Prospecting Behaviour in Wild Jackdaws

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I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree or any other University has been acknowledged.

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Abstract

Habitat suitability must be carefully considered when an animal is trying to locate a potential breeding site. Acquiring information on the quality of potential nest sites helps an individual to reduce their environmental uncertainty and to better respond to the fluctuating environmental changes. Decisions on where and when to breed are critical determinants of an animals' reproductive success and can directly affect individuals' fitness. It is therefore expected that animals will invest considerable time and energy into collecting information. Prospecting behaviour, whereby an animal gathers information about possible future breeding sites, helps individuals to reduce environmental certainty and make better and more informed decisions on where to breed. When assessing prospecting behaviour, it is important to consider the societal structures which may affect the propensity of prospecting to occur. Some individuals, such as those with greater dominance, commonly have higher reproductive success as their fitness affords them greater access to, or monopolization of, essential resources such as breeding sites. Yet, prospecting has received limited attention, despite its important role in breeding success. To understand this more, this study assesses wild jackdaws (*Corvus monedula*), who prospect breeding sites prior to breeding and who live in a hierarchical society. Investigation of how individuals and pair-bonded pairs gather information throughout the breeding season revealed that prospecting frequency did not significantly change throughout the breeding season. Prospecting did not occur more often at nest boxes with higher breeding success, nor do successfully breeding prospectors gather more information after their chicks have fledged. Pair-bonded individuals were not more likely to prospect with their partner. Yet, when they prospected together, the trips were longer. Dominance, however, had no effect on who prospected and for how long. Yet, a non-significant trend suggests that females prospect for longer than males. How information is gathered from prospecting trips, whether alone or with a breeding partner, and its role in individual decision-making processes may influence breeding habitat selection and is likely to affect dispersal and population dynamics of not just an individual but the species.

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Chapter 1: General Introduction and Research Methods

1.1. Introduction

1.1.1. What is prospecting behaviour and why is it important?

Fluctuating environmental conditions across different spatial and temporal scales can create uncertainty. Animals may therefore benefit from acquiring information to reduce that uncertainty. (Dall et al., 2005; Valone, 2007). When habitat quality is variable, collecting such information allows an individual to better respond to the environment in which it lives and to make an informed and accurate decision on which habitat to choose. It has been argued that habitat selection is a primary focus in an animal's life, as their chosen habitat will cater to many other life history requirements, including reproductive output and survival (Block & Brennan, 1992; T.R.Birkhead, 1977). A growing number of studies are showing that individuals are capable of tracking habitat quality and that habitat selection may be informed by previous experience and knowledge of nest sites and habitats (Boulinier & Danchin, 1997; Klopfer, P.H. and Ganzhorn, 1985; Marzluff, 1988). Prospecting is the exploratory behaviour used to collect information about potential future breeding sites, which includes gather information on nest sites, territories, foraging sites and mating opportunities. This allows individuals to make the best decisions that they can (Calabuig et al., 2008). Prospecting has been observed in a range of vertebrates, including birds, mammals, fish, and invertebrates (Jungwirth et al., 2015; Van Bergen et al., 2004; White et al., 2017; Young et al., 2005).

Both personal and public information can be collected when prospecting (Fig 1). Sampling the environment through direct interactions with habitats and the individuals within, such as searching for and finding a foraging site, provides personal information. Public information is gained from observing the behaviour or interactions of other individuals, such as where other individuals have chosen to nest, but also from inadvertent cues left behind in the environment (Nocera et al., 2006). However, personal information may not always be available, nor will it always be advantageous to collect since its trial-and-error method of collection can be costly. Individuals selecting breeding locations should incorporate knowledge of available mates, territories and foraging grounds (Aebischer et al., 1996; Patrick & Weimerskirch, 2014), information that can be obtained through prospecting. However, if incorrect or unreliable information is used to inform breeding decisions, individuals may inadvertently choose lower quality breeding sites that will impact their immediate and future reproductive success. (Spencer, 2002). The speed with which public information can permeate throughout a community may facilitate the transmission of correct information but could be costly when it concerns incorrect information. When prospecting for new nest sites, territories, mates or foraging locations, it is therefore important to assimilate information from reliable sources (Boulinier et al., 1996). Recognizing when to use public information preferentially over personal information, and vice versa, can positively influence an individual's breeding success (Giraldeau et al., 2002). Nine-spined sticklebacks (*Pungitius pungitius*), for example, are able to discern the most reliable source of information when faced with sources of both personal and public information, enabling them to make optimal foraging decisions (Van Bergen et al., 2004). It may therefore be beneficial to scrounge information from multiple cues, with certain attributes becoming more influential than others (Van Bergen et al., 2004). Using a multitude of factors as part of a complex decision-making process, allows for a prime breeding location to be selected, increasing the possibility of breeding success (Franks et al., 2003). In this review, I will discuss and evaluate studies on the use of prospecting in birds and its importance for breeding success.

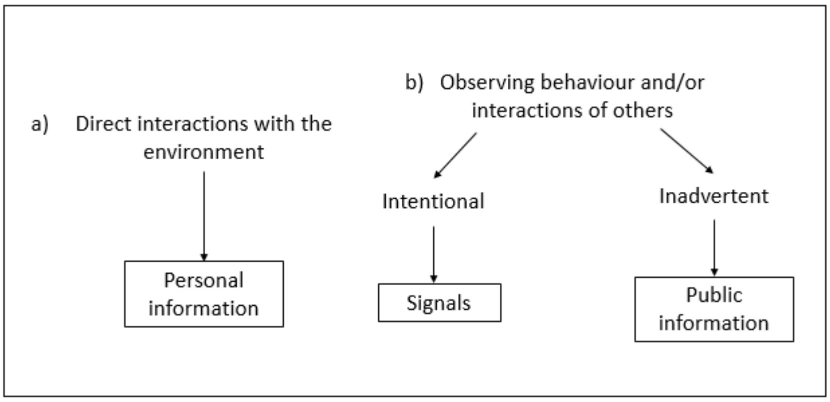

Figure 1. Potential sources of information available to animals. a) Information obtained from direct interactions with the environment provides personal information. b) Information obtained from observing the behaviour of other can be sub-categorised into intentional (signals) and inadvertent (public information) information. Adapted from (Dall et al., 2005)

1.1.2. What we already know about avian prospecting behaviour

1.1.2.1. Nest sites

Habitat suitability must be carefully considered to locate the prime breeding location as a means to increase one's potential breeding success (Block & Brennan, 1993). Breeding site quality is inextricably linked to an individual's breeding success and it is therefore thought that birds will invest considerable effort into gathering information about possible breeding sites (J. Michael Reed et al., 1999). Gathering information prior to settlement has been documented in numerous species, including kittiwakes (*Rissa tridactyla*) and brown-headed cowbirds (*Molothrus ater*) who use public information when selecting a habitat for the current or future breeding season. Kittiwakes are attracted to the nest sites of conspecifics whilst brown-headed cowbirds use host species' activities to locate nests to parasitize. (Boulinier et al., 2008; White et al., 2017). Samplonius et al (2017) illustrate this well in their study of nest site selection by late-arriving migratory pied flycatchers (*Ficedula hypoleuca*) nest site selection. When given the option to copy the nest site choices of other pied flycatchers or tits, individuals seemed to be influenced not by species identity, but rather by the density of either pied flycatchers or tits, using the species with higher density to gather their cues from, subsequently nesting in habitats most similar to those used by the species with higher density. Gathering public information flexibly in this way may allow individuals to copy cues with greater abundance according to the context they're within to assess and choose the most reliable source of information.

Using knowledge of the success and breeding stage of local birds allows individuals to target their prospecting efforts to particular parts of the breeding season. Although occurring in all seasons, prospecting is more common during the latter stages of the breeding season due to the quality of information available (Boulinier et al., 1996; Pärt & Doligez, 2003). As suggested by the "optimal timing hypothesis", information gathering should be conducted at a time that will maximally increase an individual's fitness (McNamara et al., 2011). Prospecting later in the breeding season, when information more accurately represents breeding success and is more reliable, may therefore reduce the overall energy expended by an individual when searching for information (Campioni et al., 2017; J. Michael Reed et al., 1999; J. Michael Reed & Oring, 1992; Sánchez-Tójar et al., 2017; Schjørring et al., n.d.; Ward, 2005). The ability to adjust prospecting rates to best reflect an individual's current reproductive state can increase breeding success and may reflect individual's different life history strategies (Stamps, 2007).

Beyond species-level characteristics, individual identity also influences prospecting behaviour. In some species, exploration for new sites occurs in both juveniles and adults (Kesler & Haig, 2007; Aurore Ponchon et al., 2017). Nest site prospecting appears to be particularly prevalent in juvenile birds who are approaching reproductive age, as these individuals may lack personal information gained through previous breeding experience (Dittmann & Becker, 2003; Firth, Verhelst, et al., 2018a). Adults also prospect at other breeding sites, despite being in possession of more personal information, especially if the local breeding habitat is variable in quality (Fijn et al., 2014; Ponchon et al., 2017). Both successful and failed adult breeders will take advantage of reliable public information to inform their next breeding season (Boulinier & Danchin, 1997). Failed breeding adults have been shown to abandon nests almost immediately after nest failure and commence prospecting. By doing so, they can allocate their time to exploration of future possible nesting sites (Boulinier et al., 1996; A. Ponchon et al., 2014; Aurore Ponchon et al., 2017).

When assessing the breeding success of current and potential nest sites, both adults and juveniles are able to hone in on an array of cues that may offer reliable information, each dependant on the time of year as to their availability and reliability (Block & Brennan, 1992). Adult collared flycatchers (*Fidecula albicollis*) and lesser kestrels (*Falco naumani*), for example, monitor other conspecific parents' chick provisioning rates. Higher rates of provisioning are correlated with more successful nests, so by using provisioning rates as a cue, prospectors were later able to select successful sites for breeding in (Calabuig et al., 2010; Pärt & Doligez, 2003). Studies have also shown that nests with bigger broods will be attended by more prospectors, including in common goldeneyes (*Bucephala clangula*) and pied flycatchers (*Ficedula hyoeleuca*) (Schuett et al., 2017; Zicus & Hennes, 1989). By using a playback experiment to replicate large and small broods, Brandl et al (2019) have provided evidence of zebra finches (*Taeniopygia guttata*) locating larger broods through begging calls. Auditory cues have been found to be utilised in multiple other species, including ancient murrelet (*Synthliboramphus antiquus*) and barn swallows (*Hirundo rustica*). The use of these cues can be explained by the “conspecific attraction hypothesis”, which theorizes that individuals use conspecific presence as a predominant influence in settlement decisions (Campomizzi & Lebrun-Southcott, 2020; Major & Jones, 2011).

Exploration of potential sites should inform individuals not only of preferred, high-quality sites, but also of habitats that should be avoided. Predation is a predominant reason for nest failure in birds and is a key factor to consider when deciding on a nesting location (Forstmeier & Weiss, 2004; Pöysä et al., 2001). Adult birds are able to react to the presence of predators and adjust their reproductive strategies, reduce proximity to avian predators and will even forego breeding in some extreme cases (Fontaine & Martin, 2006; Meese & Fuller, 1989; Møller, 1988). Orange-crowned warblers (*Vermivora celata*), for example, have demonstrated adaptive phenotypic plasticity in their nest-site preference when prospecting (Peluc et al., 2008). When predators are seen in the vicinity of the nest site, these warblers will change nesting sites preferences and prospect to find other viable sites with reduced proximity to the danger. The ability to monitor and respond to unpredictable environmental conditions, such as the presence of predators, may afford them a fitness advantage (Taper et al., 1995).

However, when thinking about the cues available within a nest, eggshell colour and patterning has been overlooked in the literature. In some species, males use eggshell colour as an indicator of their partner’s quality and make investment decisions in response to this cue (Moreno & Osorno, 2003). Additionally, egg size has been correlated with chick survivability. Lapwing (*Vanellus vanellus*) chicks from larger eggs are not only heavier at hatching, but also had a better chance of survival (Blomqvist et al., 1997). But it is not known whether prospectors use this cue when prospecting for future high-quality nest sites or territories. Females able to invest heavily in their offspring may also be able to attain high-quality nest sites and territories and is an area of study that future research should focus.

