Review

Prospecting for informed dispersal: reappraisal of a widespread but overlooked ecological process

Aurore Ponchon *

Posted Date: 4 January 2024

doi: 10.20944/preprints202401.0428.v1

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Review

Prospecting for Informed Dispersal: Reappraisal of a Widespread But Overlooked Ecological Process

Aurore Ponchon [1,2]

[1] School of Biological Sciences, University of Aberdeen, Aberdeen, UK; aurore.ponchon@gmail.com
[2] IMBE, Aix Marseille Université, Avignon Université, CNRS, IRD, Marseille, France

Abstract: Prospecting for a future breeding site is an essential component of informed dispersal. It allows individuals to reduce the uncertainty of their environment by gathering personal and social information about the local quality of alternative breeding areas, and to make informed emigration and settlement decisions. Although this process has been studied in territorial and social animal species for decades, it is still not well-understood and spatial patterns of prospecting movements are hard to generalize over taxa or even species due to substantial intra and inter-specific variability. Using 124 empirical studies which have explicitly described prospecting in a context of breeding habitat selection in birds, mammals, fish and invertebrates, I review why, how, when and which individuals prospect depending on their life history traits and sociality. From this synthesis, I identify persisting knowledge gaps which explain why prospecting is still understudied and sometimes overlooked. I finally propose key objectives and research directions, to shed light on prospecting movements and their consequences on informed dispersal strategies, individual fitness and population dynamics, both empirically and theoretically. A better understanding of the mechanisms underlying prospecting, their causes and their consequences will fully reveal how prospecting could constitute a powerful adaptive response to environmental changes for many social and territorial species which will help them persist on the long-term. It will also significantly enhance our ability to predict species responses to environmental changes and thus, inform more effective management plans for threatened species.

Keywords: behavioural decisions; breeding habitat selection; environmental change; exploratory movements; extra-territorial forays; incursions; information use

I. Introduction

Finding a place to breed is a vital decision for an individual, since the quality of a breeding site or territory can directly and indirectly affect individual breeding success and survival (Boulinier *et al.*, 2008). Some individuals can decide to breed where they were born and remain faithful to their breeding site for their entire life. Yet, environmental conditions vary over time and one breeding site can enhance individual productivity one year and annihilate it the next year. Consequently, philopatry is not always the best strategy to maximize individual lifetime fitness in a variable environment (Ponchon *et al.*, 2015b). In addition, kin competition, inbreeding avoidance or degrading local environmental conditions may lead individuals to seek for a new breeding site (Clobert *et al.*, 2012). When individuals decide to leave their natal or current breeding site, they enter into the dispersal phase, which corresponds to the movement between the natal/current breeding site and a new one. It is generally subdivided into three main stages: (1) emigration, when individuals actually leave their breeding site, (2) transience, when individuals move through the landscape, and (3) settlement, when individuals eventually settle in a new breeding site.

One crucial component of dispersal which affects emigration and settlement decisions is the prospecting phase. Prospecting is defined as the visits of individuals to breeding areas or territories other than their current one, from where they can gather information about the local quality of breeding sites (Reed *et al.*, 1999). When sampling their environment during prospecting, individuals can gather different types of information that are available to them. On the one hand, they acquire personal information from their direct interaction with their environment (Dall *et al.*, 2005). On the other hand, they take advantage of the presence or performance of their conspecifics to gather social information (sensu Danchin *et al.*, 2004). Overall these sources of information help individuals leave habitats of low environmental quality and settle in better ones (Ponchon *et al.*, 2021).

Even though prospecting has been identified in many colonial, territorial and social species (Reed *et al.*, 1999; Ponchon *et al.*, 2013), no synthesis covering a wide range of taxa currently exists. One difficulty to assess the universality of prospecting is due to the difficulty of concomitantly studying large scale movements of free-ranging individuals at a fine temporal resolution and over their entire life cycle (Ponchon *et al.*, 2013). Moreover, because observations in the field of the whole process of dispersal can be tricky due to potential disruptions in individual life cycle such as migration, studies often focus on one dispersal stage: either emigration, or settlement. Hence, prospecting, which can occur before or after emigration, is most of the time missed, or ignored, and empirical studies rarely manage to detail all the stages of dispersal including prospecting, except when dispersal can be monitored over limited spatial scales or within closed populations (e.g. Kingma et al., 2016).

On the other side, a lot of different terms are used, depending on the species and ecological context of the study. Prospecting can be called exploratory movements, extra-territorial visits, extra-territorial forays, hidden long-dispersal movements, pre-dispersal excursions, intrusions or incursions. This complicates the literature search when looking for studies addressing prospecting. Moreover, visits of individuals in alternative breeding sites are sometimes reported but prospecting is not explicitly named and its implications in a context of breeding habitat selection are not discussed (e.g. Zangmeister *et al.*, 2009; Bentzen & Powell, 2015). In other cases, the term 'prospecting' itself is sometimes misused. For example, prospecting usually refers to the immaturity period in seabirds. It defines the period starting after the first observed return of immatures to the natal colony, and ending when individuals recruit as first time breeders in the colony (Becker & Bradley, 2007; Bosman *et al.*, 2013). Immatures are sometimes called "prospecting pre-breeders" while attending their natal colony, before recruitment (Bradley *et al.*, 1999; Bicknell *et al.*, 2014). Yet, this does not fully correspond to the actual definition of prospecting, as it does not imply visits to other breeding areas than the natal one and thus, does not involve dispersal to a breeding area other than the natal one (Reed *et al.*, 1999). Due to this confusion, prospecting is often described in very specific social contexts, which hampers its general comprehension in a broader context and over many taxa. Finally, the type of information collected and its use for breeding habitat selection has been widely addressed in the field but those studies are only correlative and do not aim at describing the mechanisms involved in information gathering during prospecting movements (Blanchet, Clobert & Danchin, 2010).

