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Tracking prospecting movements involved in breeding habitat selection: insights, pitfalls and perspectives

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Summary

1. Prospecting allows individuals to gather information on the local quality of potential future breeding sites. In a variable and heterogeneous environment, it plays a major role in breeding habitat selection and potentially helps individuals make optimal dispersal decisions. Although prospecting movements, involving visits to other breeding sites, have been observed in many species at relatively fine spatial scales, little is known about their occurrence at larger scales. Furthermore, the adaptive value of dispersal strategies in response to environmental changes remains poorly investigated.

2. Here, our main objective is to highlight in what ways tracking devices could constitute powerful tools to study prospecting behaviour at various spatial scales. First, we stress the importance of considering prospecting movements involved in breeding habitat selection and we detail the type of data that can be collected. Then, we review the advantages and constraints associated with the use of tracking devices in this context, and we suggest new perspectives to investigate the behavioural strategies adopted by individuals during breeding habitat selection processes and dispersal decisions.

3. The rapid development of new powerful electronic tools for tracking individual behaviour thus opens a wide range of opportunities. More specifically, it may allow a more thorough understanding of the role of scale-dependent dispersal behaviour in population responses to environmental changes.

Key-words: biotelemetry, breeding habitat choice, dispersal decisions, individual strategies, social information, spatial population ecology

Introduction

Dispersal, defined as the movement of an individual from its natal or previous breeding site to a new breeding site, is a key process in ecology and evolution (Clobert *et al.* 2001; Ronce 2007). In a context of rapid environmental changes at large scales due to global warming and anthropogenic activities, the role of individual dispersal among populations has recently been highlighted as an essential research topic (Kokko & Lopéz-Sepulcre 2006; Grémillet & Boulinier 2009). Indeed, dispersal is a key process involved in the spatial distribution of populations and species ranges, as well as gene flow within metapopulations (Clobert *et al.* 2001; Hanski & Gaggiotti 2004).

A key component of the dispersal process is the selection of a new breeding habitat (Danchin, Heg & Doligez 2001). As variability in habitat quality can strongly affect individual fitness (Boulinier & Lemel 1996), numerous species have developed adaptive behavioural strategies to select high-quality habitat sites (Boulinier *et al.* 2008a). In particular, individuals may perform prospecting movements, that is, visits to breeding sites where they do not currently breed (Reed *et al.* 1999). During such visits, individuals may gather personal information from environmental cues and social information from the local presence or performance of conspecifics to assess the quality of breeding sites (Reed *et al.* 1999; Danchin, Heg & Doligez 2001; Danchin *et al.* 2004; Dall *et al.* 2005). Prospecting often occurs before dispersing and settling in a new breeding site, when individuals are expected to choose a suitable site to

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maximize their future fitness, and has mainly been reported in immatures, non-breeders or failed breeders (Reed *et al.* 1999). Theoretical studies have stressed that such behaviour should be observed if local environment quality and the used cues are temporally predictable at the spatial scale considered (Boulinier & Danchin 1997; Doligez *et al.* 2003).

Prospecting behaviour has been extensively documented in colonial (Boulinier *et al.* 1996; Danchin, Boulinier & Massot 1998; Frederiksen & Bregnballe 2001; Dittmann, Zinsmeister & Becker 2005; Calabuig *et al.* 2010) and territorial birds (Doligez, Danchin & Clobert 2002; Ward 2005; Parejo *et al.* 2007; Arlt & Pärt 2008), because their movement behaviour can be conspicuous and easily observed in the field compared to other taxa. Nevertheless, prospecting and information use in a breeding habitat selection context have also been suggested in insects (Seeley & Buhrman 2001; Francks *et al.* 2007; Canonge, Deneubourg & Sempo 2011), mammals (Young, Carlson & Clutton-Brock 2005; Selonen & Hanski 2010; Rémy *et al.* 2011), amphibians (Gautier *et al.* 2006) and reptiles (Aragón *et al.* 2006). Furthermore, visits of non-local breeders have been reported in many other species (Hamel, McMahon & Bradshaw 2008; Jorgensen *et al.* 2010; Stevick *et al.* 2011), even if these specific movements have not been described as prospecting movements or related to breeding habitat selection.

