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Albatrosses prospect before choosing a home: intrinsic and extrinsic sources of variability in visit rates

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In long-lived species with delayed maturity, prebreeders are expected to gather information by visiting and sampling the quality of potential nesting areas (prospecting), before they choose where to breed. In most seabirds, this process is important because, once recruited, individuals generally remain site-faithful throughout their long reproductive life. As many seabirds are believed to display low levels of natal dispersal, it is possible that natal philopatry is an obligate strategy for most individuals, with prospecting being a negligible activity during the prebreeding stage. Using ringing information and GPS technology, we tracked breeding adults and prebreeder black-browed albatrosses, *Thalassarche melanophris*, from a colony of the Falkland Islands, during the breeding season. Breeding adults rarely engaged in prospecting, whereas prebreeders showed a high propensity to visit other colonies. Most prebreeders started prospecting ashore when 4–5 years old and most of the younger individuals prospected more than one breeding colony, with some prospecting up to five colonies in just 9 days. Prospecting activity did not differ between males and females and rapidly declined as prebreeders aged, by which time individuals had probably already selected their future nesting site. Nestling body mass at 60 days of age and hatching date did not influence prospecting behaviour later in life. Prospecting was mostly directed at colonies within 10 km from the natal place, but occurred regularly up to 55–65 km. While distance from the natal place was a strong predictor of the probability of a colony being prospected, colony size and growth rate were not. Our results provide new insights into the role of prospecting in the process of recruitment, showing that even for highly philopatric birds, recruitment to the natal colony (or to another nesting site) has the potential to be informed, not done blindly.

Recruitment to a breeding population is a gradual and poorly understood process for long-lived species with delayed maturity (Danchin, Cadiou, Monnat & Rodriguez, 1991; Peter, Becker, & Bradley, 2007). During the prebreeding period immatures are expected to gather information to make the critical choice of where to breed. By visiting and sampling the quality of potential nesting areas, i.e. prospecting (Reed, Boulinier, Danchin, & Oring, 1999), individuals acquire and process environmental and social information needed to select the most suitable breeding site, with implications for lifetime fitness (Boulinier & Danchin, 1997; Clobert, Le Galliard, Cote, Meylan, & Massot, 2009; Danchin, Boulinier, & Massot, 1998; Enfjäll & Leimar, 2009). Dispersal strategies often appear to be informed (Clobert et al., 2009) by knowledge gathered during prospecting, resulting in nonrandom dispersal which also modulates gene flow, and thus population persistence and connectivity (Delgado, Ratikainen, & Kokko, 2011; Ponchon, Garnier, Gremillet & Boulinier, 2015).

Although prospecting may represent a successful strategy to maximize individual fitness, not all individuals show the same willingness to engage in it (Delgado et al., 2011). This suggests that the quality and value of, and access to, external information (personal and social) and the internal state of individuals (phenotype dependent) are crucial in their decision-making process regarding prospecting and dispersing (Clobert et al., 2009).

Prospecting behaviour is a general feature in both colonial and territorial species (Boulinier & Lemel, 1996; Calabuig, Ortego, Aparicio, & Cordero, 2010; Ponchon et al., 2013; Pärt & Doligez, 2003). In most seabirds, which include several philopatric

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species, breeding site selection is especially important because, once recruited, individuals generally remain site-faithful throughout their long reproductive life (Coulson, 2002). In fact, prospecting behaviours are mostly performed by pre-, non- or failed breeders (Fijn, et al., 2014; Ponchon, Chambert, et al., 2015; Ponchon, Iliszko, Gremillet, Tveraa, & Boulinier, 2017) and are generally less frequent among successful breeding adults (Reed et al., 1999). The limited occurrence of prospecting by active breeders could be related to the fact that individuals are busy with their own breeding attempts at the most profitable time for gathering valuable public information, notably the chick-rearing stage (Cadiou, Monnat, & Danchin, 1994; Doligez, Pärt, & Danchin, 2004; Zicus & Hennes, 1989).

The available information on highly philopatric species (Gauthier, Milot, & Weimerskirch, 2010; Prince, Rothery, Croxall, & Wood, 1994) may suggest that in these species (1) natal philopatry is an obligate strategy for the majority of individuals, with prospecting being a negligible activity during prebreeding. However, (2) if prospecting occurs, we might expect large and growing colonies to attract more prospectors because they provide more potential mates and putatively better local breeding conditions (Boulinier, McCoy, Yoccoz, Gasparani, & Tveraa, 2008; Coulson & Coulson, 2008; Dittmann, Zinsmeister, & Becker, 2005). Time and energy invested by prospectors are costs expected to differ with the distances travelled to prospect new breeding sites, and, because in some species long-distance dispersal is less frequent than short-distance dispersal (Prince et al., 1994), (3) colonies nearby might be more frequently visited than those further away.