This review aims at providing evidence for the widespread occurrence of prospecting in different species and social contexts based on 124 empirical studies which have explicitly described prospecting in a context of breeding habitat selection. Those empirical examples, covering birds, mammals, fish and invertebrates, are used to explain why, how, when and which individuals prospect. Then, persisting knowledge gaps are identified and discussed. Finally, key objectives and research directions are proposed to shed light on prospecting movements and their consequences for dispersal strategies, individual fitness and population dynamics.

II. Study of prospecting movements over the last two decades

A first extensive review documenting prospecting in birds was published 25 years ago (Reed *et al.*, 1999). Most of the studies cited relied on the direct observations of ringed birds. Yet, this method for observing prospecting is time consuming, requires a monitoring survey conducted in multiple areas at the same time, which limits the detection of prospecting individuals outside monitored areas but also the spatial scale at which such movements can be detected. Since then, a broader range of approaches for tracking organisms have yielded new perspectives in the study and understanding of prospecting (Ponchon *et al.*, 2013).

This section compiles examples of prospecting based on a search of papers published from 1999 to 2022 for birds and any time up to 2022 for other animal taxa because of their rarity. It syntheses why, how, when and which individuals prospect according to species life history traits, sociality and environmental conditions.

Studies were identified through Google Scholar searches and via citations by relevant articles. The following search terms were used: ‘prospecting’ AND breeding habitat selection; ‘prospecting’ AND ‘information use; ‘prospecting’ AND ‘dispersal’; ‘extra-territorial movements’ AND dispersal; ‘exploratory movements’ AND ‘breeding habitat selection’. Only cases documenting prospecting in a context of breeding habitat selection based on conspecific public information were retained.

I found 106 studies which discussed or at least explicitly mentioned prospecting in a context of dispersal and breeding habitat selection, 12 studies reporting extra-territorial movements in a context of extra-pair copulation and 6 studies addressing prospecting in a context of parasitic breeding birds (see Supplemental material Table S1 for all references). Among taxa, birds were the most represented (71%), followed by mammals (24%; Fig 1a). Most of studies (65%; 80/124) used a tracking system to follow prospecting but only 25% (31/124) deployed devices recording the continuous movement of animals in their environment (e.g. GPS or PTT; Figure 1b), all focusing either on birds or mammals (Table 1). The number of publications documenting prospecting increased in the 2000s, but later remained stable (Figure 1c) despite the development of tracking devices which facilitated the identification of prospecting (Ponchon *et al.*, 2013).

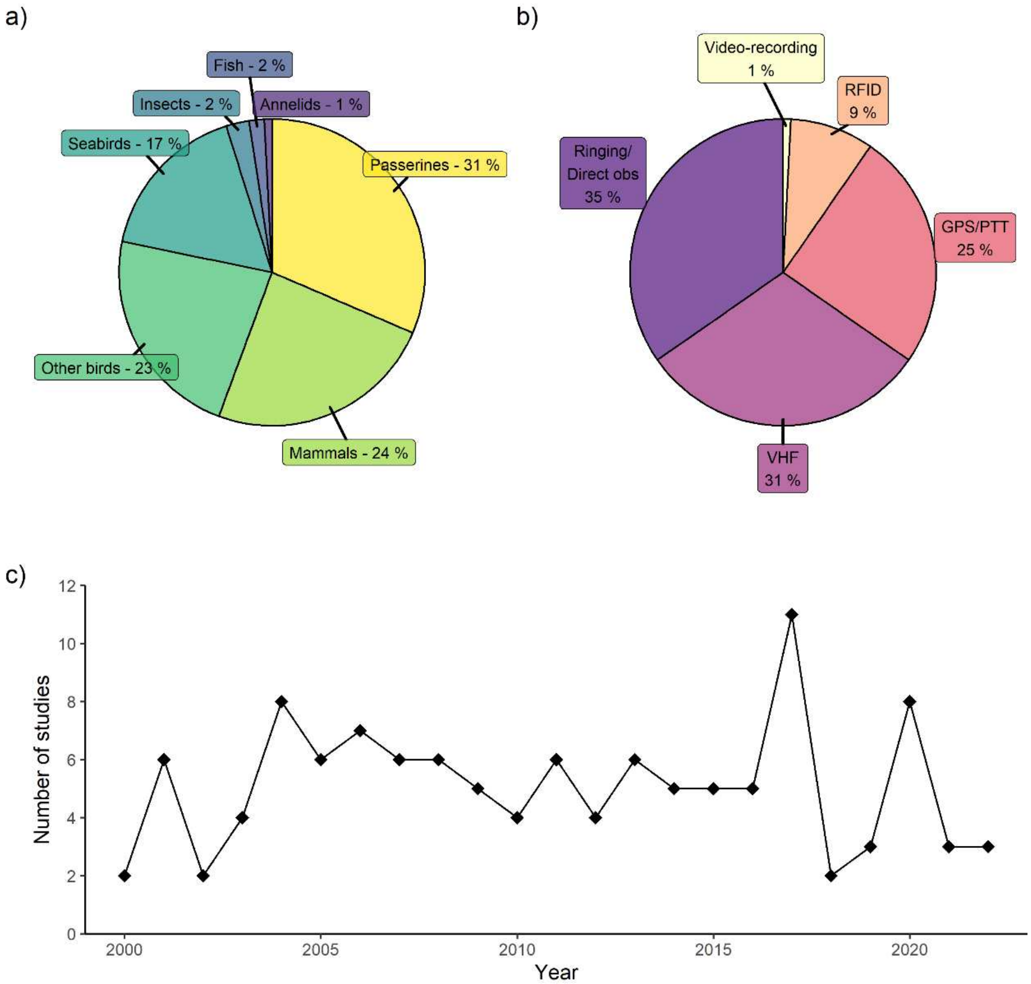

Figure 1. (a) Percentage of the different taxa studied (b) Percentage of the different methods used and (c) number of publications per year among the

124 publications reporting prospecting in a context of breeding habitat selection.