Additionally, ectoparasites are known to have potentially huge fitness costs to chicks and parents (Christe et al., 1996; Wegmann et al., 2015). However, research to address the use of prospecting to assess parasite abundance in visited nest sites and territories has yet to be conducted. This may be because individuals are limited in their defence strategies against parasite abundance within their nests, or it may be too difficult to accurately assess during short prospecting forays.

1.1.2.2. Territories

Deciding how and when to disperse to a new territory can directly impact gene flow across populations and is an important factor in reducing the possibility of inbreeding (Garant et al., 2005). Habitat availability is often a limiting factor for dispersal and can mean some individuals' breeding attempts rely wholly on finding a territory for themselves (Aebischer et al., 1996).

When without a territory, both adult and juvenile birds may prospect during and outside of the breeding season to find available territories (Hogstad, 1999; Piper et al., 2006). House sparrows, for example, exhibit high fidelity to their sites all-year round. Juveniles will prospect twice as much as adults in their first winter available territories, so the long-term benefits of finding a good-quality site should outweigh the initial cost of prospecting (Sánchez-Tójar et al., 2017).

Finding a seasonal territory that meets a species' spatial and temporal requirements for breeding may necessitate an individual to relocate to a new location.. Migratory species, such as common nightingales (*Luscinia megarhynchos*) and collared flycatchers, may be constrained by time and can face trade-offs between breeding and collecting information (Kokko, 1999). Utilizing the post-breeding season to gather information about potential territories can save time and energy for migratory species in future breeding seasons. Some experienced individuals are able to take advantage of the public information still available in the form of cues and remember it through to the following breeding season (Arlt & Pärt, 2008; Brandl et al., 2019; Ward, 2005). Male Northern Wheatears, for example, combine information collected post-breeding through to the following spring, in a two-part decision-making process of territory acquisition (Arlt & Pärt, 2008). Taking advantage of cues, when constrained by time, may speed up the territory selection, allowing migratory individuals to relocate more quickly and invest more time in breeding.

Unlike migratory species, resident individuals are afforded the opportunity to gather information outside of the breeding season. Conspecific social associations can be an important factor in an individual's decision-making process (Firth & Sheldon, 2016). For instance, familiarity between individuals has been shown to influence some individuals' territory acquisitions. Male great tits (*Parus major*) will search for and form territories near individuals they socially associated with during their time in winter flocks (Firth & Sheldon, 2016). These relationships may help to reduce aggressive interactions with neighbouring conspecifics and promote mutual neighbour defence, leaving more energy and time to be allocated to other needs (Firth, Cole, et al., 2018; Grabowska-Zhang et al., 2012; Johnson et al., 2017). Resulting proximity and familiarity to certain individuals may also increase the opportunity for extra-pair copulations which may lead to elevated breeding success (Choudhury & Black, 1994).

Whilst some species use social associations to decide on territory locations, others rely heavily on favourable environmental conditions. The life-history traits of certain species may impact the time an individual has to gather information about available territories (Pärt & Doligez, 2003). In cooperatively breeding species, where offspring receive care from not just their parents, but also other members of the group, the decision on whether to disperse to a new territory or stay as a subordinate within the natal group is often dependant on environmental conditions. (Hatchwell & Komdeur, 2000). Limited breeding habitat availability, as suggested by the "ecological constraints hypothesis" causes for an individual's breeding success to become reliant on, and inextricably linked with, that of its natal group (Hatchwell & Komdeur, 2000; Heg et al., 2005). A study on Seychelles warblers found that 73% of prospectors were able to secure an external breeding position compared to only 50% of philopatric subordinates (Kingma, Bebbington, et al., 2016). Prospecting subordinates may therefore be able to locate new territories that provide better breeding positions, often achieved through changing rank from a subordinate to a dominant individual within the group. (Kingma, Bebbington, et al., 2016).

When prospecting for new territories, it is known that individuals use a variety of cues as sources of information. Prospecting Northern wheatears (*Oenanthe oenanthe*) for example are significantly more likely to prefer a site occupied by successful breeders when it is housed in short vegetation. These birds subsequently have elevated breeding success when they return to breed in prospected sites the following year (Pärt et al., 2011). Nightingales (*Luscinia megarhynchos*), for example, use singing of territory-holding males during the dawn chorus (Amrhein et al., 2004). Interestingly, a study on wood warblers (*Phylloscopus sibilatrix*) has shown that individuals preferred nesting sites inhabited by low-quality individuals. Using male song as a cue on individual quality, prospecting males preferred breeding sites inhabited by low-quality males instead of high-quality males. Choosing territories with neighbours of lower quality than one's self may reduce aggressive interactions and subsequently the effects of intraspecific competition (Szymkowiak, Thomson, & Kuczy, 2016). Common loons (*Gavia immer*) intrude territories based on the presence of chicks, in an attempt to claim the territory for their own (Piper et al., 2006). Prospecting loons that employed this method of habitat copying, produced chicks 31% more often than when vacant territories were taken over (Piper et al., 2006). Using prospecting forays to gather information, individuals may be able to evaluate a conspecific's ability to defend their territories, using auditory and visual cues as predictors of their breeding success, including territorial calling and head-dipping displays, as witnessed in interactions between Micronesian kingfishers (*Todiramphus cinnamominus reichenbachii)* (Kesler & Haig, 2007).

However, with active breeders visiting nest sites and territories belonging to other birds, the benefits of prospecting whilst provisioning and caring for a brood, and the trade-off associated with such a situation, should be quantified. To my knowledge, no studies have quantified the increase in future breeding success for individuals that prospect whilst caring for young. Conversely, nor has it been assessed how their prospecting activity impacts on the success of the current brood, nor their ability to defend a territory.

1.1.2.3. Finding a mate

Mate choice is an important contributor to an individual's breeding success (Naves et al., 2006). Potential mate quality is often assessed via phenotypic traits, provisioning of resources or the quality of a territory provided (Hoelzer, 1989; Moody et al., 2005). Given the importance of choosing a high-quality mate, choosiness has evolved across the animal kingdom, presenting itself more frequently in certain mating systems than others (Johnstone et al., 1996). Systems that rely on the female to provide most, if not all, of the parental care, for example, exhibit a high degree of female choosiness, where she relies on the male to impart as much heritable quality as possible (Slagsvold & Lijfeld, 1997). However, choosiness can be costly as finding a mate can be a long and energy-demanding process. Picking a mate requires not only an assessment of their suitability, but also the best choice available relative to the time constraints an individual may be facing (Botero & Rubenstein, 2012; Slagsvold et al., 1988).

When prospecting for a potential mate, parental quality may not be observable (Hoelzer, 1989). Instead, individuals may rely on intersexual cues (Carlos, 2006). Acoustic signals, such as song use can illustrate quality, age and readiness for mating. Female zebra finches (*Taeniopygia guttata*), for example, prefer males who have a higher amplitude song (Eens et al., 1991; Ritschard et al., 2010; Roth et al., 2009). However, females of certain species also sing to attract mates. Female alpine accentors (*Prunella collaris*) use complex songs during the breeding season to encourage copulations with males (Langmore et al., 1996; Slater & Mann, 2004). Visual traits are often used as a signal for mate choice and are present in both males and females (Amundsen et al., 1997; Byers et al., 2010). When prospecting for a mate, ornamentation which is often costly to produce as predicted in “the handicap principle”, may provide an obvious and reliable signal for a good mate (Zahavi, 1975). Male and female yellow-eye penguins (*Megadyptes antipodes*), for example, both use caretonoid-based eye and plumage colourations as a signal of quality and parental abilities as part of a mutual mate choice (Massaro et al., 2003). Similarly, male great tits with greater levels of ornamentation are able to provision young with a higher proportion of spiders than caterpillars, resulting in chicks with better body condition (Pagani-Núñez & Senar, 2014). There is evidence that, in some species, kin recognition may be mediated by olfactory cues: European storm petrels (*Hydrobates pelagicus*) are able to recognise kin odours distinct to non-kin odours. Using olfactory cues to reduce the chances of inbreeding in philopatric species is therefore important when prospecting for new mates, and thus may potentially increase the survival and quality of one's offspring (Bonadonna & Sanz-Aguilar, 2012).

Mate finding can impact the behavioural traits of a species (Celis-Murillo et al., 2016; Roth et al., 2009). Female nightingales conduct prospecting forays during the night when many territorial unmated males sing, rather than at dawn when both mated and unmated males sing in more equal numbers (Roth et al., 2009). Conversely, in response to the strong selection pressure of female choice and movement patterns, leks are formed of conspicuous male groups. This grouping allows for many males to be assessed simultaneously (Gibson et al., 1991; Westcott, 1994). However, only one or a few males tend to receive attention from a disproportionate number of the prospecting females (Duval, 2012). When visiting the leks, females are looking for signals indicative of male quality (Höglund et al., 1990). Great snipe (*Gallinago media*) females, for instance, prefer males with a higher percentage of white on their tails, whereas sage grouse (*Centrocercus urophasianus*) females assess acoustics and repetition rate of the male's strut display, and will keep searching until they find their preferred mate (Gibson, 1996; Höglund et al., 1990). Such aggregations have led to mate-searching females using the choices of conspecifics as reliable cues, resulting in mate-searching females being attracted to males seen copulating with other females (Balmford, 1991; Danchin & Wagner, 1997).

To my knowledge there is no research on how pairs prospect together. In socially monogamous species, nest site, foraging site and territory selection may have similar impacts on both the male and the female's fitness. Prospecting new sites together may help to defend against site owner aggressions and to share the energetic costs of prospecting. To investigate this further, research should focus on how and when pairs prospect together compared to prospecting alone. As well as this, it should be investigated how the division of labour in vigilance and information gathering is adjusted when pairs prospect together. Understanding the criteria of cues used during prospecting and how they may differ between males and females would help in our understanding of what makes a good nest site, how this differs between the sexes, and how a nest site plays into an individual's breeding success.

1.1.2.4 Cognitive demands of prospecting behaviour

For some species that form long-term pair bonds, a partner may not be for life. Birds may decide to re-evaluate their mate choice, and divorce their partner following reproductive failure, if it seems likely they can increase their breeding success with another partner (Choudhury, 1995). Finding a new partner is likely to be very costly and it is generally thought that breeding success is closely tied with nest site and mate fidelity (Dubois & Cézilly, 2002; Friedrich et al., 2015; Naves et al., 2006). Decisions as to whether to divorce a partner, therefore, are likely to be influenced by the integration of personal information about current mate quality with information gathered through prospecting about the availability and quality of other mating partners. Common murres (*Uria aalge*), for example, breed in large colonies. Prospecting individuals leave their partner at the nest whilst they gather information about their neighbours' chick provisioning ability, using this information to inform divorce and re-partnering decisions (Moody et al., 2005). However, whilst it is believed birds are able to remember information gathered during the same season (Scardamaglia et al., 2017; Schuett et al., 2017), very few studies have been conducted to assess an individual's ability to remember locations of high-quality potential mates. Whilst it may be that this information begins to become outdated and unreliable, individuals may be using it in combination with new information to make an accurate assessment of a breeding site.