However, most studies directly dealing with breeding habitat selection and using marked individuals have recorded prospecting movements at limited spatial scales, covering a few kilometres at best. Consequently, the relative importance of large- vs. small-scale prospecting movements is little known. Moreover, both the influence of prospecting behaviour on large-scale population dynamics (Morales *et al.* 2010) and the use of information gathered by individuals on the quality of a site in response to large-scale environmental fluctuations remain unexplored (Grémillet & Boulinier 2009). Capture–mark–recapture approaches (Lebreton *et al.* 2003) genetics tools (Broquet & Petit 2009), and to some extent, intrinsic biogeochemical markers (Ramos & González-Solís 2012) allow estimating dispersal rates within metapopulations. Yet, these methods give limited insights into the behavioural mechanisms underlying breeding habitat selection which lead to the observed dispersal patterns. Furthermore, direct observations and modelling approaches conducted so far paid little attention to large-scale prospecting movements and their consequences on dispersal strategies and population dynamics.

In the last decades, powerful tracking devices have been developed to allow the remote tracking of individuals (Ropert-Coudert & Wilson 2005). Strikingly, the enormous potential of these tools for addressing crucial questions regarding information gathering and dispersal at various spatial scales has been so far poorly exploited (Grémillet & Boulinier 2009; but see Votier *et al.* 2011). Therefore, our main objective here is to highlight in what ways tracking devices can constitute powerful tools to study prospecting behaviours at various spatial scales. For this purpose, we first outline the importance of investigating prospecting behaviour for breeding habitat selection studies and we review the type of required data. In a second step, we describe how to collect such data in wild populations using tracking devices and we provide illustrations of prospecting movement data collected using different tracking devices. Finally, we highlight the strong potential of these approaches to explore the role of prospecting in breeding habitat selection and dispersal processes.

Why investigate prospecting behaviour?

As an important part of habitat selection process, prospecting can have potential consequences on dispersal strategies at the individual, population and species levels.

First, investigating prospecting behaviour can shed light on decision-making processes involved in dispersal and thereby help understand the mechanistic responses of individuals to environmental conditions fluctuating at different spatial scales (Boulinier & Lemel 1996). The spatio-temporal patterns of prospecting behaviour can help reveal the different cues used by individuals to make dispersal decisions (Doligez *et al.* 2003). Comparing the frequency of prospecting movements at different spatial scales with the spatial variability of the environment can provide information about the scale at which dispersal might be adaptive (Boulinier & Lemel 1996). For instance, repeated large-scale prospecting movements of individuals are predicted to be associated with large scale changes in habitat quality (Boulinier & Danchin 1997). Similarly, comparing the timing of prospecting with the temporal variability of the value of different information sources that reflect the quality of breeding sites can help identify the specific cues individuals rely upon to select suitable breeding sites (Boulinier *et al.* 1996). If an individual misses the optimal timing of a specific cue, a mismatch between the information gathered and the real value of this cue could have potential impacts on individual fitness (see McNamara *et al.* 2011). Thus, prospecting movements are expected to occur when the cue is the most valuable and reliable.

Second, investigating prospecting behaviour can help understanding how selective pressures affect individual investments in different activities and thus how constraints acting on prospecting can shape the evolution of dispersal strategies at different scales (Pärt & Doligez 2003). Time and energy spent prospecting for a potential future breeding site are traded off against other activities such as foraging or resting. As a result, the ability of individuals to gather information via prospecting can affect fitness components and thus lead to the joint evolution of dispersal strategies and life-history traits such as age at first reproduction (Boulinier & Danchin 1997; Frederiksen & Bregnballe 2001).

Third, understanding the behavioural mechanisms underlying breeding habitat choices and dispersal is crucial to predict population responses to environmental changes, especially in the case of management or conservation of fragmented populations (Bowler & Benton 2005; Van Dyck & Baguette 2005). One possible response of populations to changing constraints and selective pressures is the colonization of new suitable breeding sites, including sites out of the current species range (Thomas *et al.* 2001). Thus, dispersal can shape spatial shifts in species' ranges and investigating how breeding habitat selection processes can affect dispersal decisions is essential to predict how species' ranges could change (Kokko & Lopéz-Sepulcre 2006). Investigating prospecting movements can also help understand how different levels of natural selection may affect the responses of populations to environmental variability (Delgado, Ratikainen & Kokko 2011).