In particular, the use of GPS and satellite transmitters has been particularly crucial recently, as prospecting movements has been explicitly revealed over distances up to hundreds of kilometres (Table 1). So far, the most distant implicit prospecting movement has been identified in a Tristan albatross *Diomedea dabbenena* ringed as an immature in Crozet archipelago, and reobserved a few years later as an adult breeding in Gough Island, 5000 km away (Bond *et al.*, 2021). The most distant prospecting movement actually recorded with tracking devices is in a black-legged kittiwake breeding in Hornøya (Norway), prospecting colonies up to 550km away in Russia (Table 1), 10 times further than the usual foraging range during the breeding season in this colony (Ponchon *et al.*, 2015a, 2017b). Other studies have identified prospecting movements at smaller spatial scales, with distances similar to the distances travelled for other activities such as foraging (Table 1; (Kelly *et al.*, 2020))

Table 1. Species tracked with devices allowing the recording of continuous movements of individuals over time and associated maximal prospecting distance.

Species	Scientific name	Taxon	Class of prospectors	Tracking device	Maximal prospecting distance (km)	Reference
Black-legged kittiwake	*Rissa tridactyla*	seabird	Failed breeders	GPS-UHF	550	(Boulinier *et al.*, 1996)
Bonelli's eagle	*Aquila fasciata*	raptor	Juveniles	PTT	435	(Cadahía Lorenzo *et al.*, 2009)
Audouin's gull	*Larus audouinii*	seabird	Failed and successful breeders	GPS + PTT	360	(Oro *et al.*, 2021)
Golden eagle	*Aquila chrysaetos*	raptor	Juveniles and subadults	PTT	> 300	(Poessel *et al.*, 2022)
Black-legged kittiwake	*Rissa tridactyla*	seabird	Failed breeders	GPS-UHF	220	(Ponchon *et al.*, 2017a)
White-tailed sea eagle	*Haliaeetus albicilla*	raptor	Juveniles	GPS-GSM	200	(Engler & Krone, 2022)
Sandwick tern	*Thalasseus sandvicensis*	seabird	Failed breeders	GPS-UHF	170	(Fijn *et al.*, 2014)

Black-browed albatross	*Thalassarche melanophris*	seabird	Immatures	GPS	160	(Campioni, Granadeiro & Catry, 2017)
Wolf	*Canis lupus*	mammal	Adults	GPS	147	(Mancinelli & Ciucci, 2018)
Northern gannet	*Morus bassanus*	seabird	Immatures	GPS-PTT+VHF	> 100	(Votier *et al.*, 2011)
Cory's shearwater	*Calonectris diomedea*	seabird	Immatures	PTT	> 100	(Péron & Grémillet, 2013)
European badger	*Meles meles*	mammal	Subadults (2-3 years-old)	GPS	> 100	(Gaughran *et al.*, 2019)
Black-legged kittiwake	*Rissa tridatyla*	seabird	Failed breeders	GPS	40	(Ponchon *et al.*, 2015a)
Roe deer	*Capreolus capreolus*	mammal	Juveniles	GPS	25	(Debeffe *et al.*, 2013)
Gray fox	*Urocyon cinereoargenteus*	mammal	Adults	GPS	23.2	(Deuel *et al.*, 2017)
Common tern	*Sterna hirundo*	seabird	Successful and failed breeders	GPS-UHF	19.5	(Martinović *et al.*, 2019)
Eurasian beaver	*Castor fiber*	mammal	Dominants and subordinates	GPS	11.3	(Mayer, Zedrosser & Rosell, 2017)

Californian spotted owl	*Strix occidentalis occidentalis*	raptor	Female breeders	GPS-UHF	> 10	(Blakey *et al.*, 2019)
Mallard, gadwall, cinnamon teal	*Anas platyrhynchos - Mareca strepera –* *Spatula cyanoptera*	waterfowl	Juveniles, immatures and adult females	GPS-GSM	3	(Casazza *et al.*, 2020)
European badger	*Meles meles*	mammal	Juveniles and adults	GPS	2	(Kelly *et al.*, 2020)
White-tailed deer	*Odocoileus virginianus*	mammal	Breeding females	GPS	< 2	(Kolodzinski, Jeffrey J. *et al.*, 2010)

doi:10.20944/preprints202401.0428.v1

(1) Why? Function of prospecting

The ultimate goal of prospecting for individuals is to make informed decisions in a context of dispersal and breeding habitat selection. Yet, depending on the timing of prospecting, the type of cues available, and the breeding or social status of individuals, the finer goal and thus the function of prospecting can vary.

First, prospecting individuals aim at assessing the local environmental quality of alternative breeding areas by gathering personal information from their direct interaction with the environment (Dall *et al.*, 2005), relying on all the visual, hearing, olfactive or chemical cues that are directly available to them. They can hence directly determine the physical structure of the environment (e.g. temperature, vegetation cover), the potential presence of predators or parasites and the current availability of vacant territories (Vangen *et al.*, 2001; Bruinzeel & van de Pol, 2004; Soulsbury *et al.*, 2011; Veiga *et al.*, 2012). By repeatedly prospecting and spending extensive time in the same area, individuals accumulate information and progressively get more familiar with the surroundings. This sole factor can affect individual settlement decision (Haughland & Larsen, 2004; Selonen & Hanski, 2006) but also survival (Brown, Bomberger Brown & Brazeal, 2008; Jungwirth, Walker & Taborsky, 2015) and breeding success (Saunders *et al.*, 2012). Repeated prospecting visits also allows individuals to update information to fine-tune current investment in reproduction and territory defence according to variable environmental conditions such as predation (Thomson *et al.*, 2013) or changes in neighbouring family groups (Mayer *et al.*, 2017; Barve *et al.*, 2020).

A second essential purpose of prospecting is to locate and start acquiring a new breeding site (Reed *et al.*, 1999). At the scale of a habitat, prospecting has the same purpose for all species, which is to gather information on the local quality of the breeding habitat for emigration and/or settlement decisions. At a local spatial scale, the purpose of prospecting might be slightly different depending on the social structure and sex of species. In territorial and colonial birds, males tend to acquire a territory while females tend to acquire a mate already possessing a territory (Greenwood, 1980). Therefore, while a male bird would actually be searching for breeding sites of good quality, implying a competition for breeding sites, females may search for mates rather than territories, implying a competition for mate (Betts *et al.*, 2008).