However, collecting the most reliable information will only be beneficial if individuals can use it to their advantage. Different life history attributes can affect different selection pressures on prospecting. Species that are brood parasites for example, require specialised cognitive abilities for breeding site selection, including heightened spatial memory capabilities so that multiple different nest site locations can be remembered simultaneously (White et al., 2017). Female brood parasites, such as cowbirds and cuckoos, must not only prospect for viable nests but assess their suitability and the stage of breeding each nest has reached to make sure the host has reached the incubation phase (White, 2020; Yang et al., 2017). Female brown-headed cowbirds show a clear preference for laying their eggs in nests in which the host's egg number corresponds with the number of days since her last visit and avoid nests in which the number of eggs has not increased since the previous visit. This enables the females to choose nests most suitable for parasitism to give her offspring the best chance of competing with the host's chicks, thereby increasing the chances of a successful breeding season (White et al., 2009). Furthermore, cowbirds seem able to integrate information regarding egg-laying date of the host with multiple other features. The hippocampus, which is associated with storing spatial memory, is larger in females than in males, in cowbird species where the female searches for host nests. This is not the case for species where both females and males search for host nests or for cowbird species that are not brood parasites. This allows the females to gather information about host eggs, whilst simultaneously assessing characteristics such as host species and nest quality (Banks & Martin, 2001; Reboreda et al., 1996; Scardamaglia et al., 2017). Looking at prospecting from this perspective highlights how adaptive the behaviour is and how it is intertwined with a species' life-history strategy, allowing individuals to gather multiple different types of information simultaneously.

The ability to remember information not only within breeding seasons, but between breeding seasons, may help to increase an individuals' breeding success when environmental characteristics are sufficiently stable over time. Prospecting a new each breeding season may provide reliable information, but it may also incur substantial time and energy costs (Pärt & Doligez, 2003). Remembering the location of high-quality sources of information may help to reduce some of these costs. Resident great tits, for example, are able to remember and implement such nest site preferences from one year to the next (Forsman et al., 2014). This will be advantageous in allowing individuals to focus prospecting efforts on particular nests, thereby increasing the proportion of their time budget that can be allocated to other important tasks.

The ability to discriminate or recognise different individuals may be paramount when assessing potential future mating opportunities or having to respond to aggressive outsiders. This is particularly helpful if an individual lives in a location where interactions that occur are not predictable, for example, when courtship and mating opportunities occur away from the nest (Pardo et al., 2018). In acorn woodpeckers (*Melanerpres formicivorus*), for instance, individuals form coalitions to find and take over breeding vacancies in other territories (Pardo et al., 2020). There is some evidence that as a result these birds show third party recognition whereby they can determine whether third party individuals (i.e. individuals outside of their own group) belong to the same group or not. The ability to gather this information will help individuals navigate many difficult social interactions and highlights the need to gather and use public information to one's advantage.

1.1.3. Improving conservation efforts via prospecting behaviour

Combining what is already known about prospecting patterns can help to create effective conservation plans tailored to a particular species. Increased knowledge on how and why an individual chooses a breeding location means efforts can be made to attract individuals to new sites of known high-quality containing fewer predators or parasites, via these specific cues (Reed & Dobson, 1993). Efforts have already been made to re-establish certain seabird colonies, with perhaps the most iconic of them all being a study on Atlantic puffins (*Fratercula arctica*) (Kress & Nettleship, 1988). Using chick translocation and adult puffin decoys, they were able to re-establish the once locally decimated population. Conspecific attraction, as exemplified in Kress' use of decoys, allows animals to gather inadvertent social information from conspecifics that have the same needs (Stamps, 1991). More recently, studies on species such as the grasshopper sparrow *(Ammodramus savannarum*) and the endangered black-capped vireo (*Vireo atricapilla)* have proven how social cues, such as conspecific playback, attract individuals to establish themselves in new habitats and territories (Andrews et al., 2015; Ward & Schlossberg, 2004). It is thought that by using this method to pick higher-quality habitat, individuals are able to reduce energy expenditure of searching for a new habitat and increase fecundity (Fletcher Jr, 2006). One of the biggest drivers of reducing biodiversity is habitat loss (IUCN, 2014). Encouraging individuals to disperse and settle in created and restored habitat via conspecific attraction or translocation has become a reliable tool in the fight against extinction.

1.2. Relevance of my research

Gathering reliable information in preparation for a future breeding season is important for optimal decision making. It reduces an individual's uncertainty about the environment in which it lives and is generally thought to increase an individual's breeding success (Giraldeau et al., 2002). Reducing uncertainty is an important factor in habitat selection, affects population dynamics and encourages the dispersal of individuals to areas that may offer the greatest fitness benefits (Delgado et al., 2011; Fretwell, 1969). Prospecting, as a form of information gathering, therefore allows individuals to make the best decisions that they can, whether relating to nest sites, territories, foraging sites or mates.

However, there are still many aspects of prospecting behaviour that remain poorly understood. For example, we do not know if individuals prospect whilst still rearing chicks, if there is a trade-off between prospecting and parental care, nor have we quantified the improvement in future breeding success for prospecting active breeders. It is still unknown if, and how, pairs prospect sites together and if they collect the same types of information. Nor has the effect of dominance status on prospecting behaviour been studied; do dominant individuals prospect less frequently and for less time? This thesis aims to address these questions by studying a free-living population of wild jackdaws. Jackdaws are long-lived birds who exhibit strong pair-bonds and dominance hierarchies. Pair-bonds are essential for breeding success in jackdaws, as without them, they cannot commence breeding. They exhibit non-territorial foraging, with large winter flocks gathering through the winter (Röell, 1978). As well as to collect information on the nest sites around them (i.e. who owns which nest site, how successful other nests have been), I expect prospecting in jackdaws to help reinforce the social bonds between individuals that don't breed together (Bayern et al., 2007; Valone, 2007). Social bonds in group-living species are very important for sharing of information regarding food availability and predator avoidance (Braun & Bugnyar, 2012). As well as this, dominance often has an influence on social structure, with fewer individuals having greater access to certain resources, such as mates and food (Wechler, 1988). I therefore would predict that jackdaws with greater dominance would be able to monopolize resources, such as nesting sites, and would therefore be less likely to need to prospect.

Increasing our understanding of prospecting behaviour in wild birds is important for two reasons. Firstly, looking at prospecting from a ‘blue-sky’ perspective will further our understanding of the behavioural ecology, evolutionary ecology and the cognitive ecology of a species. We can then apply these findings to inform conservation policy to help species in need. While much headway has been made into exploring prospective behaviour in multiple species of birds, there is still much we do not know. As a result, we do not have a holistic view of how species use public and personal information to make decisions regarding where they will breed, who they will mate with and where they will forage. In this study, I have highlighted what we do know and where future work must focus to increase our understanding of prospecting behaviour.

1.3. Research Methods

1.3.1 Study System

Fieldwork took place as part of The Cornish Jackdaw Project which researches free-living populations of jackdaws. The project began in 2012 and contains 85 nest boxes across three field sites in West Cornwall (Fig 2). As part of the BTO ringing scheme, over 3000 individuals have now been ringed. Each ringed individual has a unique ring colour combination and life-history data collected. Jackdaws provide an excellent study system to assess prospecting behaviour and public information use. Naturally nesting semi-colonially in cavities, jackdaws readily nest in nest boxes. This allows for life-history data to be collected and breeding site selection to be monitored.

1.3.2 Changes to Data Collection

When planning data collection for my thesis, I had planned to collect RFID (Radio Frequency Identification) (IB Technology, Leicester, UK) data from all 72 nest boxes in the study system, throughout the whole breeding season (March-July). RFID data would have allowed me to assess which individuals in the community were prospecting, where they preferentially visited, and the characteristics of nest boxes, and box owner of the most prospected nest sites. As part of the ongoing research conducted by The Cornish Jackdaw Project, each bird ringed as part of the project had 3 colour rings and 1 metal ring. The majority of ringed birds had a Passive Integrated Transponder (PIT) tag embedded into one of their colour rings. I attached perches to the front of the nest boxes, beneath the entrance hole, which detected the direction of movement into the nest box via two antennae. Data collected from the PIT tags were collected by RFID logger boards, located beneath the nest box. During the 2019 breeding season, it became apparent that many tags had malfunctioned due to manufacturer error and needed to be replaced. I could not replace tags until much later in the breeding season but planned to recollect data in the 2020 breeding season. However, due to the COVID-19 pandemic, data collection could not go ahead during the 2020 breeding season. This meant I was not able to collect new data to better analyse prospecting behaviour. As a result, I was only able to use data from the 2019 breeding season video records.

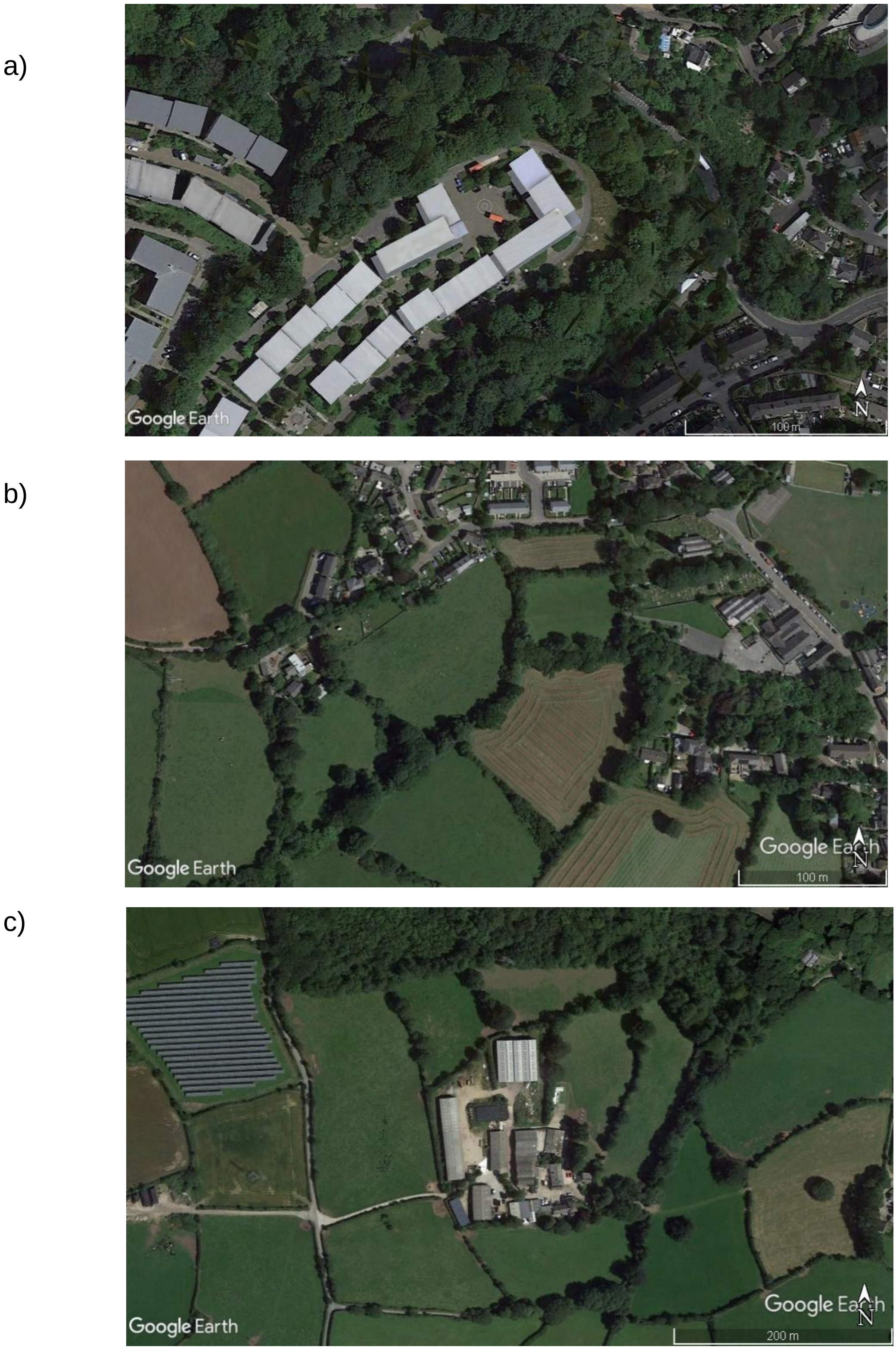

Figure 2. Maps showing the location of the three field sites of The Cornish Jackdaw Project. a) Penryn Campus, b) Stithians Village and c) Pencoose Farm.