Finally, non-random dispersal patterns may have major evolutionary consequences via directed gene flow. On the one hand, they could promote genetic divergence and ultimately speciation, when individuals choose their habitat according to their phenotype and/or their natal environmental conditions (Edelaar, Siepielski & Clobert 2008; Bolnick *et al*. 2009). On the other hand, non-random dispersal may promote gene flow between populations, preventing local adaptation and genetic differentiation between populations (Lenormand 2002).

What do we need to know about prospecting behaviour?

Knowledge on the role of prospecting varies greatly among taxa and according to the considered spatial and temporal scales. The general framework presented here aims at highlighting a series of key questions that can be addressed to investigate prospecting.

Understanding how information regarding the quality of a breeding site is gathered and used by individuals for dispersal decisions requires monitoring individual movements at the time of breeding to determine (i) whether individuals visit breeding sites other than their own, which are potentially suitable for future reproduction (Figs 1–3), (ii) whether they visit sites at random or are attracted by specific sites that they visit more frequently (Figs 1 and 2), (iii) whether the sites visited differ in quality, (iv) what cues are used by individuals, (v) whether the timing of prospecting matches the timing of information reliability and availability, (vi) whether subsequent site selection is related to previous prospecting visits, and finally, (vii) how time spent prospecting is traded off against other activities such as foraging or resting. A careful study design, potentially integrating experimental manipulations of environmental or social cues (e.g. Seeley & Buhrman 2001; Doligez, Danchin & Clobert 2002; Boulinier *et al*. 2008b), can be relevant to address prospecting occurrence, information use and their consequences on dispersal decisions. Data on the spatial and temporal variability of environmental factors such as food availability, predation risks and parasite presence are also important to collect as they may contribute to explain the occurrence of prospecting at different spatial and temporal scales (Boulinier & Lemel 1996).

The frequency, duration and timing of prospecting are likely to differ between life stages (e.g. immatures, successful breeders, failed breeders or non-breeders) and sexes (see Fig. 1), which can potentially shape differences in dispersal strategies (Boulinier & Danchin 1997; Clobert *et al*. 2001; Bowler & Benton 2005; Votier *et al*. 2011). Therefore, prospecting behaviour needs to be investigated in different categories of individuals to understand how constraints linked to age, sex and individual reproductive status influence dispersal decisions.

How should this knowledge be gathered?

Prospecting can be studied by direct observations of marked individuals in the field (e.g. Young, Carlson & Clutton-Brock