In social or cooperative species, the purpose of prospecting is somewhat different, as individuals are not directly searching for a territory but rather a social group defending a common territory. In this specific context, prospecting allows individuals to get accepted by the targeted group and potentially acquire a new social status when they have decided to leave their current group (fish: Jungwirth *et al.*, 2015; birds: Hale, Williams & Rabenold, 2003; Williams & Rabenold, 2005; Kingma *et al.*, 2016; mammals: Teichroeb, Wikberg & Sicotte, 2011; Mares *et al.*, 2014). It can also be an opportunity for males to acquire new mates via female transfer or group take-over, creating new breeding opportunities (Sicotte & Andrew, 2004) or expand their territory (Mayer *et al.*, 2017).

Some avian brood parasites such as cuckoos or cowbirds lay their eggs in nests of other bird species which provide parental care for the parasite eggs and chicks. For those species, prospecting allows females to search for a nest site where they can safely lay eggs and where hosts are assessed as being of good-quality (Honza *et al.*, 2002; White *et al.*, 2007, 2017; Scardamaglia *et al.*, 2016). In addition, it can allow females to identify successful active nests cavities with lower predation risk and lay their parasite eggs in safer places (Pöysä *et al.*, 1999; Pöysä, 2006).

Finally, some species visit other territories during the breeding/fertility period to increase extra-pair copulation opportunities (Naguib, Altenkamp & Griessmann, 2001; Stutchbury *et al.*, 2005; Young, Spong & Clutton-Brock, 2007; Ward *et al.*, 2014; Carter, Vorisek & Ritchison, 2018). Nevertheless, this type of prospecting is unlikely to trigger dispersal, as individuals are not directly searching for a breeding site but rather a temporary mate (Debeffe *et al.*, 2014 and references therein; but see Williams & Rabenold, 2005). Moreover, those movements may differ from prospecting in their behavioural and space use patterns, as observed in red foxes *Vulpes vulpes* (Soulsbury *et al.*, 2011). Therefore, movements related to sporadic extra-pair copulation involving fidelity to the initial breeding site should not be considered as "prospecting".

doi:10.20944/preprints202401.0428.v1

Overall, regardless of the precise purpose of prospecting (acquiring a territory, a mate, finding a new social group or parasitizing a nest), it is not only essential for individuals to inform final settlement decision but also, to inform emigration decision. Indeed, prospecting is not always followed by dispersal and individuals can decide to remain philopatric if they consider that their current breeding site is of better quality than the ones they have prospected (Ducros *et al.*, 2020). Likewise, individuals prospecting the highest number of patches or travelling the furthest are not necessarily those which are the most likely to disperse (Jungwirth *et al.*, 2015; Ponchon *et al.*, 2017b). For example, although failed black-legged kittiwake breeders nesting in a completely unsuccessful depredated area deserted their breeding site after failure and spent considerable time prospecting in other alternative distant breeding areas, half of them still came back to the same nesting site the following year (Ponchon *et al.*, 2017b). The same trend was observed in koalas *Phascolarctos cinereus*, where after spending some time exploring their environment, up to 3 km, some sub-adults and adults eventually came back to their initial territory (Dique *et al.*, 2003). Prospecting is therefore a powerful way of gathering and updating information on the environment to ultimately decide both whether to leave the natal/current breeding territory and subsequently, where to settle.

(2) Who? Classes of prospectors

In mammal species where individuals quickly become sexually mature and can breed as soon as their first year, juveniles have to rapidly leave their natal patch when becoming independent. Therefore, they engage in prospecting not only to explore and get familiar with their environment but also locate potential other breeding territories where they can subsequently settle to breed. This is notably the case in coyotes *Canis latrans* (Harrison, Harrison & O'Donoghue, 1991), North American red squirrels *Tamiasciurus hudsonicus* (Haughland & Larsen, 2004), flying squirrels *Pteromys volans* (Selonen & Hanski, 2006, 2010), brush mice (Mabry & Stamps, 2008), root vole *Microtus oeconomus* (Rémy *et al.*, 2011) and roe deer *Capreolus capreolus* (Debeffe *et al.*, 2013).

In colonial or territorial species with a longer immaturity period such as seabirds or raptors, individuals can take several months/years before selecting a territory and settling to breed for the first time. Yet, immatures/subadults are regularly observed as prospecting during the years before actually acquiring their first territory (Bradley *et al.*, 1999; Dittmann & Becker, 2003; Balbontín & Ferrer, 2009; Cadahía Lorenzo *et al.*, 2009; Campioni *et al.*, 2017; Wolfson, Fieberg & Andersen, 2020; Engler & Krone, 2022). This behaviour affects their age at recruitment and enhances their subsequent breeding success, as they settle in habitats of better quality (Schjørring, Gregersen & Bregnballe, 1999; Dittmann, Ezard & Becker, 2007; Davis *et al.*, 2017).

For social species becoming highly faithful to their breeding territory once they have settled, young individuals tend to prospect more than adults (Sánchez-Tójar *et al.*, 2017; Campioni *et al.*, 2017; Wolfson *et al.*, 2020; Kelly *et al.*, 2020; Poessel *et al.*, 2022). On the contrary, when breeding adults reassess their site fidelity regularly, prospecting becomes more frequent, especially in birds willing to renest within the same breeding season after an early breeding failure (Ward, 2005; Pakanen *et al.*, 2014; Martinović *et al.*, 2019).