Chapter 2: Individual Characteristics of Wild Prospecting Jackdaws

2.1 Abstract

Gathering information is key to animals' ability to assess their surroundings and adapt their behaviour to changing environmental conditions. Decisions regarding where and when to breed are critical determinants of animals' reproductive success and can directly affect individuals' fitness. Prospecting behaviour, the act of gathering information about potential future breeding sites, helps individuals to assess habitats and to reduce environmental uncertainty. By collecting breeding information on conspecifics and their nesting sites, individuals may be able to locate high-quality breeding sites for future breeding events. Here, I investigated prospecting behaviour in a free-living, nest box-breeding population of western jackdaws (*Corvus monedula*). I assessed the relationship between prospectors' own breeding success and the changes in prospecting frequency and duration throughout the breeding season, for individuals and for breeding pairs. I assessed whether prospecting occurred most frequently at nest boxes with higher breeding success, if prospecting behaviour occurs more frequently at nest boxes in the nestling stage (when one or more chicks are in the nest) of the breeding season as compared to the nest-building stage, egg-laying stage and post-fledging stage (once all chicks have left the nest), if successful individuals will prospect at other nest boxes more frequently once their chicks have fledged the nest, if pair-bonded individuals are more likely to prospect with their partner than without their partner and if individuals prospecting with their partner will prospect for less time than those without their partner. Jackdaw prospecting frequency was not significantly greater in the chick-rearing phase, compared to the nest-building stage, egg-laying stage and post-fledging phase. Pair-bonded partners were more likely to prospect alone than together, but those that did prospect together, did so for significantly longer, which may allow these individuals to collect more information and potentially make more informed and accurate decisions. How information is gathered from prospecting trips, whether alone or with a breeding partner, and its role in individual decision-making processes may influence breeding habitat selection and is likely to affect dispersal and population dynamics.

2.2 Introduction

Breeding site quality is of prime importance for an individual's breeding success (Boulinier et al., 1996). Finding and acquiring a high-quality breeding site not only impacts individual fitness but can shape patterns of dispersal for individuals and the population (Cox & Kesler, 2012; Danchin et al., 2004). Increasing our knowledge and understanding of individual breeding site selection, and the challenges this entails, is vital for evolutionary and applied conservation purposes such as population regulation (Cody, 1985; Morris, 2003).

It has been argued that individuals will invest substantial time and effort into gathering information about potential breeding sites (Mori & Nakata, 2008; J. Michael Reed et al., 1999). If environmental conditions are spatially and temporally variable, gathering information can reduce an individual's uncertainty about the surrounding environment (Dall et al., 2005). Collecting and processing information, therefore, is crucial for animals to make informed and accurate decisions on the habitats they choose to live and breed in (Block & Brennan, 1992). Prospecting behaviour, where an individual visits potential future breeding sites, allows habitat and breeding site quality to be monitored (J. Michael Reed et al., 1999; Szymkowiak, Thomson, & Kuczyński, 2016), facilitating adaptive decision-making. Individuals can prospect by collecting personal information derived from direct interactions with their environment (Nocera et al., 2006). Alternatively, animals may use public information by attending to signals or cues produced by other individuals (Morand-Ferron et al., 2009). Whilst both types of information have the potential to provide more certainty about environmental states, greater time and energy costs may be incurred when collecting personal information compared to the lower costs entailed from gathering public information (Schjørring et al., n.d.). Additionally, using outdated or unreliable information provided by others can negatively impact an individual's breeding success (Pärt et al., 2011). Animals may need to consider the trade-off between costly but accurate personal information, compared to cheap but potentially inaccurate, or outdated, public information. It may therefore be beneficial for individuals to flexibly switch between gathering public vs. personal information depending on the relative costs and benefits (Giraldeau et al., 2002; Morinay et al., 2020).

Social information is well documented to be used in breeding site selection (Valone, 2007; Ward, 2005). For instance, the conspecific attraction hypothesis, where individuals are attracted to a site due to the presence of conspecifics, has been argued to play an important role in species distribution and dispersal (Campomizzi & Lebrun-Southcott, 2020; Pizzatto et al., 2016). In many bird species, individual habitat selection strategies that use social information may rely on the breeding success of conspecifics for inferring the suitability of a breeding site (Pärt & Doligez, 2003). Pied flycatcher (*Ficedula hypoleuca*) nests with larger broods receive significantly more prospecting visits than smaller broods (Pärt & Doligez, 2003). Another example is provided by zebra finches (*Taeniopygia guttata)*, where individuals take advantage of begging calls as a cue of breeding success, prospecting at nests with larger broods (Brandl et al., 2019; Schuett et al., 2017). Using social information may allow individuals to make quick assessments of breeding habitat quality, helping to reduce the time spent prospecting and ultimately reduce energy expended.

Prospecting for public information may be costly and increase aggressive interactions with conspecifics, but the potential advantages of prospecting may outweigh the risk and potential cost of aggression. Individuals may be particularly likely to take risks associated with prospecting if they stand to gain substantially from gathering social information. Public information is thought to be especially important for failed breeders and immature individuals, who may lack knowledge from personal experience (Danchin et al., 1998). A black-legged kittiwake (*Rissa tridactyla*) study, which manipulated the breeding success of breeding pairs, demonstrated a distinct difference between successful and unsuccessful breeders. In total, 33% of failed breeders prospected other breeding sites after nest failure, but successful individuals never prospected (Aurore Ponchon et al., 2017). Another example of the importance of prospecting is provided by cormorants (*Phalacrocorax carbo sinensis*), where individuals have higher breeding success in their first breeding season if they have actively prospected conspecific nest sites prior to breeding (Schjørring et al., n.d.). Thus, using public information to inform decisions can increase future breeding success.

Selecting an optimal breeding site requires information to be collected at the right time. The 'optimal timing hypothesis' suggests information should be collected when it will maximally increase an individual's fitness (McNamara et al., 2011). In birds, information is generally thought to be more reliable later in the nestling stage of the breeding season, as compared to the nest-building, egg-laying and post-fledging stages (Table 1), because there is more information available on the reproductive success associated with breeding locations. At this stage, prospectors are able to cue in on brood size and begging calls (Brandl et al., 2019; Schuett et al., 2017). First-time breeding great cormorants (*Phalacrocorax carbo sinensis*), for example, prospected at conspecific nests throughout the breeding season, but with greater frequency later in the season. Prospecting rates peaked once most eggs had hatched but before the chicks had fledged, which suggests individuals were able to discern when the most 'valuable' information was available (Schjørring et al., n.d.). Choosing when to prospect potential breeding sites, can therefore be plastic and appears to depend on different cue availability.

Whilst research has been conducted on the cues used and consequences of prospecting, no studies to my knowledge have investigated if breeding pairs prospect together. It is estimated that over 90% of bird species are socially monogamous, meaning that a male and female form a pair-bond and breed together (Lack, 1968). However, there is great variability in the duration of pair-bonds. Some last only for a single nesting attempt, whilst others last a lifetime (Griffith, 2019; Owen et al., 1988). For species that mate for life, such as albatrosses, swans and some corvids, breeding site quality may be inextricably linked to not just one individual, but both members of the pair. Prospecting with a partner may allow the cost of prospecting to be shared between both individuals. Prospecting together creates the potential for a division of labour, where one individual can prospect, whilst the other watches for danger, which may help to reduce the number of aggressive interactions with nest site owners. Therefore, breeding pairs that prospect together may be able to gather information more quickly, thus increasing time and energy allowance for other behaviours.

The aim of this study was to investigate the prospecting behaviour of wild jackdaws, focusing on the prevalence of prospecting in successful and unsuccessful breeders, how the rates of prospecting events vary throughout the breeding season and whether jackdaw pairs prospect together. Jackdaws are a monogamous, site-faithful, passerine species. They have one brood per season, regardless of breeding success or failure. Brood failure may therefore be detrimental to the lifetime breeding success of an individual (Röell, 1978). They breed semi-colonially in cavities and take to nest boxes which allows for direct behavioural observations. As such, jackdaws provide a great study system as individual prospecting movements and breeding site selection can be readily observed.

Based on the previous research described above, I formulated five predictions. 1) Prospecting will occur more frequently at nest boxes with higher reproductive success. 2) Failed breeders will prospect more than successful individuals. 3) Prospecting behaviour occurs more frequently at nest boxes in the nestling stage of the breeding season as compared to the nest-building stage, egg-laying stage and post-fledging stage. 4) Successful individuals will prospect at other nest boxes more frequently once their chicks have fledged. 5) Higher rates of prospecting will be linked to higher reproductive success the following year. 6) Pair-bonded individuals are more likely to prospect with their partner than without their partner. 7) Individuals prospecting with their partner will prospect for less time than those without their partner.

2. 3 Methods

2.3.1 Study System

RFID Data Collection

I conducted my research at 72 nest boxes across two field sites in West Cornwall, UK: Site Y (N 50°11’25.98”, W 5°10’49.00”) at Stithians Village and Site Z (N 50°11’ 55.37”, W 5°10’7.48”) at Pencoose Farm, from February to July, 2019. My study was conducted as part of The Cornish Jackdaw Project, which began ringing and studying jackdaws in 2013. All individuals ringed as part of the project were given a unique colour ring combination to allow for identification. The majority of ringed birds had a Passive Integrated Transponder (PIT) tag embedded into one of their colour rings. I attached perches to the front of the nest boxes, beneath the entrance hole. Perches were embedded with two tag-detecting antennae to detect the direction of movement into our out of the nest box (IB Technology, Leicester, UK). The perches were large enough for only one bird to land at a time. Data collected from the PIT tags were collected by RFID (Radio Frequency Identification) logger boards. I rotated 15-20 RFID logger boards every 2-5 days around all 72 of the nest boxes throughout each stage of the breeding season (nest-building/ egg-laying/ nestling/ post-fledging). The two perch antennae were connected to the logger board. All logger boards were located directly beneath the nest box. Logger boards sampled the environment twice per second for PIT tags and bird identity was logged. I replaced active logger boards with dummies when they were removed to ensure individuals remained habituated to them.

Individual Characteristics

Individuals were ringed by members of the Cornish Jackdaw Project under BTO licenses. Individuals were trapped using remote-controlled trap-doors or large walk-in traps. Each individual was fitted with one metal ring and three colour rings, one of which contained an embedded PIT-tag. I determined the age of all individuals (ringed and unringed) using plumage. Adults have black feathers all over the body, with the nape and sides of the neck silver/grey. Eyes are silvery white. Juveniles have uniform brown/black feathers and dull brown eyes. When first trapped, small blood samples are taken from all individuals. Sex is determined for each ringed individual using blood analysis (Griffiths et al., 1998). Birds without rings, or with missing rings could not be reliably sexed. Partnerships, (i.e. pair-bonds), are defined from nest box ownership and from behavioural observations of joint nest-building, parental care, nest site defence, foraging and aggressive interactions with other pairs. Jackdaw pair-bonds are established as early as their first-year and their pair-bonds often last a lifetime in this monogamous species. Jackdaws usually begin breeding in their second-year, once pair-bonds have been established (Röell, 1978). For individuals that were box owners, I could be confident they were also pair-bonded as they were breeding. If a prospector and its pair did not own a box, I could not be confident that they were breeding and therefore couldn’t make an association between ‘pair-bonded’ and ‘breeding’.

Breeding Success

Given that jackdaws disperse after fledging and it is difficult to measure their long-term survival, I used the total number of chicks that survived to fledging as a proxy for the breeding success of each nest. I calculated the breeding success for all nest boxes and box owners in 2018 and 2019. This measure of breeding success was used to analyse whether boxes with higher breeding success receive more prospecting visits. However, several studies, including on jackdaws, have shown that heavier chicks are more likely to survive (Grant, 1991; Henderson & Hart, 1993; Kersten & Brenninkmeijer, 1995). I therefore ran additional analyses to see if the total mass of fledglings produced predicts the number of prospecting events. I considered individuals to own a nest box once nest building began. When assessing whether successful breeders prospect more frequently after their chicks have fledged, breeding individuals were considered ‘successful’ if they had at least one chick fledge the nest. If they had zero chicks fledge, the nest was considered ‘failed’. I could not calculate breeding success in 2020 due to the COVID-19 pandemic resulting in reduced data collection.