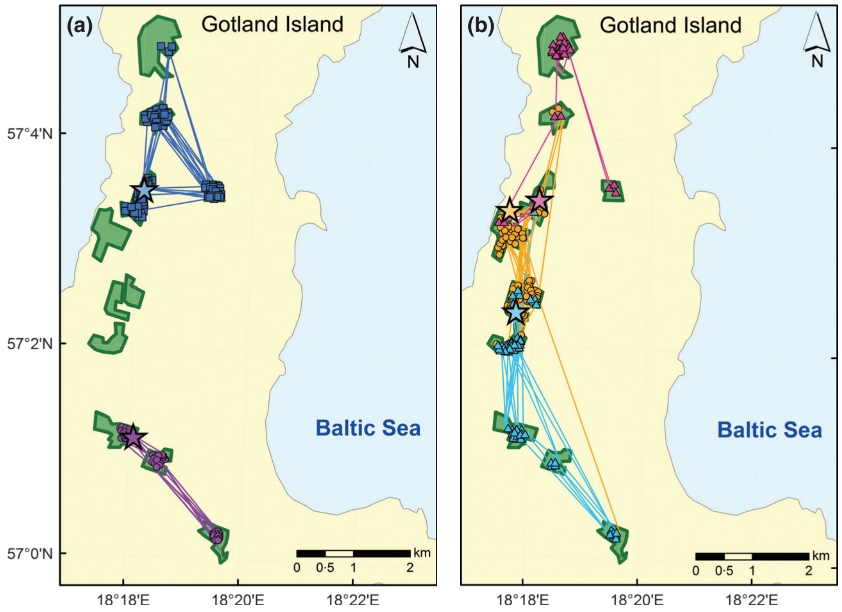

Fig. 1. Example of post-fledging prospecting movements recorded with Very High Frequency (VHF) in the collared flycatchers *Ficedulla albicolis*. Green areas indicate available breeding sites and stars represent the location of the breeding site of each individual. (a) One successful breeding male (blue squares) and one fledgling (purple points) showing numerous repeated movements to the same neighbouring breeding patches. (b) Two failed females (pink and blue triangles) and one fledgling (orange points) showing high prospecting movements (maps created from unpublished data by Doligez and collaborators).

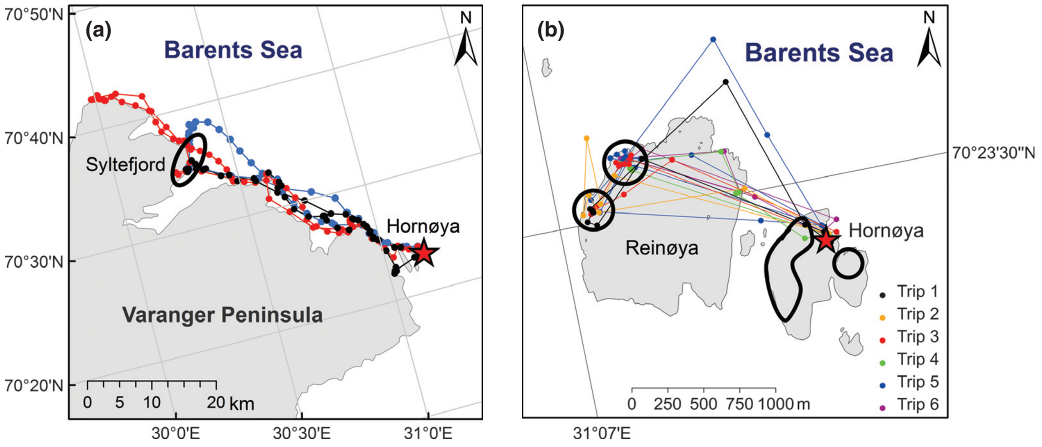

Fig. 2. Example of prospecting trips recorded in two black-legged kittiwakes *Rissa tridactyla* tracked with Global Positioning System (GPS) after their breeding failure: (a) three large scale prospecting trips to the colony of Syltefjord; (b) six fine scale prospecting trips from a different individual to colonies of Reinøya. The red star represents the current nesting colony and the black ellipses, potential prospected colonies (maps created from unpublished data by Ponchon and collaborators).

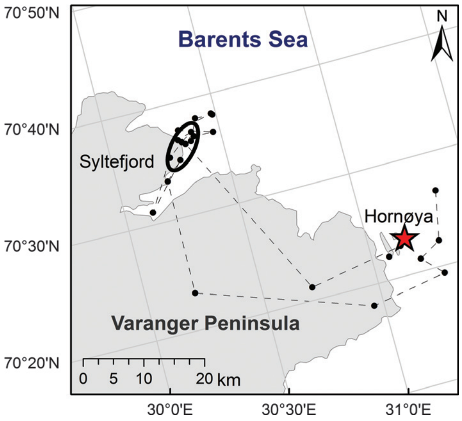

Fig. 3. Example of a prospecting trip recorded in a black-legged kittiwake *Rissa tridactyla* tracked with a Platform Terminal Transmitter (PTT) after a breeding failure. The red star represents the current nesting colony and the black ellipse, the prospected colony (maps created from unpublished data by Ponchon and collaborators).

2005). However, such observations (i) are extremely time-consuming, (ii) provide incomplete information about movements of individuals and (iii) are usually biased towards a few sites and time periods that can be monitored simultaneously. Over the last decades, a great variety of miniaturized electronic tags have been developed, providing the location and physiological, behavioural and energetic status of a large number of wild animals at different temporal scales (Cooke *et al.* 2004). Among them, tracking devices have been widely used to record animal movements and their interactions with the environment and other individuals at scales ranging from a few metres to several thousands of kilometres, both on land and at sea (Cagnacci *et al.* 2010).