Even though individual breeding failure is most often assumed to be an important trigger of prospecting (Reed *et al.*, 1999), its role might be overestimated. Indeed, in short-lived species, both successful and failed breeders prospect (Doligez *et al.*, 1999; Wischhoff *et al.*, 2015; Barve *et al.*, 2020). In long-lived bird species, prospecting is commonly expected to occur in failed breeding or non-breeding (=floater) birds, because those individuals had to decide whether to emigrate and where (Bruinzeel & van de Pol, 2004; Calabuig *et al.*, 2010; Fijn *et al.*, 2014; Ponchon *et al.*, 2015a, 2017b). Active successful breeders are expected to fully invest in reproduction to maximize offspring survival, potentially leaving no time for prospecting. Yet, a recent study on 14 species of gulls and terns has revealed that prospecting was actually common in active breeding seabirds, especially for species living in ephemeral/unstable environments (Kralj *et al.*, 2023). Those findings challenge the general assumption that prospecting mostly follow individual breeding failure and this requires a complete reassessment of prospecting occurrence based on a wide range of life history traits and environmental conditions.

According to its primary function, prospecting is expected to depend on sex. In birds, females tend to prospect more and potentially further than males (Eikenaar *et al.*, 2008; Trainor *et al.*, 2013; Kingma *et al.*, 2017; Martinović *et al.*, 2019; but see Balbontín & Ferrer, 2009). The reverse is generally observed in mammals: males tend to prospect more than females (Selonen & Hanski, 2010; Rémy *et al.*, 2011; Cram *et al.*, 2018; Kelly *et al.*, 2020; but see Debeffe *et al.*, 2013). Yet, it is difficult to *draw generalities, as* many taxa do not show any difference (Dique *et al.*, 2003; Therrien *et al.*, 2015; Campioni *et al.*, 2017; Poessel *et al.*, 2022). The effect of sex could therefore depend on the fine purpose of prospecting in selecting a breeding site and the direction of competition to acquire a new breeding site or a new mate.

In cooperative species, subordinates and helpers tend to prospect more than dominants or breeders, as they are more likely to seek for new breeding opportunities in neighbouring social groups and evaluate potential competitors (Young, Carlson & Clutton-Brock, 2005; Eikenaar *et al.*, 2008; Kingma *et al.*, 2016; Barve *et al.*, 2020; Cram *et al.*, 2018). Yet, dominants can still prospect to find opportunities to expand their current territory, especially when they own small or low-quality territories (Mayer *et al.*, 2017; Barve *et al.*, 2020).

Individuals that have already decided to disperse (=dispersers) performed more prospecting trips before definitely leaving their territory compared to philopatric individuals that remained on their territory (Debeffe *et al.*, 2014; Oro *et al.*, 2021). Hence, the amount of prospecting movements was positively correlated with whether an individual was a disperser or not.

Finally, individuals can prospect in groups: males of social species such as meerkats or badgers can form coalitions to prospect (Doolan & Macdonald, 1996; Roper, Ostler & Conradt, 2003; Sicotte & Andrew, 2004), while trogons, territorial passerines, constitute assemblages of both sexes (Riehl, 2008). Visiting other breeding territories in groups may allow individuals to acquire information more safely, such as through diluting predation risk and possibly outcompeting conspecifics more easily to acquire new social status or extend an existing territory. This thereby provides various indirect fitness benefits which promote prospecting.

(3) When and what? Timing of prospecting and available cues

Thanks to a variety of different cues, prospecting individuals are able to evaluate the quality of habitats at various times of the year (within and outside of breeding season) to predict their expected fitness in alternative breeding habitats. Yet, most of prospecting activity has been documented during the different stages of the breeding season, when individuals need to acquire a territory or integrate a social group to reproduce.

Prospecting during the pre-breeding or nest building/territory acquisition season implies that individuals immediately use the gathered information to settle in a new breeding site. Yet, individuals cannot directly rely on the breeding performance of their conspecifics, as mating has not taken place yet. Instead, they can rely on physical features of the environment (e.g. snow cover and depth for snowy owl *Bubo scandiacus* (Therrien *et al.*, 2015), breeding status and timing of singing around dawn in nightingales (Amrhein, Kunc & Naguib, 2004; Roth *et al.*, 2009) or the general activity of conspecifics (brown jays *Cyanocorax morio* Williams & Rabenold, 2005). When prospecting occurs during laying and egg incubation in birds, public information becomes available for prospecting individuals. The number of incubating conspecifics and the number of eggs in nests can be a good proxy of the current environmental quality (Martinović *et al.*, 2019; Oro *et al.*, 2021), especially for avian brood parasite birds (Honza *et al.*, 2002; Pöysä, 2006; White *et al.*, 2017).

A peak of prospecting is generally observed during the chick-rearing period, when public information is the most available and the most reliable (Doligez, Pärt & Danchin, 2004; Ward, 2005; Veiga *et al.*, 2012). At that time, the breeding success of conspecifics is conspicuous, more representative of the general environmental quality of a breeding patch and individuals can hence gather finer information from the number and quality of fledging (Pärt & Doligez, 2003; Parejo *et al.*, 2007). Even if the information gathered can be used at any time during the breeding season, the later prospecting occurs, the more likely individuals to use information for the next breeding season. Prospecting can happen during the post-breeding season, after nestlings have fledged. During this period, social information is less available but individuals can still use reliable cues to assess the quality of breeding sites such as the location of occupied breeding sites (Arlt & Pärt, 2008; Ciaglo *et al.*, 2021; Patchett *et al.*, 2022) or rests of eggshell fragments and membranes in successful nests (Pöysä, 2006). The seasonality of prospecting during the breeding season is exacerbated in migratory species: the later migrants arrive on their breeding ground, the shorter the prospecting period. The same happens at the end of the breeding season, when migrants are constrained by their departure.

Outside the breeding season, prospecting has mainly been reported in non-migratory mammals (Deuel *et al.*, 2017; Mayer *et al.*, 2017; Mancinelli & Ciucci, 2018; Kelly *et al.*, 2020; but see Sánchez-Tójar *et al.*, 2017 for birds). Social information about future breeding conditions might not be directly available but prospecting still help individuals monitor neighbouring group composition, conspecific competitive abilities and sexual status, notably through olfactory cues. This may ultimately facilitate emigration and settlement decisions.