Video Data Collection

To further assess prospector behaviour at nest boxes, I randomly selected 20 breeding pairs and their nest boxes for video data collection (Appendix I Table 1). Nine nest boxes were at Pencoose Farm and 11 nest boxes at Stithians Village (Fig 3). I filmed each nest box inside and outside simultaneously, once in the morning and once in the evening whilst RFID data were being collected. I used RFID data collected in the 2018 breeding season to see which times of day were optimal for prospecting. I then filmed the nest boxes at these times. I used the video data to validate the RFID data and to collect data on unringed individuals that were prospecting. I fitted CCTV cameras inside the nest boxes prior to nest building commencing. Camcorders were set-up in a nearby hide, erected at least 12 hours before filming, or in a car, located >10m from the nest box to reduce disturbance to the birds. I standardised the camcorders to film a 2m^2 area around the nest boxes. Within this 2m^2, it could reliably be stated that an individual was prospecting at the observed nest box. CCTV videos were stored on Digital Video Recorders (DVRs) and powered by battery packs, all of which were controlled at ground level, beneath the nest boxes to reduce disturbance for the birds. I set up the CCTV equipment at sunrise (+/- 20 mins) and three hours before sunset (+/- 20 mins). Internal recording of the nest boxes commenced when trained observers arrived on site. Recording by the external cameras began after a one-hour habituation period, or when a bird arrived at the box, whichever came first. I filmed the nest boxes externally for one hour. At the end of this hour, I ceased both the external and internal recording of the nest box. If no bird arrived during the habituation period, filming did not occur. Filming times were informed by peak prospecting activity observed in RFID data from 2018. A trained observer was present at each filming session, noting the date, time and the activities and individuals seen. Video data were collected from March – July 2019. Data collection ceased when prospecting rates had dropped significantly lower than peak rates.

Video Transcription

I transcribed videos using BORIS software version 7.9.7 (Friard & Gamba, 2016). I used BORIS to record the activity of box owners and prospectors on and near nest boxes. I considered a prospecting event to have occurred when an individual arrived at, or near, a box that they did not own and stayed for more than 1 second (transcribed as ‘In Frame’). Arrival and departure times near the box and on the box were noted. Near box was anywhere within the standardised 2m^2 area around, but not on, the nest box. Where possible, I identified all individuals using their colour rings. If an individual did not have colour rings, or the rings were incomplete, the individual was given a unique number beginning with U. I considered individuals to prospect with their partner if they arrived within 5 seconds of one another. For partnership analysis, only known individuals (i.e. those that could be identified by their rings) were used. If an individual left and returned after 10 seconds, within the same recording session, I considered it a separate prospecting event. To check video transcriptions for observer bias, randomly selected videos (20%) were transcribed by one other trained observer who was blind to my predictions. Transcriptions for the same video were then checked for inter-rater reliability in R. Inter-rater reliability was >80% accuracy for each behaviour transcribed (Appendix I Table 2).

Figure 3. Nest boxes used for video data collection at a) Stithians Village (site Y) and b) Pencoose Farm (site Z).

Ethics

All procedures pertaining to the birds operated under the appropriate licences from the BTO and Home Office (project licence 30/3261). Data collection was approved by the University of Exeter Biosciences Ethics Committee (eCORN002589 v3.3.)

2.3.2 Data Analysis

Due to high levels of RFID tag failure due to manufacturer errors, RFID data was not reliable enough for use until June 2019 when the majority of failed rings had been replaced. For this reason, the RFID tag data was not used for data analyses.

Each nest box received 50 hours of external filming, with 25 hours in the morning (between 6:00-9:00am) and 25 hours in the evening (between 17:00-20:00pm) between March and July 2019, giving a total of 1000 hours of video material across the 20 nest boxes. Internal camera footage was watched but I decided not to analyse it due to only one individual going inside a nest box whilst prospecting. For each prospecting event, I noted the breeding stage it occurred in (Table 1). I also recorded for each prospecting event, the amount of time the prospector spent on the perch, on top of the box, and on the side of the box, and summed these to give a single duration spent at the nest box for each prospecting event. Only two prospecting events were conducted by failed breeders so this data could not be analysed. When assessing the ages of prospecting birds, precise hatching dates were not known for many individuals. Therefore, for consistency, birds were only aged as ‘adult’ or ‘juvenile’. When assessing whether successful breeders prospect more after their chicks had fledged, only one value was used per pair when both the male and female had prospected. As such, 2 males and 1 female were randomly selected and deleted from the dataset. Analysis of birds prospecting with their partner was conducted after the removal of 3 female and 3 male randomly selected datapoints from the dataset. These data were removed to account for repeated measures when both the male and female of the pair prospected together.

Table 1. Description of each breeding stage.

Breeding Stage	Description
Nest-build	1 or more pieces of nest material in the nest box. 0 eggs laid.
Egg-lay	1 or more eggs have been laid. 0 chicks have hatched.
Nestling	1 or more chicks have hatched. 0 chicks have fledged.
Post-fledging	All chicks have fledged.

All analyses were conducted in R version 4.0.4 (R Core Team, 2021). Plots were made in *ggplot2* and the lme4 package was used for analyses. Model reduction was not performed on any of these analyses. All data analysed had a non-normal distribution and the statistical tests were chosen to meet that requirement. To test the relationship between nest box breeding success and prospecting visits, I used a GLM with total times a box was prospected as the response variable and breeding success (total number of chicks) of the prospected box as the predictor variable. As chick weight can have a profound effect on post-fledging survival of chicks and therefore potentially the quality of a nest site, I ran a GLM to assess the relationship between the total weight of chicks that fledged as the predictor variable, and the total times a box was prospected as the response variable. In order to investigate the relationship between frequency and duration, I ran a GLM with total number of prospecting events as the predictor variable and total time spent prospecting as the response variable for each known prospector. To test whether prospecting behaviour occurs more frequently in the nestling stage, I used a GLMM with prospecting frequency as the response variable, breeding stage (nest-build/ egg-lay/ nestling/ post-fledging) as the fixed effect and nest box ID as the random effect. The model was fitted with a Poisson error distribution and used a log link. When assessing the prospecting rates conducted before and after fledging for successful individuals, I used a Wilcoxon signed-rank test appropriate for the repeated measures being analysed. To test if pair-bonded individuals are more likely to prospect with their partner than alone, I used a Wilcoxon signed-rank test to compare the total prospecting events conducted with and without a partner. This test was the most appropriate for the repeated measures analysis. To test if individuals prospect for longer when prospecting with their partner, I used a GLMM with total time spent prospecting as the response variable, whether the individual was with their partner (yes/no) as the fixed effect, and prospector ID as the random effect. The model was fitted with a Gamma error distribution using a log link.

2.4 Results

In total, 67 individuals were detected prospecting at 14 of the focal nest boxes. These individuals prospected a total of 92 times with an average of 1.3± 0.1 prospecting events per individual (mean± SE). Of these 67 individuals, 66 were adults, 30 were known individuals (ringed) and 37 were unknown (unringed/ missing rings). Of the known individuals, sex was known for 25 individuals. 11 of the prospectors were females and 14 of the prospectors were males. On average, females conducted 1.5± 0.3 (mean± SE) prospecting trips for an average of 65.5± 23.4 seconds (± SE), whereas males conducted 1.7± 0.3 (mean± SE) prospecting trips which lasted an average of 51.3± 13.5 seconds (± SE) (Fig.4). Fifteen of the known individuals were box owners and 34 of the 92 prospecting events involved individuals prospecting with their partner. When looking at the spatial distribution of the known box owners (n=15), it could be seen that 93.3% of individuals conducted only one prospecting visit and all but one of the known box owners stayed at the site in which they were breeding to prospect. For example, birds that owned a nest box in site Z only prospected in site Z. 46.7% of prospecting visits were to a neighbour’s nest box. A nest box was considered to be a neighbour if there were no other nest boxes between itself and the nest box the prospecting individual owned. The data showed no clear signature of reciprocation of prospecting visits. However, when observing the jackdaws at both sites Y and Z, I did see on multiple occasions instances of a pair visiting a neighbouring box, causing for the pair that owned the neighbouring (prospected) box to then reciprocate the behaviour.

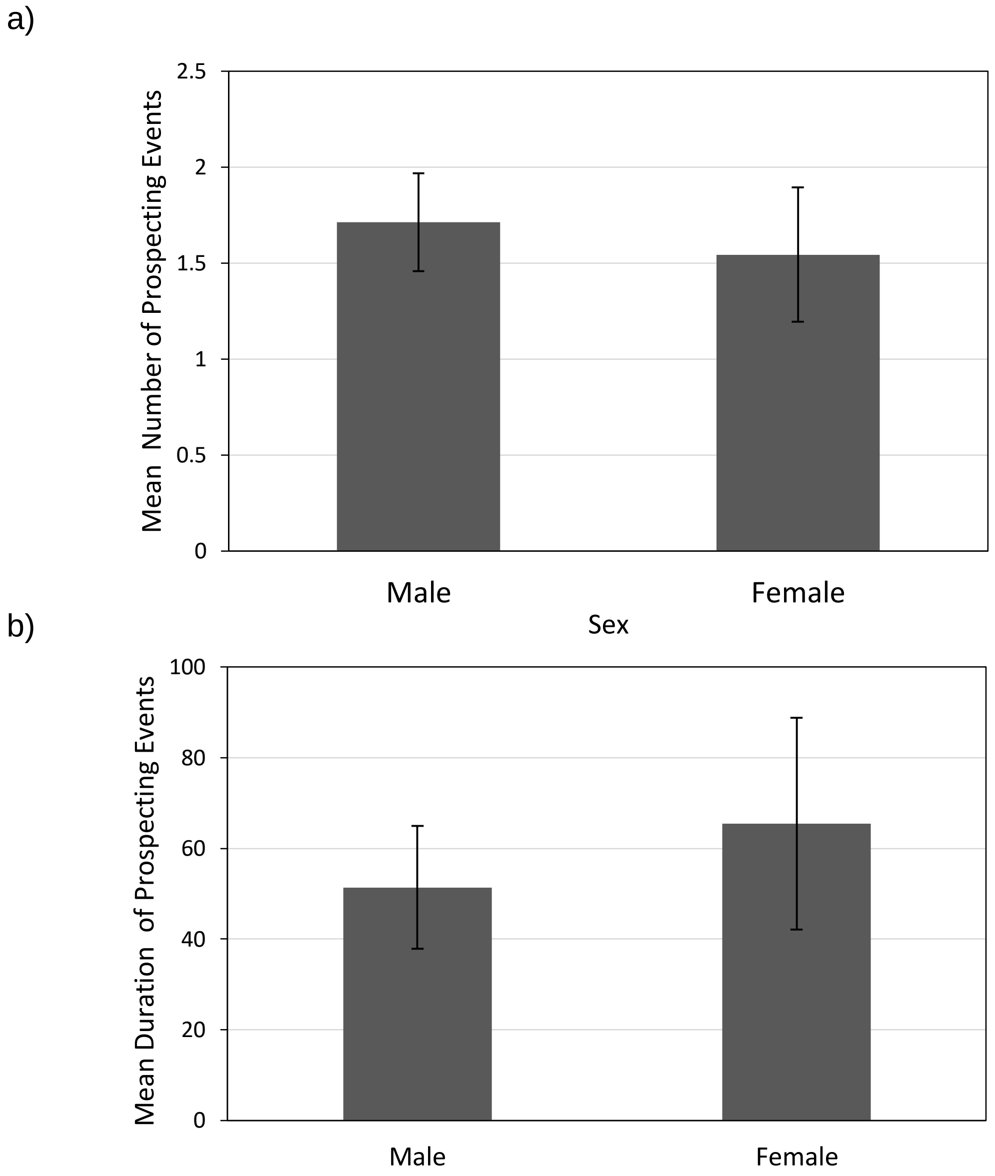

Figure 4. The mean number (a) and the mean duration (b) of prospecting events conducted by male and female prospecting individuals.