Individual investment in time and energy for prospecting is also expected to change according to individual experience, age and sex, as well as conditions experienced in early life (Barbraud, Johnson, & Bertault, 2003; Dittmann et al., 2005; Tilgar, Mänd, Kilgas, & Mägi, 2010). As such, (4) we might expect prebreeders to prospect less as they mature and decide to recruit at a given colony. Moreover, because, in birds, females generally tend to disperse more (Greenwood, 1980), (5) we might predict males to be less inclined to prospect non-natal breeding sites. Similarly, (6) birds in poor condition during early growth (indicative of worse local conditions) might be more willing to prospect and disperse (Tilgar et al., 2010). Finally, if breeders are engaged in breeding duties at the time when suitable information on conspecific breeding performance is available, (7) we might expect few or none of them to be detected prospecting other colonies.

Prospecting movements concerning selection of breeding habitat during the immature phase have rarely been studied in seabirds (common guillemot, *Uria aalge*, Halley & Harris, 1993; kittiwake, *Rissa tridactyla,* Cadiou et al., 1994; common tern, *Sterna hirundo*, Dittmann et al., 2005; northern gannet, *Morus bassanus*, Votier, Grecian, Patrick, & Newton, 2011; Scopoli's shearwater, *Calonectris diomedea*, Péron & Grémillet, 2013) and the predictions formulated above scarcely tested. Here, we studied prospecting movements of prebreeder and adult back-browed albatrosses, *Thalassarche melanophris*, by means of GPS tracking. For the purposes of this study, prospecting behaviour was defined as visits of individuals to breeding areas where they were not currently breeding (Reed et al., 1999) including waters adjacent to the colonies, where seabirds congregate in large numbers and where the exchange/sharing of social or personal information is possible (Carter et al., 2016; Daniels, Heath, & Stevenage, 1994; Evans, Dall, Bolton, Owen, & Votier, 2015; Granadeiro, Campioni, & Catry, 2017; Weimerskirch, Bertrand, Silva, Marques, & Goya, 2010). We described the occurrence of this behaviour in our study population and examined its prevalence in relation to intrinsic (i.e. age, sex, early history) and extrinsic factors (i.e. distance from natal colony, size and demographic trend of visited colonies).

METHODS

Study Area and Data Collection

The black-browed albatross is the most abundant albatross species in the southern hemisphere. In Chile, albatrosses breed at six known sites (see Fig. 1a) whereas the Falkland archipelago (southwest Atlantic Ocean) supports one of the largest black-browed albatross concentrations in the world including 12 breeding colonies (Tickell, 2000; Fig. 1b). Since 2003, the black-browed albatross colony on New Island (51°43′S, 61°18′W) known as Settlement rookery has been the focus of a long-term monitoring

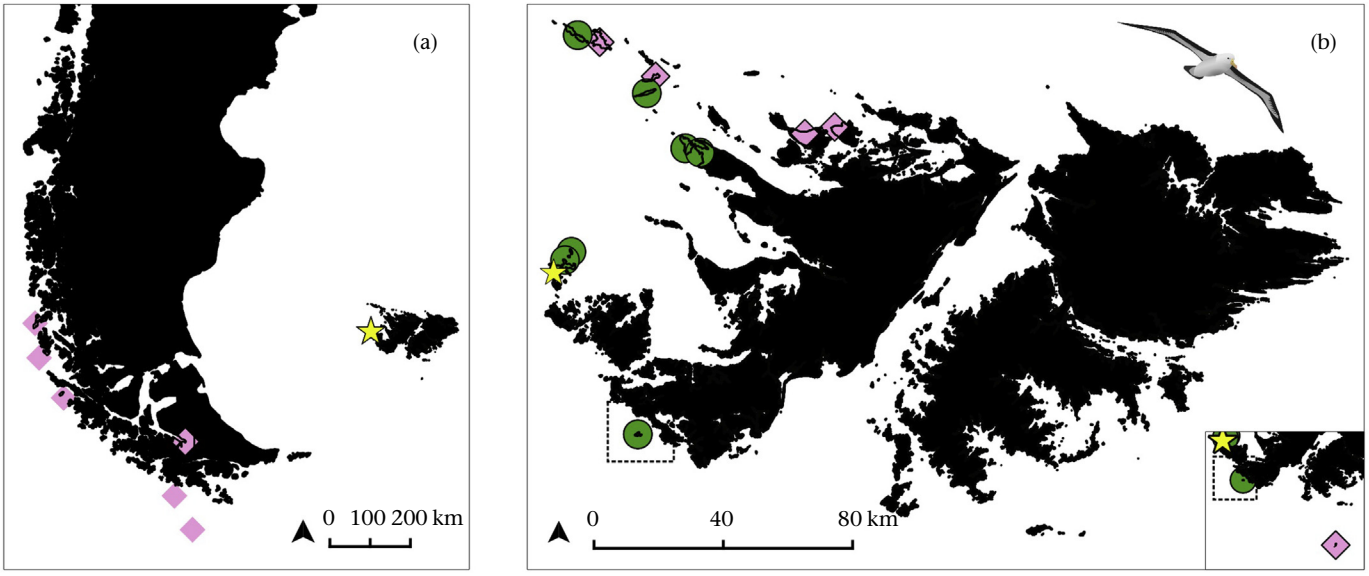

Figure 1. Map of the southwest Atlantic region showing black-browed albatross colonies of (a) Chile and (b) Falkland Islands. Beauchene Island is shown in the small insert. Colonies prospected and not prospected by prebreeders from New Island (study colony, star symbol) are shown as circles and diamonds, respectively.