(4) How? Patterns of prospecting

Prospecting can be displayed based on alternative behavioural tactics among which the '*best-of-n*' strategy and the '*sequential sampling*'. The best-of-n strategy consists for prospecting individuals to visit one or several alternative breeding areas while still regularly coming back to their natal/current breeding site. It allows individuals to gather information about different breeding areas and eventually select the one they consider the best among the ones visited. This strategy is usually observed in species with high mobility abilities but facing limited number of alternative breeding areas (Balbontín & Ferrer, 2009; Kesler & Haig, 2007; Weston *et al.*, 2013; Gaughran *et al.*, 2019).

The sequential sampling occurs when individuals prospect continuously after definitely leaving their current natal or breeding area. They visit one patch after the other and based on an implicit threshold, they settle in the first breeding site they consider suitable enough. This strategy is notably displayed by species with more limited mobility (Mabry & Stamps, 2008) or species with high constraints in breeding site selection (Armstrong, Braithwaite & Huntingford, 1997; Dale *et al.*, 2006; Therrien *et al.*, 2015).

Although probably crucial in shaping the spatial patterns of prospecting, inter-individual variability is rarely accounted for. It is likely that individuals from the same population exhibit different prospecting patterns and different uses of the information they gather. For instance, both prospecting strategies have been observed in flying squirrels *Pteromys Volans*, where the best-of-n strategy was linked with short-distance dispersal and sequential search for long-distance dispersal (Selonen & Hanski, 2010). Hence, some individuals may be more prone to engage in prospecting than others, possibly due to a cost/benefits trade-off between remaining in the same breeding site/social group and leaving it to acquire a new one which in turn depends on individual factors (Jungwirth *et al.*, 2015), environmental factors such habitat type (Rioux, Amirault-Langlais & Shaffer, 2011; Swift *et al.*, 2021; Kralj *et al.*, 2023), habitat quality (Rémy *et al.*, 2011; Barve *et al.*, 2020), habitat availability (Dale *et al.*, 2006) or foraging opportunities (Davies & White, 2018).

Alternatively, dispersal strategies as a whole can greatly vary, with some individuals from the same population exhibiting prospecting while others fully remaining philopatric to their natal patch and others just dispersing directly to a new territory without any previous assessment of their environment (Harrison *et al.*, 1991; Armstrong *et al.*, 1997; Mabry & Stamps, 2008; Ducros *et al.*, 2020; Engler & Krone, 2022).

Another crucial factor to consider when addressing prospecting patterns is the spatial scales at which individuals move. In a breeding habitat selection context, the environment is often seen as a mosaic of small homogeneous good patches embedded in a larger matrix whose quality varies spatially and temporally (Kotliar & Wiens, 1990; Orians & Wittenberger, 1991). Consequently, a species' response to environmental quality is expected to be scale dependent (Wiens, 1976). For instance, a movement of an individual over a few hundred meters in the same breeding patch may be considered as prospecting as soon as the movement is a response to the local environment, such as local poor quality territory features, increased presence of parasites or strong competition to acquire a territory. Hence, if prospecting is used by individuals to assess the local quality of other areas, the spatial scale of their movements is expected to be greater than the spatial scale at which poor conditions apply and this can occur from a few meters to hundreds of kilometers. At the same time, prospecting and subsequent dispersal movements at large spatial scale might be more risky and time consuming for individuals (Stamps, Krishnan & Reid, 2005) so there may be an important trade-off between the spatial scale of the environmental factor to escape from and the spatial scale of prospecting movements. Despite its obvious importance in the understanding of individual response patterns to environmental variability, the hierarchical spatial aspect of the environment is often overlooked and needs to be better considered (Gaillard *et al.*, 2010).

The newly-developed tracking devices and advanced analytical tools available to infer individual behaviour and underlying spatial patterns of habitat selection (Ponchon *et al.*, 2013), would allow such considerations. It would further be possible to derive individual breeding or social status, based on space use stability, exploration behaviour and the directionality of movements. Indeed, some prospecting individuals have been shown to travel faster, further and avoid conspecifics in occupied territories, creating typical movement patterns that can be objectively discriminated from other movements (Kesler, Walters & Kappes, 2010; Soulsbury *et al.*, 2011; Ponchon *et al.*, 2017a; Mayer *et al.*, 2017; Ducros *et al.*, 2020; Barve *et al.*, 2020).

Table 2. Factors likely driving prospecting.

Class of factors	Factors	Class of prospectors	Example of references
Individual factors	Sex	Males, females	(Selonen & Hanski, 2010; Trainor *et al.*, 2013)
	Age	Juveniles, immatures, subadults, adults	(Campioni *et al.*, 2017; Wolfson *et al.*, 2020)
	Breeding status	Failed or successful breeders, non-breeders (=floaters)	(Ponchon *et al.*, 2015a, 2017b; Kingma *et al.*, 2016; Kralj *et al.*, 2023)
	Dispersal status	Philopatric or dispersing individuals	(Debeffe *et al.*, 2013; Kingma *et al.*, 2016)
Social factors	Social status	Dominants, helpers, subordinates	(Kingma *et al.*, 2016; Cram *et al.*, 2018)
	Inbreeding	Kin-related individuals	(Kingma *et al.*, 2016)
Environmental factors	Habitat size/quality	Territory owners	(Dale *et al.*, 2006; Mayer *et al.*, 2017)
	Habitat familiarity	All	(Armstrong *et al.*, 1997)
	Territory quality	Territory owners	(Barve *et al.*, 2020)
	Predation risk	All	(Pakanen *et al.*, 2014)

(5) How? Costs of prospecting

As for dispersal (Bonte *et al.*, 2012), prospecting is likely to entail multiple costs (Stamps *et al.*, 2005). First, prospecting requires time and energy to access the different breeding areas, and thus, it needs to be traded against other essential activities such territory defence, mate bonding, grooming or foraging for food. In black-legged kittiwakes *Rissa tridactyla*, prospecting failed breeders spent less time foraging compared to non-prospecting successfully breeding ones (Ponchon *et al.*, 2015a).