2.4.1 Nest Box Visits

Do boxes with higher breeding success receive more prospecting visits?

Overall, 70% of the 20 focal nest boxes received at least 1 prospecting visit. On average, I recorded 4.6 ±1.3 (mean± SE) prospecting events per nest box throughout the breeding season. The mean breeding success of boxes that received prospecting was 1.9 ± 0.2 (mean number of fledglings ± SE) and 1.8 ± 0.4 for boxes that did not receive prospecting (mean number of fledglings ± SE).

Boxes with higher breeding success did not receive more prospecting visits (model slope estimate +/- SE = -0.052+/- 0.116, z=-0.446, P=0.656; Fig.5a).

When considering the relationship of total fledgling weight and its effect on the number of prospecting events a box received, I found that the average total weight of fledglings across the 20 nest boxes was 398.1 ± 42.9 grams (± SE). The total weight of fledglings did not predict the total number of prospecting events at a nest box (model slope estimate +/- SE = -0.0001+/- 0.0005, z=-0.343, P=0.732; Fig.5b).

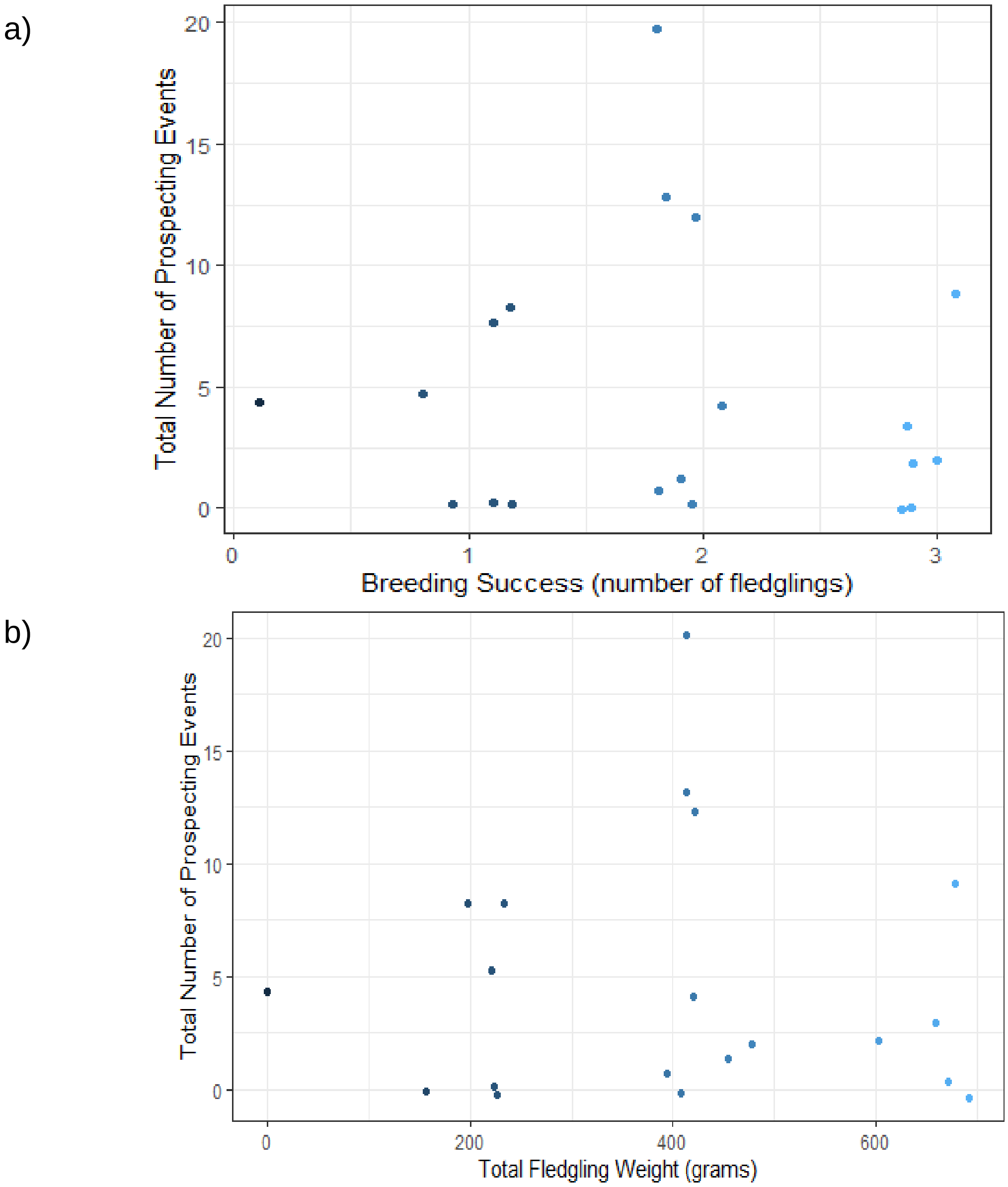

Figure 5. The relationship between a) breeding success and b) the total weight of chicks that fledged with the total number of prospecting events at each nest box.

2.4.2 Individual Characteristics

Prospecting Occurrence

Do individuals that conduct more prospecting trips, spend more time prospecting throughout the breeding season?

Of all the 67 unique prospecting individuals, 44.8% were by known individuals. (n=30). Known individuals prospected a total of 1.6± 0.2 (mean± SE) times across the breeding season, for an average of 57.1± 11.1 (± SE) seconds. Individuals who conducted higher numbers of prospecting trips to potential breeding sites, spent significantly more time prospecting in total throughout the breeding season (model slope estimate +/- SE = 0.3968+/- 0.1611, z=2.464, P<0.020; Fig.6).

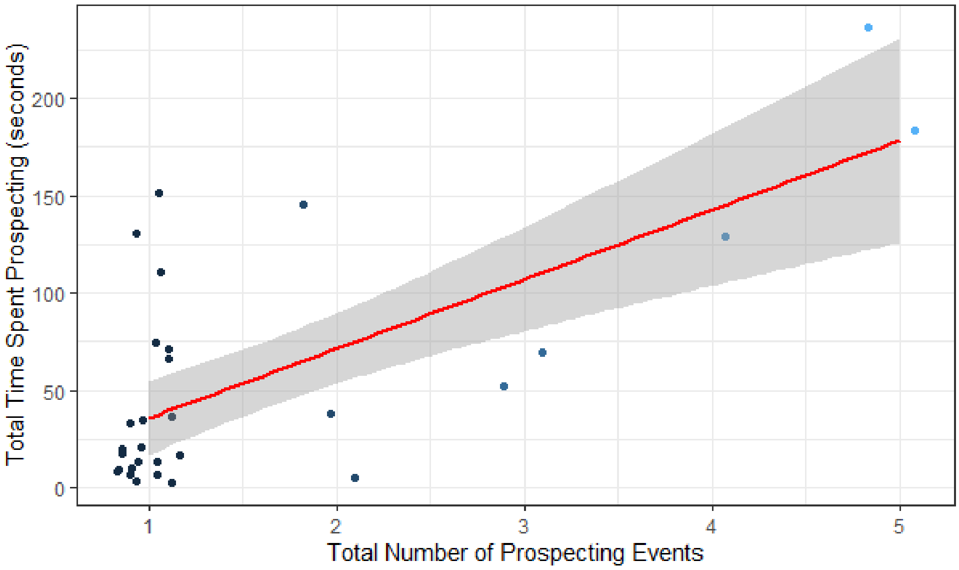

Figure 6. The relationship between the total number of prospecting events and the total time an individual spent prospecting.

Does prospecting occur more frequently in the nest box owners' nestling stage?

The nest-building stage received 10.9% of all the prospecting events (out of n=92 in total), the egg laying stage received 14.1%, the nestling stage received 47.8% and the post-fledging stage had 27.2%. However, the nestling stage did not have significantly more prospecting events than the other breeding stages (Fig 7a; Table 2).

Do successful breeders prospect more frequently after their chicks have fledged?

Of all recorded prospecting events, 27.2% were by box owners (n=15). 86.7% of prospecting box owners were successful breeders in the 2019 breeding season (n=13). There was a trend for successful breeders to prospect most frequently (81.3% of all events) once their chicks had fledged, compared to 12.5% in their nestling stage, 6.3% in their egg laying stage and 0% in their nest building stage (Fig 7b). However, this pattern was not statistically significant: successful breeders were not significantly more likely to prospect after their chicks had fledged (V=13.5, n=10, p=0.1449).

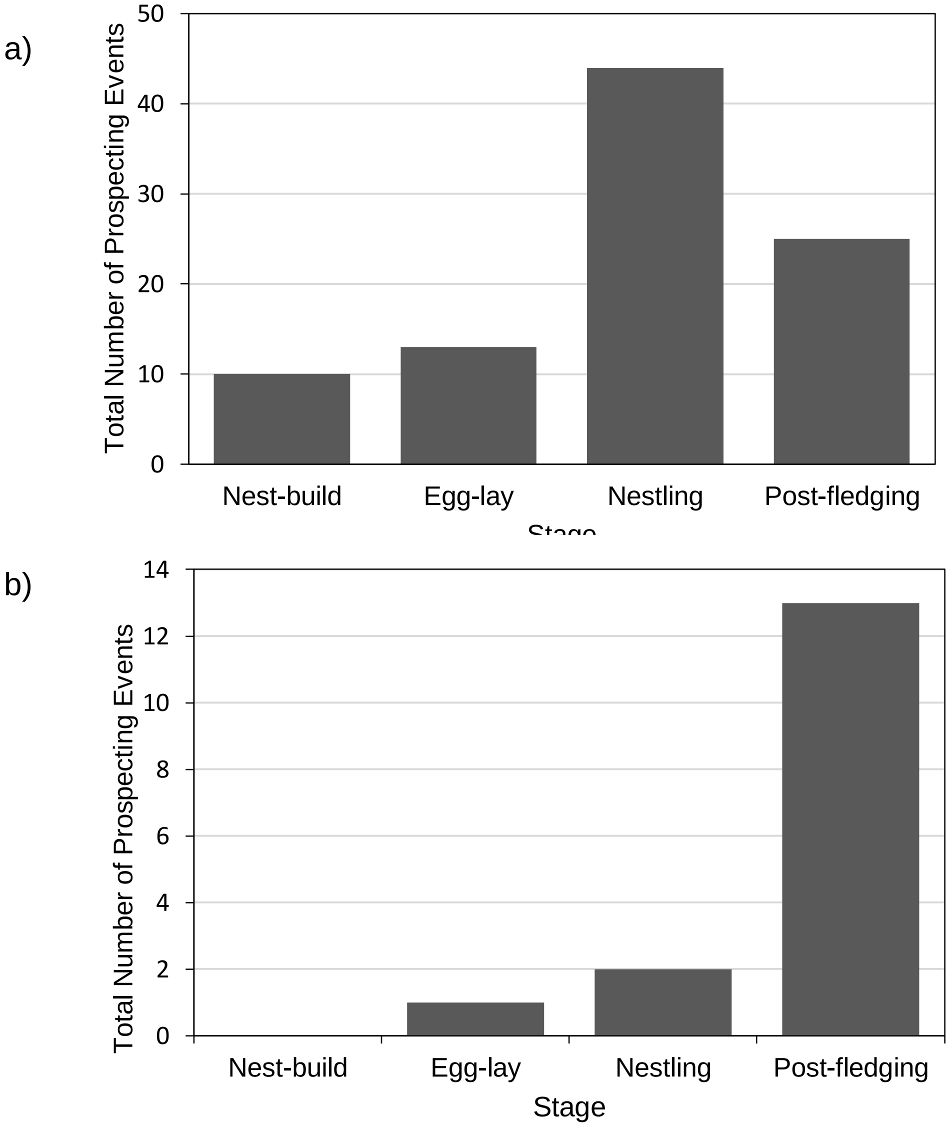

Figure 7. Total prospecting events in each stage of the breeding season. a) For the nest boxes visited by prospectors b) The stage of the clutch of prospecting individuals.