Recent reviews highlight the potential of tracking devices in ecological studies, especially in marine vertebrates (Wilson *et al.* 2002; Cooke *et al.* 2004; Ropert-Coudert & Wilson 2005; Hart & Hyrenback 2009; Wakefield, Phillips & Matthiopoulos 2009). However, most tracking studies to date have focused on habitat use, foraging strategies or migration routes, potentially neglecting large-scale movements related to breeding habitat selection. Moreover, they have often been biased towards individuals that are currently breeding successfully, and thus unlikely to prospect. Here, we present five tracking systems that can be used to reveal and investigate prospecting movements in free ranging species (Table 1).

1 *Very High Frequency (VHF) radio tracking* was the first system used to track animals without retrieval of the device, starting in the middle of the twentieth century. Thanks to directional antennas, individuals tagged with miniaturized radio emitters can be located precisely in the field by triangulation. When using non-directional antennas or remote receiving stations, only their presence is detected within a larger area. As radio signals can only be received within a limited range, from a few metres to a few kilometres, VHF radio-tracking system mainly addresses movements at relatively small spatial scales (but see Irons 1998; Wikelski *et al.* 2006). Therefore, it is particularly suitable for addressing habitat selection issues at such scales (Calabuig *et al.* 2010). For instance, following several categories of individuals using radio tracking could reveal different prospecting patterns according to sex or reproductive status (Fig. 1). Despite relatively low material costs allowing large sample sizes (Table 1), this system is nowadays less used compared to recent electronic remote sensing tools that allow more refined tracking of individuals (Wilson *et al.* 2002). Because VHF tags can be very light (down to 0·2 g, Naef-Daenzer *et al.* 2005), it nevertheless remains the only remote sensing tool available to track small species.

2 *The Radio Frequency IDentification (RFID) technology*, first developed in the early 1990s, uses miniaturized Passive Integrated Transponder (PIT) tags that are detected at a specific site thanks to fixed antennas. Data acquisition is automated but because transponders do not emit signals actively, the reading range of antennas is currently limited to 1 m at best (Bonter & Bridge 2011). Thus, antennas have to be placed where prospecting might be potentially detected, which

Table 1. Possible use of the different tracking systems to address the occurrence, frequency and characteristics of prospecting movements at different spatial and temporal scales

System	Applications	Spatial scale	Advantages	Disadvantages	Price for the lightest tags[1] and equipment
VHF	Prospecting intensity Prospecting patterns	Fine	Low cost per tag Low tag mass Large sample size	Relatively low receiving range (<1 km)	170€ for 0·2 g + 1200€ for receiver + antenna
RFID	Prospecting intensity Territory attendance	Fine	Automated system Low cost per tag Low tag mass Large sample size	Low reading range (<1 m) *A priori* knowledge of the potential prospected breeding sites No information on ancillary activities	3€ for 0·1 g + 500€ for each antenna
GPS	Prospecting intensity Mapping of prospecting trips Prospecting time budgets	Fine to large	High spatial accuracy High temporal resolution Complete trips recorded	Need for individual recapture (if not combined with downloading stations) Relatively short acquisition duration (days)	From 50 to 800€ for 12 g; 3000€ for 22 g when combined with a PTT + ARGOS subscription
PTT	Prospecting intensity Potential consequences on other life stages	Large	No need for individual recapture Long-term acquisition duration (months)	Low spatial accuracy (*c.* 1 km) Very high cost per tag	2500€ for 9·5 g + ARGOS subscription
GLS	Comparisons between different life stages of individuals	Large	Large sample size Low device mass Long-term analysis Attachable to a ring	Need for individual recapture Very low spatial accuracy Only two locations a day No locations at equinoxes	160€ for 1 g

The pros and cons are listed for the currently commercially available equipment. Note that the miniaturization of systems is still improving with time. VHF, very high frequency system; RFID, radio frequency identification system; GPS, global positioning system; PTT, platform terminal transmitter; GLS, global location sensing

[1] Lightests tags are the most miniaturized and often the most expensive.