When individuals visit other breeding areas than their own, they can potentially cross unfamiliar environments, where predation risk and confrontation with aggressive conspecifics can entail injuries (Crawford, 2015; Kingma *et al.*, 2016; Mayer *et al.*, 2017). Long-distance and risky movements can increase energetic demands and stress levels (Young & Monfort, 2009), potentially leading to lower body condition (Kingma *et al.*, 2016; Melzheimer *et al.*, 2018). Further, an increase of the frequency of prospecting over years can drastically reduce individual survival (Cram *et al.*, 2018).

As active breeding individuals can prospect (Kralj *et al.*, 2023), if the mate or other group members are not present to defend the current territory, there is a risk of losing the territory and thus, jeopardizing the current reproduction or the cohesion of the social group (Barve *et al.*, 2020).

Locally, prospecting often involves a close inspection of the environment and encounters with conspecifics, which facilitates disease transmission, especially when the infectious agents is transmitted through direct contact or through infected parasites (e.g. ticks or flees; (Boulinier *et al.*, 2016; Gaughran *et al.*, 2019). As prospecting can occur at large spatial scales (Table 1), it could further facilitate disease circulation and accelerate propagation to distant populations and thus contribute to strong and rapid disease spread. Yet, linking prospecting to disease propagation still remains a challenge, as both the infectious status of prospectors and individuals present in the visited breeding areas would have to be monitored regularly, which might not be easy at large spatial scales and in dense populations. Nevertheless, integrating prospecting in eco-epidemiological models might be key to better understand the dynamics of host-pathogens interactions and their effects on population dynamics (Boulinier *et al.*, 2016).

III. Future research directions

(1) Issues and limits in studying prospecting in the field

The study of prospecting still faces multiple challenges which complicates its thorough understanding.

Species life history traits

- Long-lived species are generally difficult to monitor in the field during several years and over large spatial scales so it may be difficult to relate prospecting and actual dispersal movements to a new breeding site for a large number of individuals and in dense populations.
- Mammals with larger body size may be tracked more easily but they usually live in low-density habitats. So studies on large mammals may end with small sample sizes and low statistical power when investigating the causes and consequences of prospecting, either at the individual or population level.
- In some species, individuals may be more or less easy to capture based on intrinsic factors. For example, in seabirds, successfully breeding individuals are more likely to be tracked compared to juveniles, immatures or failed breeding individuals because they are attached to their nest site and thus, are more accessible and easier to capture. On the other side, it is not always possible to determine individual age, sex or breeding stage, which complicates the fine understanding of movement patterns.
- Prospecting is sometimes hard to describe from tracking data, as the function of different observed movements may be unclear due to similarity of movement patterns between activities (e.g. Poessel *et al.*, 2022)

Field bias

- A detailed knowledge of the locations of all colonies, social groups or territories is required. This can be easily feasible over small spatial scales but it can quickly become complicated when prospecting occurs over long periods and/or large spatial scales (e.g.(Therrien, Pinaud et al. 2015)) or when breeding and foraging areas are mixed. Accordingly, if the best-of-n-rule strategy is easy to detect, with individuals regularly coming back to their current territory, the sampling strategy is more difficult to monitor, because all potential breeding patches/territories have to be known *a priori*.

- Monitoring prospecting preceding new colony formation and territory acquisition outside current occupied areas is still a challenge. It mostly relies on opportunistic observations of individuals resting in unoccupied areas (Munilla *et al.*, 2016).
- The spatial scale of observation sometimes does not match the spatial scale individuals actually use for prospecting and dispersal (Doligez *et al.*, 2008).

(2) How to fill the persisting knowledge gaps?

Objective 1: Acknowledging prospecting as a movement as important as foraging or migration.

This may help researchers identify prospecting more easily and may foster further research in the field. This may start by using the same word and definition for all species and social context. Then, even if time-consuming and potentially costly, an effort should be set to identify potential territories and suitable patches directly in the field, especially in colonial species, which are easier to locate compared to less aggregated species or social species which are more likely to move in their environment.

Objective 2: Using tracking devices.

The constant improvement of miniaturized tracking devices, with longer batteries, higher temporal and spatial resolution, and measurement of ancillary data (e.g. accelerometry, altitude, heart rate etc) have offered new opportunities to study prospecting, notably by decreasing constraints linked with monitoring effort in the field (Ponchon *et al.*, 2013). But this will imply a careful and thorough inspection of individual tracks, as some prospecting may be missed just because they are not searched for.

Objective 3: Using appropriate analytical tools

The rapid development of cutting-edge statistical models and machine learning tools examining space use from individual movement trajectories have opened large avenues for inferring animal behaviour (Nathan *et al.*, 2022) and offers promising tools for the study of prospecting at a hierarchy of spatial scales. For example, R package *recurse* (Bracis, Bildstein & Mueller, 2018) may be used to quantify systematically and robustly recurrent visits of individuals in breeding habitats at a fine spatial scale while *momentuHMM* (McClintock & Michelot, 2018) may infer distinct behavioural states including prospecting from hidden Markov models. Additionally, habitat selection functions may be used to examine how individuals select particular habitats according to different covariates and different life stages (Northrup *et al.*, 2022).

Objective 4: Combining field-based monitoring surveys with tracking data

This step will be key to assess prospecting at a hierarchy of spatial and temporal scales which will reflect the scales at which individual collect information on their environment and thereby, the scale at which individual decisions regarding emigration and settlement are made (Doligez *et al.*, 2008).