Table 2. Estimated regression parameters, standard errors, *z*-values and *P*-values for the Poisson GLMM for number of prospecting events for each breeding stage. The nest-building phase was the baseline to which the other breeding phases were compared.

	Estimate	Std. error	*z* value	*P*-value
Intercept	1.0347	0.3262	3.172	0.002
Nestling	-0.1377	0.5005	-0.275	0.783
Egg-lay	0.5612	0.3813	1.472	0.141
Post-fledge	0.1453	0.4030	0.360	0.713

Prospecting with a Partner

Are individuals more likely to prospect with their partner?

Individuals were significantly *less* likely to prospect with their partner as compared to prospecting alone (V=16.5, n=15, p=0.020). Of the 92 prospecting events, 15 known individuals with known partners prospected 27 times. Of these events, 0% prospecting events were conducted with a partner in the nest build and egg laying stages, but 19% did occur with a partner in the nestling phase and 33.3% in the post-fledging stage, but these differences were not significant (Fig 9a).

Do individuals prospect for longer if they are with their partner?

The duration of prospecting events was nearly three times longer when conducted with a partner, namely 65.4±16.3 seconds (mean± SE, n=6) compared to 22.7± 5.0 for prospecting events conducted alone (n=21). Prospecting duration was significantly longer if individuals prospected with their partner (model slope estimate +/- SE = 1.3271+/- 0.3899, z=-3.404, P=0.0007; Fig 9b).

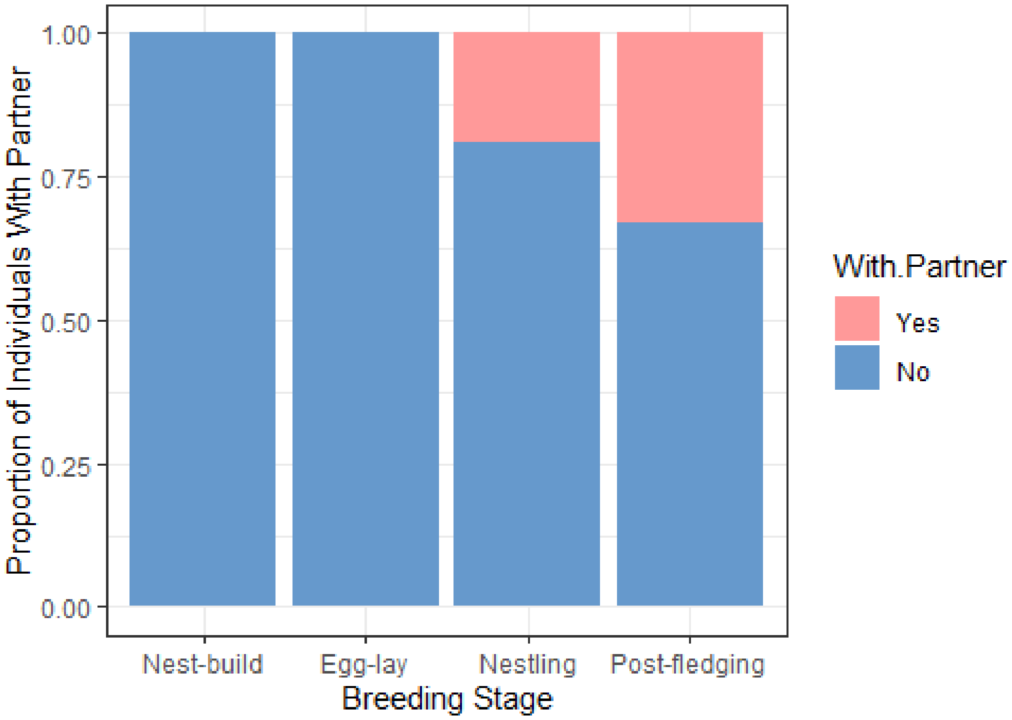

Figure 8a Proportion of known individuals that prospected with their partner in each of the breeding stages**.**

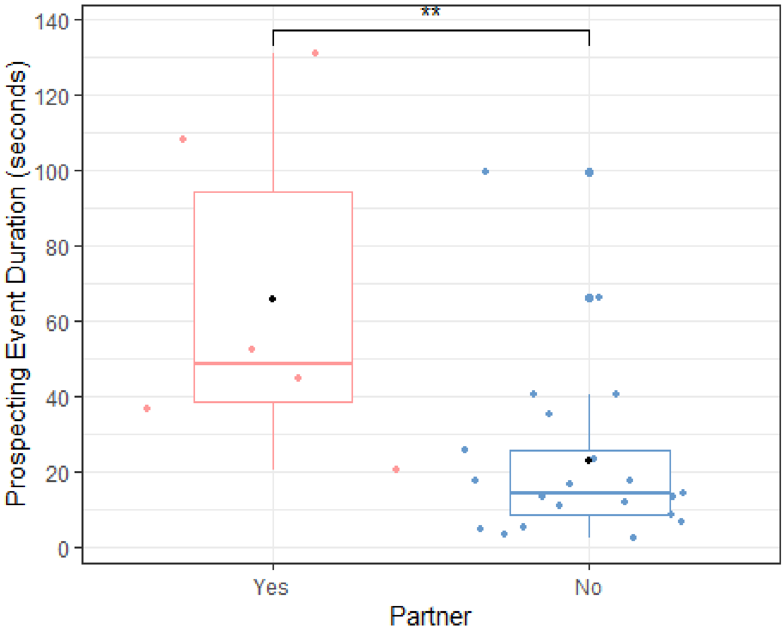

Figure 8b. A comparison of prospecting duration when individuals that prospected were with or without their partner. Mean prospecting duration for each category is labelled on the figure with a circle. Boxplots show the median prospecting event duration with the hinges of the box showing the 25% and 75% quartiles. The whiskers represent the 95% confidence intervals. Asterisks denote statistically significant difference ($p<0.001$).

2.5 Discussion

Prospecting behaviour in wild jackdaws was not more prevalent in the nestling stage of the breeding season, nor did successful breeders wait until their chicks had fledged to gather information on other nest sites. Breeding success (total chicks that fledged the nest) and total fledgling weight did not predict the amount of prospecting visits a nest box received. While pair-bonded individuals were significantly more likely to prospect alone than with their partner, pairs that did gather information together, had prospecting visits of longer duration.

Although much research has been conducted on how information gathering strategies differ across the breeding season and for different species' of wild birds (Fijn et al., 2014; McNamara et al., 2011; Valone, 2007), this is the first study to report that some breeding pairs prospect together. Prospecting events conducted with a partner were significantly longer than those without a partner. As a species that establishes long-term pair bonds, individual jackdaw breeding success may be inextricably linked with their partner's. Losing either the male or female in the partnership can cause nest failure and will likely result in the loss of a nest site (Kubitza et al., 2015; Röell, 1978). Pair-bonds, which are influential for breeding success, may help to mitigate some of the costs associated with prospecting for potential high-quality nesting sites (Kingma, Komdeur, et al., 2016). It has been suggested that social monogamy affords benefits to both individuals. Sentinel behaviour, exhibited in socially monogamous zebra finches (*Taeniopygia guttata*), is used to protect a partner from predators (Mainwaring & Griffith, 2013). Prospecting in pairs may therefore afford individuals greater protection from aggressive conspecifics, allowing individuals to be bolder when gathering information. Males and females may also have preferences for different cues and when able, may gather different types of information. However, the majority of ringed, pair-bonded jackdaws (56%) did not prospect with their mate and prospecting in pairs did not occur in the nest building or egg laying stages. Future studies should assess the relationship between breeding success and the propensity of pairs to prospect together to better assess the value of gathering information in pairs, as well as the division of labour when prospecting so that one is vigilant whilst the other prospects the nest site. Additionally, research should be conducted on the relationship between individual and pair dominance, and how this affects prospecting behaviour.

This study found that prospecting frequency in jackdaws was not significantly greater in the nestling stage, as compared to other breeding stages. This finding contrasts with previous studies, which have suggested a preference for gathering information in the nestling phase due to the quality of information available regarding the site owners' breeding success and habitat quality (Brandl et al., 2019; Piper et al., 2006; Veiga et al., 2012). It could be argued that information available during the nestling stage is more conspicuous and reliable, as prospectors can evaluate the number and size of chicks to better determine whether a nest site is good quality. Therefore, it could be theorized that the process of collecting information is most efficient at this stage, which reduces a prospecting individual's time and energy demands (Boulinier et al., 1996). However, the consistency of prospecting duration across the season may also be attributed to the perpetual time and energy costs associated with gathering information (Kingma, Komdeur, et al., 2016). Consistent prospecting may increase site owners' familiarity with prospectors, helping to reduce aggressive interactions with conspecifics. Extending the duration of prospecting trips provide more information than shorter prospecting trips and allow individuals to make more accurate assessments of nest sites and habitats. Future studies should assess if individuals instead increase the frequency of their prospecting trips to collect the necessary information.

In contrast to previous studies of different species, prospecting jackdaws were not more attracted to nest boxes with higher breeding success (Doligez et al., 2004). This may be because higher reproductive success has been associated with other individual traits that are less attractive to prospectors. Breeding success, for example, has been found to occur in animals with higher dominance (Henderson & Hart, 1995). Prospecting more frequently at these sites may increase aggressive interactions at nest boxes, but also nesting near dominant individuals could increase food stealing behaviour from dominant birds (Goss-Custard et al., 1982). Consequently, prospectors may aim to nest away from dominant individuals. It is worth considering what constitutes a 'higher-quality' nest site in this jackdaw population. The study sites in this system provide little for comparison, nor do the nest boxes. Nest boxes are identical and in similar locations and similar access to food sources. If a prospector had no preference for boxes exhibiting greater breeding success, and other more ‘obvious’ cues aren’t available in this study system, we must consider what an individual might stand to gain from this potentially costly behaviour. It should be noted, though, that the sample size in this study was smaller than anticipated and a more highly-powered study might have picked up more patterns in the prospecting data. Secondly, whilst there are some cases where box ownership changes between breeding seasons and boxes become vacant (e.g. when a box owner dies), jackdaws in our population tend to be site faithful to the same nest box year on year. This lack of potential to gain ownership of a new nest site may have affected the visitation rates of the prospecting individuals.

Whilst there was a trend for successful breeders to visit prospective nest sites most frequently after their own chicks had fledged, prospecting visit frequency did not differ significantly between breeding stages. Unfortunately, I could not assess box owner breeding success for the 2020 breeding season due to the COVID-19 pandemic, nor could I assess the difference in prospecting rates between successful and failed breeders to due insufficient data. It therefore remains unclear whether prospecting individuals had higher breeding success the subsequent year as compared to non-prospectors and if failed breeders prospect more often than successful breeders. In other bird species, prospecting by successfully breeding adult birds is thought to be rarer than that exhibited by juveniles and failed breeders (Martinović et al., 2019). The trend for the prospecting, successful individuals in this study to gather information most frequently after their chicks had fledged, implies that it may be beneficial to commence breeding, and subsequently complete breeding earlier in the season. For a long-lived species like jackdaws, such a decision can be very valuable and may allow for maximal information to be collected from their neighbours for future breeding attempts. Whilst successful, pairs that fledged at least one chick may still have scope for increasing breeding success and increasing the number of fledged chicks in later breeding seasons. Most research to-date has focussed on juveniles or failed breeders and the effects of prospecting on their breeding success (Hogstad, 1999; Aurore Ponchon et al., 2017; Röell, 1978). However, the impact of prospecting on future breeding success of successful breeders is not well documented, and it is here that future research should focus.