requires an *a priori* knowledge of prospecting locations prior to tracking individuals, as in burrow-nesting species (Zangmeister *et al.* 2009). The RFID method has been proved to be useful in investigating prospecting movement patterns and dispersal decisions according to sex, age, habitat quality or social information use (Dittmann & Becker 2003; Dittmann, Zinsmeister & Becker 2005; Robinson *et al.* 2009). For now, several studies based on RFID but not investigating habitat selection processes have incidentally revealed prospecting events without discussing them (e.g. Ottosson *et al.* 2001; Zangmeister *et al.* 2009). Thus, the current development of the use of RFID in various species may greatly increase the acquisition of data on prospecting intensity during breeding. The low cost of the tags and automatic data storage may allow tracking a large number of individuals over their whole life. Thus, high statistical power can be reached using RFID to test the influence of individual natal conditions, age or experience on their subsequent movements (Dittmann & Becker 2003). As PIT tags are very light, RFID can also be used to monitor very small species (e.g. Robinson *et al.* 2009).

3 *Global Positioning System (GPS)* performs well to record individual movements at fine spatial and temporal scales since 2000 (Hulbert & French 2001). Animal position can be recorded up to every second, 24 h a day, and location accuracy varies between 5 and 30 m (Frair *et al.* 2004). For a 10 g GPS programmed with a 4 min acquisition frequency, individual positions can be recorded for a week, allowing estimating individual time budgets and prospecting intensity (Fig. 2). When GPS loggers are not connected to downloading stations, equipped individuals have to be recaptured to recover the loggers and access the data. Due to this constraint, these loggers have to be preferentially used on individuals showing high fidelity to their breeding site, for example, failed breeders nesting among successful conspecifics (Fig. 2). However, the current development of GPS devices combined with other transmitting systems such as Platform Terminal Transmitters (PTTs), GSM (Sundell, Kojola & Hanski 2006) or Bluetooth/radio signals (Shamoun-Baranes *et al.* 2011) allows more efficient tracking, without the need to recapture individuals. Therefore, these systems decrease time and effort spent in the field and they secure data more efficiently via regular downloads. Furthermore, spatial accuracy can be improved to a few centimetres when using differential GPS (see Pépin *et al.* 2004). Recently, the use of GPS loggers in small species (< 1 kg) has strongly increased (Cagnacci *et al.* 2010) and has provided valuable data on individual movements with a very high spatial and temporal resolution. Yet, so far, most studies focused on foraging and migrating behaviours (e.g. Grémillet *et al.* 2004; Schofield *et al.* 2007) while potentially missing information about visits to other breeding sites. Therefore, GPS loggers should be particularly appropriate in studies dealing with prospecting behaviour from relatively fine spatial and temporal scales to larger ones but only for species heavier than *c.* 200 g (Table 1). In addition to revealing prospecting occurrence and intensity at different spatial scales (Fig. 2), GPS loggers can provide valuable data on individual time budgets and habitat use (Owen-Smith, Goodall & Fatti 2012). In particular, GPS data can reveal how the time spent prospecting is traded off against other activities such as feeding or resting and what consequences it can have on energetic or body condition.

4 *Platform Terminal Transmitters*, relying on ARGOS satellite network, are used since the late 1980s. They have been particularly useful when the devices are difficult to recover (e.g. when individuals have a lower probability to return to the site of capture) or when animals are tracked over large spatial scales for a long time. PTTs could thus be especially suitable to track juveniles or immatures before recruitment (Votier *et al.* 2011) and failed breeders from low success breeding sites (Fig. 3), as they are expected to engage in intense prospecting activity and are unlikely to come back to their breeding site the following year (Danchin, Boulinier & Massot 1998; Boulinier *et al.* 2008b). Location accuracy fluctuates from a few 100 m to several kilometres for standard PTTs (Hays *et al.* 2001), but the emergence of new devices combining PTTs and GPS such as Fast-Loc GPS-PTTs (Costa *et al.* 2010; Witt *et al.* 2010) strongly improves location accuracy and can efficiently reveal prospecting visits to other breeding sites (Votier *et al.* 2011). Due to their low spatial accuracy, standard PTTs have to be used to address mostly large and meso-spatial scale processes, when the potential prospected sites are located tens of km away from each other (Fig. 3).