Objective 5: Improving theoretical models

Despite its crucial ecological and evolutionary consequences on population dynamics, structure and persistence (Delgado *et al.*, 2014; Ponchon *et al.*, 2015b; Schmidt *et al.*, 2015; Ponchon & Travis, 2022), prospecting has rarely been explicitly and thoroughly implemented into theoretical models (Ponchon *et al.*, 2021). Two relatively simple models had pointed out that prospecting was only beneficial when the environmental was temporally predictable and spatially heterogeneous (Boulinier & Danchin, 1997; Pärt & Doligez, 2003). Yet, a recent empirical study has shown that individuals could prospect in ephemeral or unstable environments, contradicting those long-standing theoretical hypotheses (Kralj *et al.*, 2023). There is thus an urgent need to develop more complex modelling approaches that link prospecting to dispersal and demography in a highly variable environment (Ponchon *et al.*, 2021). One way to stimulate theoretical studies would be to explicitly implement the different phases of informed dispersal: 1) emigration decision, 2) prospecting ("best-of-n strategy; (Ponchon *et al.*, 2021)) or spatially explicit searching phase (sequential sampling; (Delgado *et al.*, 2014)) and 3) settlement decision. This would help develop novel knowledge on how and which individuals prospect and what the ecological and evolutionary consequences are on individual fitness and population functioning. In particular, there is a much-needed work on sex-biased and age specific prospecting strategies to better understand the underlying mechanism of informed dispersal, which would help describe the different patterns observed in the different taxa according to specific life-history traits and sociality. Newly developed theory would then become testable, driving new experiments in the field with the use of tracking devices. Such results would in turn feed back in the theory to fine-tune the way prospecting is modelled. Overall, with a strong fundamental understanding and modelling capability of prospecting, we will be in a better position to build more realistic predictive models of species' response to environmental changes, fully embedding informed dispersal (Urban *et al.*, 2016).

(3) Prospecting in a changing world

Prospecting allows individuals to assess the local environmental quality of a breeding area by gathering information from various social and environmental cues to make informed dispersal choices. It has been identified as one key individual behavioural strategy to respond to rapid environmental change, as it helps individuals leave habitats of low quality and settle in habitats of better quality and productivity (Ponchon *et al.*, 2015b, 2021). The resulting dispersal at the individual level has direct and immediate consequences at the population level, with a non-random redistribution of individuals in space, leading to a longer-term persistence of populations through extinction-recolonization or source-sink dynamics (Ponchon *et al.*, 2015b). Yet, climate change and the occurrence of extreme climate events may disrupt the availability and reliability of the cues used by individuals and may jeopardize the benefits of informed dispersal. In particular, if environmental or social cues incorrectly reflect the local quality of the environment at the time of prospecting, individuals will gather erroneous information about the environment and will end making bad settlement decisions, thereby jeopardizing their fitness (McNamara *et al.*, 2011). The use of such cues would become maladaptive and would lead the population to ecological traps (Kloskowski, 2021).

Conversely, if individuals are able to appropriately switch the cues they rely on and adjust the timing of their collection, prospecting could constitute a powerful way to efficiently overcome environmental change and track more efficiently breeding habitats of good quality. Nevertheless, the time of adaptation of using new cues will have to be quicker than environmental changes (Ponchon *et al.*, 2015b). In particular, prospecting could lead to the colonization of new breeding areas, including some out of the current species range (Kokko & Lopéz-Sepulcre, 2006). Yet, the speed and success of colonization will highly depend on individual preferences between settling in an empty habitat or settling in habitats already occupied by conspecifics. This implies that in addition to the timing prospecting and the types of cues, the balance between the use of personal information *versus* public information will be crucial in the success of populations to track climate change (King & Cowlishaw, 2007; Ponchon & Travis, 2022).

New evidence of prospecting from species living in ephemeral environments and during active breeding have also challenged classic theory (Kralj *et al.*, 2023), suggesting that prospecting could actually constitute an adaptive response to rapid environmental changes or breeding failure. However, this would only be the case if individuals use the collected information immediately after prospecting, so that the value of information would still correctly reflect the local quality of the habitat and individuals would still choose habitats of better quality (McNamara *et al.*, 2011).

In addition to natural adaptation, which might sometimes be too slow for species to keep pace with environmental changes, humans could help species make better settlement decisions by providing artificial social cues such as decoys or playbacks to attract them towards habitats of better quality when their current ones suffer from severe degradation. This has already been done in birds and results have generally been encouraging (Ahlering *et al.*, 2010; Anich & Ward, 2017). Nevertheless, such conservation strategies would have to be monitored scrupulously to ensure actions are not detrimental to the population and do not trigger unforeseen negative consequences. Additionally, studying more closely prospecting during an attempt of attracting individuals to new habitats may allow identifying new breeding areas not currently used but close to attraction sites. But again, a good understanding of the mechanisms of information use and settlement decision will be crucial for the success of such strategies.

IV. Conclusions

(1) Prospecting is a crucial phase of dispersal where individuals gather information about their environment to make informed emigration and settlement decisions. By bringing together a large and scattered pool of literature, this review confirms that prospecting is widespread, not only in birds, as previously stressed, but also in many other animal taxa including invertebrates. Its ultimate goal for individuals is to collect information about the quality of different breeding areas in order to leave habitats of bad quality and settle in better ones.

(2) Various intrinsic, environmental and social factors may induce prospecting but they may not always lead to dispersal. It points out that information gathering and information use imply two distinct decisions (whether to leave and where to settle) that lead to very different outcomes. Unveiling the factors affecting both decisions and being able to address them concurrently will be key in the thorough understanding of informed dispersal.

(3) Empirical work can be enhanced with the deployment of newly-developed miniaturized tracking devices and the use of appropriate mathematical models. Alternatively, theoretical work will be boosted by explicitly implementing prospecting within informed dispersal. It will notably help understand its ecological and evolutionary consequences at the individual and population level.

(4) Prospecting might be crucial in species response to environmental changes. Fostering research on prospecting and informed dispersal will shed light on this potential adaptive response that may help species persist on the long-term thanks to active directed movements from degrading environments to better ones. It will also help inform more effective management plans

Acknowledgments: I thank Thierry Boulinier who got me into the fascinating world of prospecting and with whom I have shared so many passionate discussions over the years. This work was initiated during my Marie-Sklodowska-Curie project EcoEvoProspectS (grant agreement no. 753420) and I thank attendees of the purple patch pumpkin meeting held in Corbières (France) back in Octobre 2018 who shared their opinion about my initial ideas. I am particularly grateful to David Grémillet, Justin Travis and Valeria Romano who provided constructive comments on an early version of this review.

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