did not depart from one (Fig. 2), indicating that the estimate that could be obtained on a single visit not only allowed the comparison of the relative quality of the different cliffs, but also could provide a direct assessment of the actual reproductive success within colonies. Outside the end of the rearing period and the beginning of the fledging period, the determination coefficients were not significantly different from zero (Figs 1 and 2), meaning that on these dates the relative quality of the cliffs could not be inferred from the proportion of nests showing current evidence of success (Fig. 2).

In 1985 and 1992, the number of prospectors increased as the season progressed, and reached the highest values between the end of June and the end of July. There was a marked decline in prospectors midway through the fledging period (Fig. 1(a) and (b)). The peak occurred slightly later in 1992 than in 1985, but occurred when the value of information on local reproductive success was still high. Globally, the number of prospecting birds followed a pattern parallel to that of the quality of the information that could be gathered on the local reproductive success (Fig. 1). Thus, in both years prospectors were more prevalent when the information on the local reproductive success of the breeding patches was the most reliable.

Discussion

These results show that in the Kittiwake most of the attendance at colonies by prospectors occurred when the best information was available on the quality of the cliff breeding patches. This is consistent with the use of this information by prospectors as a proximate cue for their future settling decision.

The existence in this Kittiwake population of a restricted period when high quality information was available on patch reproductive success was notably due to the synchronisation of breeding events, as observed in most migratory species. The pattern of variation of this information before the fledging period may vary according to the timing of factors affecting local reproductive success. For instance, predation on eggs may reveal a badly exposed cliff earlier in the season than the effect of ectoparasites on chick survival (Danchin and Monnat 1992). As pelagic seabirds roam widely, low food availability is likely to be reflected in poor breeding success of several neighbouring colonies (Monaghan et al. 1989, Danchin 1992) and is unlikely to influence cliffs in a particular colony differentially. Thus, such factors acting at a larger spatial scale may affect reproductive success less clearly at the small spatial scale considered here. For similar reasons, in most species the best information on breeding patch quality is likely to be available just before the fledging period, and that is when most prospecting is observed (Catchpole 1972, Danchin et al. 1991, Reed and Oring 1992, Baker 1993). Moreover, behavioural observations showed that prospectors are likely to assess the presence of chicks on the breeding patches: in the Kittiwake prospectors are attracted to nests containing chicks (Cadiou et al. 1994) and in several cavity nesting species they enter nests (Ashcroft 1976, Podolsky and Kress 1989, Zicus and Hennes 1991). In the Kittiwake, non-breeders often visit several different colonies within a breeding season and were found to be more likely to recruit the following year in the colony, and even on the actual nest site where they were most often observed (Cadiou et al. 1994). Individual prospectors can be recorded within the same day in colonies situated more than 15 km apart (pers. obs.). Moreover, we have evidence that environmental quality is spatially heterogeneous and temporally predictable at the scale at which most of the recruitment and dispersal events are recorded. Successful cliffs attract more recruits and keep more of their former breeders the next year than unsuccessful cliffs (Danchin, Boulinier and Massot, unpublished). Thus, prospecting could be seen as a sampling behaviour that allows individuals to track fluctuations in the quality of their breeding habitat, as optimal foragers do at a different scale (Stephens 1987).

The use of reproductive success as 'public information' resembles the one identified in studies of group foraging (Valone 1989).

Prospecting birds include different categories of individuals that are at various stages of the recruitment processes (Cadiou et al. 1994), and this must be kept in mind when discussing their behaviour and pattern of appearance in the colonies. In particular, some of the birds recorded as prospectors in this study were failed breeders, which could potentially start prospecting only after they had failed. These birds may represent a large proportion of the prospectors at the time when most failures had already occurred, and thus at the time the current relative quality of the cliffs can be assessed reliably. This may explain arithmetically part of the good fit observed between number of prospectors and the quality of information available. Nevertheless these birds are true prospectors potentially looking for new sites (individuals are more likely to change sites after a breeding failure; see Switzer 1993 for a review).

Explanations of the presence of non-breeders at colonies other than assessing local reproductive success exist and may contribute to explain the pattern of prospecting observed. Attending the breeding grounds implies potential costs, such as stronger intraspecific competition for food close to colonies (Furness and Birkhead 1984) and should thus be associated with benefits. This is notably the case if their presence at colonies allows non-breeders to make early attempts of site and mate acquisition (Stutchbury 1991, Zack and Stutchbury 1992, Cadiou et al. 1994). In some species, such as the Kittiwake, a lower attendance of breeders towards the end of the breeding season may explain some form of late prospecting (prospectors that actually squat and attract potential mates on nests temporally left unattended by their owners; Danchin 1987, Cadiou et al. 1994), but this would not explain late prospecting in species with continual attendance by the breeders until the end of the season (Nelson 1978, Klomp and Furness 1990). The acquisition of knowledge about other environmental characteristics than the breeding success of conspecifics would not in itself justify a late timing of prospecting (Klöpfer and Ganzhorn 1985, Wiens 1985), unless this information is available only late in the breeding season (e.g. social interactions with successful breeders or information on food availability at the time of chick provisioning). Detailed monitoring of the physiological condition of prospectors in relation to their yearly pattern of appearance would allow to test if eco-physiological constraints may prevent young birds from reaching the breeding grounds earlier.

In conclusion, the timing of prospecting observed in the Kittiwake, as well as in most birds, parallels the seasonal variation of the quality of information available on breeding patch quality. Together with the differential recruitment observed in relation to patch reproductive success (Danchin, Boulinier and Massot, unpublished), this observation suggests that prospectors gather such information while visiting colonies. The potential adaptive significance of this behaviour depends on the value of the information gathered (Stephens 1989), which, in turn, depends on the spatial heterogeneity and predictability of the environment. Our results underline the need to study the spatial and temporal scale of variations of the local factors affecting reproductive success in relation to dispersal and recruitment behaviour.

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