5 *Global Location Sensing (GLS)* loggers, available since the early 1990s, provide two locations a day from ambient light levels (Wilson *et al.* 1992). They have a much lower location accuracy compared to GPS and PTTs, with an average error of 186 km (Phillips *et al.* 2004). Consequently, they can only be used to track large spatial and temporal movements such as seasonal migrations (González-Solís *et al.* 2007; Fuller *et al.* 2008; Stutchbury *et al.* 2009). Although the use of GLS loggers to identify and study prospecting behaviour is hampered because of their very low spatial accuracy, their low cost and mass could allow monitoring large-scale and long-term movements of a large number of individuals, even in small species (*c.* 40–50 g, Stutchbury *et al.* 2009). GLS loggers could for instance help to test whether juveniles/immatures visit other breeding sites before recruitment in their breeding site.

Conclusion

In this study, we outlined how tracking devices could be used as powerful tools to explore prospecting movements underlying informed dispersal decisions at different spatial and temporal scales. In particular, we showed that characterizing and quantifying prospecting movements using tracking devices is feasible (Figs 1–3) and brings new perspectives in population dynamics through possible investigations of breeding habitat selection behaviours and dispersal processes at large scales. Exploring prospecting behaviour could therefore enable a better understanding of the influence of different factors such as local breeding density, reproductive performance of conspecifics or food availability on dispersal movements and population responses to environmental changes.

Tracking devices may be particularly useful in the context of current global changes. As species ranges are shifting because of global warming (Parmesan & Yohe 2003; Kokko & Lopéz-Sepulcre 2006), breeding habitat selection will become a crucial life-history determinant of population dynamics and adaptive potential. Tracking devices could help identify new breeding habitats visited by individuals out of the current species range and therefore predict the expansion or contraction of species range. In a biodiversity conservation framework, knowledge about the relationship between feeding and prospecting behaviours provided by tracking tools could play a determinant role in implementing new types of protected areas. For instance, seabird conservation has so far mostly focused on foraging habitat without accounting for other related processes occurring on land (Yorio 2009). If protection was given to both foraging areas and breeding colonies connected through prospecting movements, it could lead to more efficient management and conservation of endangered species (Grémillet & Boulinier 2009).

However, tracking devices also have limitations. In many instances, prospectors are expected to collect information about the local quality of potential breeding sites (Reed *et al.* 1999). In the field, tracking devices can help detect individuals visiting breeding sites, but it is more difficult to assess whether these individuals are actually gathering information for subsequent breeding habitat choice. Thus, tracking data should be integrated in study designs allowing to collect complementary data on individual responses to changes in their environment, for example, by manipulating information cues. Moreover, the characterization of individual behaviours could be refined by using data loggers such as three-dimensional accelerometers (Wilson, Shepard & Liebsch 2008; Whitney *et al.* 2010) or miniature cameras (Grémillet *et al.* 2010) deployed simultaneously on the same individuals. Cameras placed directly in breeding sites could also record valuable information about individual and conspecifics behaviour (Calabuig *et al.* 2010). Thus, the combination of tracking devices, additional data loggers and capture–mark–recapture data eventually may help characterize (i) the prospected habitats, (ii) individual prospecting behaviour (iii) the links between prospecting and future habitat selection and (iv) the nature of information used by individuals to make subsequent breeding habitat selection decisions.

Another limitation is that data loggers could have negative effects on individual survival, reproductive success, energetic expenditure or natural behaviour (Wilson, Grant & Duffy 1986; Phillips, Xavier & Croxall 2003; Barron, Brawn & Weatherhead 2010; Bowlin *et al.* 2010; Passos *et al.* 2010; Vandenabeele, Wilson & Grogan 2011 but see Naef-Daenzer *et al.* 2005). Therefore, whenever possible, future tracking studies should aim at assessing possible alterations of prospecting behaviour due to the presence of these devices by simultaneously monitoring the behaviour of control individuals.

Because tracking technology has evolved very quickly towards smaller and lighter electronic devices, it may be soon possible to equip even very small animals. In this context, we posit that the powerful combination of tracking devices and robust study designs could lead to major breakthroughs in our understanding of breeding habitat selection and scale-dependent individual responses to environmental changes. This approach could ultimately integrate other types of movements notably involved in foraging or wintering habitat selection.

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