It is likely that many more prospecting events occurred throughout the 2019 breeding season. Unfortunately, due to high levels of RFID tag failure in 2019 and the COVID-19 pandemic ceasing data collection in 2020, I was unable to assess prospecting in more depth. Additionally, it is worth noting that only 27.2% of prospecting events were by box owners. Only individuals with complete rings were used in the analyses, yet some of the individuals that could not be accurately identified may also have been box owners, as some box owners did have missing rings. Therefore, the values for known individuals in this study may be an underestimate. As well as this, it should be considered how representative the data is of the study system. Filming only occurred for 2 hours per day. However, prospecting events will likely have occurred at other times of day. The reported rates of individuals prospecting alone and with their partner may have been higher had more filming occurred. Additionally, greater hours of filming may have found higher instances of known individuals prospecting at nest boxes and may have been a more accurate representation of prospecting behaviour in this jackdaw population. In future studies, it would be worthwhile using functional RFID tags (Firth, Verhelst, et al., 2018b), or a similar method, to gain a better understanding of nest site preferences, the characteristics of individual prospectors, and to truly assess how prolific the behaviour of pairs prospecting together is.

In gregarious species such as jackdaws, whose populations support colonial, hierarchical social structures, prospecting behaviour may provide a multitude of benefits to individuals. Whilst gathering information from neighbours can help to increase future breeding success and knowledge on territories, prospecting in semi-colonial groups may also help to increase integration and group cohesion (Jungwirth et al., 2015; Schjørring et al., n.d.). Building and maintaining these relationships could be paramount for cohesion of winter flocks when food is scarce and support important behaviours, such as predator mobbing behaviour (Firth, Cole, et al., 2018; Grabowska-Zhang et al., 2012; Johnson et al., 2017).

Chapter 3: Dominance status, and its impact on prospecting behaviour in wild jackdaws.

3.1 Abstract

Information gathering is an important process which allows animals to assess their environment and adapt their behaviour accordingly to respond to changing environmental conditions. Collecting information allows animals to make informed decisions on suitable habitats, which can directly impact breeding success and an individual's fitness. Increasing breeding success is a key aspect to an animal's life, and time and energy should therefore be attributed to achieving it. Prospecting behaviour, whereby information is gathered about potential future breeding sites, has the benefit of reducing environmental uncertainty, but may also entail trade-offs in the allocation of resources or increase the risk of aggressive encounters. It is therefore likely that resource holding potential, such as that found in dominant individuals is linked to dominance. Individuals with greater dominance would be expected to conduct less prospecting as they have often have higher breeding success and access to better breeding sites. However, the relationship between dominant individuals and prospecting individuals has not previously been assessed. The western jackdaw (*Corvus monedula*) lends itself well to this study as they exhibit dominance hierarchies within their populations and prospect for future breeding sites. Here, I assessed whether prospectors had lower dominance than non-prospectors and if dominant individuals spent less time prospecting. Prospecting individuals did not have lower dominance, nor did dominant individuals spend less time prospecting. However, females spent more time prospecting than males. This study reveals that information gathering is not affected by societal hierarchies. I discuss the broader implications of these findings and how dominance hierarchies and prospecting behaviour contribute to group living.

3.2 Introduction

Living in spatially and temporally variable environmental conditions can create uncertainty for animals (Dall et al., 2005). Investing time and energy into gathering information on habitats, and the animals that live within it, will allow individuals to reduce their uncertainty (Mori & Nakata, 2008; J. Michael Reed et al., 1999). Collecting and processing information is therefore essential in order for animals to make accurate decisions on where is best to live and breed (Block & Brennan, 1992). Whilst certain individuals may inherit, or more easily acquire, better quality breeding sites through their own, or familial, dominance, others may need to invest time and energy into looking for nest sites (Haley et al., 1994; Moore, 1990). Prospecting behaviour, where individuals gather information on potential future breeding sites, allows breeding site quality to be assessed (Szymkowiak, Thomson, & Kuczyński, 2016). Individuals may collect prospecting information through personal information, where information is gathered through direct interactions with their environment, or through public information, whereby an individual can adaptively use information from the interactions of others (Abril-de-Abreu et al., 2015; Nocera et al., 2006). Using public information allows information to be gathered on agonistic interactions between conspecifics (Abril-de-Abreu et al., 2015). For public information to be advantageous, individuals may need to be selective regarding whom they gather information from, as the quality and accuracy of information varies from one individual to another (Laland, 2004).

Gathering information prior to selecting a breeding site, and the benefits of doing so, have been well documented (Pärt & Doligez, 2003; Schuett et al., 2012). Most often, prospecting behaviour has been recorded in failed breeders and juveniles, as these individuals are lacking in the personal experience of successfully breeding (Eadie & Gauthier, 1985). Cormorants (*Phalacrocorax carbo sinensis*), for example, can increase their reproductive success in their first breeding season, if they have prospected at conspecific sites prior to breeding (Schjørring et al., n.d.). In one study on lesser kestrels (*Falco naumanni*), 50% of failed breeders were found to prospect other nests sites in both their own, and other colonies, with prospector visits correlating with colony size (Calabuig et al., 2010). Prospecting to gather social information, therefore, can help individuals make accurate assessments of potential breeding sites, and by doing so, increase future their breeding success.

However, prospecting requires an investment of time and energy to successfully gather the right information from the right locations (Kingma, Bebbington, et al., 2016). Allocating resources to gathering information, therefore, may require a trade-off between the investment that is made to either current or future reproductive success according to the quality of the individual (Kokko, 1999). Dominant individuals, who are often higher quality individuals, will be better able to find and defend high-quality sites and therefore spend less time prospecting, compared to subordinate individuals (Henderson & Hart, 1993) As well as this, travelling to new sites may increase the potential risk of aggressive interactions with unfamiliar individuals and communities (Kingma, Komdeur, et al., 2016). Seychelles warblers (*Acrocephalus sechellensis*), for example, were documented to have 5.2% lower body mass than conspecifics, if they prospected other breeding sites (Hatchwell & Komdeur, 2000). Therefore, due to the lower quality of subordinate individuals, they will more likely need to invest more time and energy into prospecting potential breeding sites.

A characteristic feature of group-living species' is the establishment of dominance hierarchies. Individuals living in these communities may strive to attain more dominant positions as dominance can have great effects on their life-history and social traits (Majolo et al., 2012). Increased dominance is typically associated with greater access to food, mates and breeding territories and can often lead to monopolization of resources and improved breeding success (Hake, 1996; Haley et al., 1994; Lemoine et al., 2020). Northern fur seal copulatory success, for example, is positively correlated with dominance in males with mid to high dominance status (Haley et al., 1994). A study by Henderson and Hart (1995), found male jackdaws who had higher dominance were better able to provision their offspring and raise larger a broods. However, this was contradicted by Verhulst and Salomons (2004), who found that dominant individuals had lower fitness and dominant male jackdaws reared fewer fledglings. Although it should be noted that the nest boxes used in this study were place unnaturally close together, which may have exaggerated 'normal' levels of dominance usually seen in jackdaws. Therefore, it can be argued that dominance hierarchies likely play a significant role in the breeding success of individuals.

The aim of this study was to investigate the relationship between prospecting behaviour and dominance status in the western jackdaw (*Corvus monedula*). Jackdaws are monogamous, pair-bonded birds that mate for life (Röell, 1978). They breed semi-colonially and will readily nest in nest boxes. They sometimes prospect potential breeding sites with their breeding partner, and when they do, they prospect for longer (Cuff, Chapter 2).They often feed in flocks, the size of which is dictated by abundance and availability of food, and they live in fission-fusion societies (Chen, 2020). Dominance in jackdaws has received much research, with several studies examining its impacts on their breeding success, life-history traits and social structure (Henderson & Hart, 1993, 1995; Verhulst et al., 2014; Verhulst & Salomons, 2004). Prospecting in jackdaws, however, has received relatively little attention (Schuett et al., 2012), with no previous studies reporting on the relationship between dominance and prospecting behaviour in not just jackdaws, but all bird species.

Given that higher reproductive success is often found in individuals with higher dominance status I formulate 2 predictions. 1) Prospectors will be less dominant than non-prospectors. 2) More dominant individuals will spend less time prospecting compared to subordinate individuals.

3.3 Methods

3.3.1 Study System

My study was conducted as part of The Cornish Jackdaw Project in West Cornwall, UK. The project has been ringing and researching wild jackdaws since 2013. I conducted my research at 72 nest boxes across two field sites: Site Y (N 50°11’25.98”, W 5°10’49.00”) at Stithians Village and Site Z (N 50°11’ 55.37”, W 5°10’7.48”) at Pencoose Farm. All individuals ringed as part of the project were given a unique colour ring combination to allow for identification, which consisted of 3 colour rings and one metal ring.

Prospecting Video Data Collection

I randomly selected 20 breeding pairs and focussed on their nest boxes for prospecting video data collection. Nine nest boxes were at Pencoose Farm and 11 nest boxes at Stithians Village (Fig 9). I filmed each nest box inside and outside simultaneously, once in the morning and once in the evening. For internal filming of the nest boxes, I fitted CCTV cameras inside the nest boxes prior to nest building commencing. CCTV videos were stored on Digital Video Recorders (DVRs) and powered by battery packs. I controlled the CCTV cameras and the DVRs at ground level, beneath the nest boxes to minimise disturbance. Internal recording of the nest boxes commenced at sunrise (+/- 20 mins) and three hours before sunset (+/- 20 mins). For external filming of the nest boxes, I set-up the camcorder in a nearby hide or in a car, located >10m from the nest box. I erected bird hides at least 12 hours before filming to reduce disturbance to the birds. I standardised the camcorders to film a $2m^2$ area around the nest boxes. Within this $2m^2$, it could reliably be stated that an individual was prospecting at the observed nest box. I began filming with the external cameras after a one-hour habituation period, or when a bird arrived at/near the box, whichever happened first. I externally filmed the nest boxes for one hour. Once this hour was complete, all filming (internally and externally) ceased. If no bird arrived during the habituation period, filming did not occur. Filming times were informed by peak prospecting activity observed in 2018. I, or another trained observer, narrated each filming session, noting the date, time and the activities and individuals seen. Video data were collected from March – July 2019. Data collection ceased when prospecting rates had dropped significantly lower than peak.

Dominance Video Data Collection

Research on dominance interactions was conducted at Site Y and Site Z from April to July 2019. Six dominance tables, measuring 40cm by 25cm, were positioned approximately 5m above the ground. A dominance table is a feeding table with a monopolizable food resource set-up to quantify the outcomes of aggressive interactions and to calculate dominance ranks (Arbon, unpublished data; Mikolasch et al., 2013; Vahl et al., 2005). Each table had a circular food well and GoPro camera housing attached. Video cameras were used without an observer to record interactions to reduce researcher disturbance. I attached wire mesh atop the food well to prevent large quantities of food being taken in one sitting. I used cheese, a high-quality food source to bait the tables. Once baited, I filmed the tables for 1-3 hours in the mornings, usually from 7am. In total, 186 hours of video were recorded.

Prospecting Video Transcription

I transcribed prospecting videos using BORIS software version 7.9.7, recording the activity of box owners and prospectors on and near nest boxes (Friard & Gamba, 2016). I considered a prospecting event to have occurred when an individual arrived at, or near, a box that it did not own and stayed for more than 1 second. I noted the arrival and departure times of prospectors at and near the box. “Near the box” was defined as anywhere within the standardised $2m^2$ area around, but not on, the nest box. I used colour rings to identify each prospecting individual, where possible. If an individual did not have colour rings, or had lost one or more rings, I gave the individual a unique number beginning with U. If an individual left and returned after 10 seconds, within the same recording session, I considered it a separate prospecting event. Randomly selected videos (20%) were also transcribed by one other trained observer who was blind to my predictions. This allowed me to check behavioural scores for observer bias. Inter-rater reliability was >80% accuracy for each behaviour transcribed (Appendix II Table 1).

Dominance Video Transcription

Dominance events transcribed from videos were determined as physical displacements when the focal bird was displaced (leaves the feeding table because of the arrival and/or aggression from an interacting bird) at the feeding table by another bird, resulting in a change of access to the food resource. For each individual, ID, arrival time and leave time were noted. Per interaction, displacement and unsuccessful displacement were noted. Video transcription ceased once all of the cheese had been eaten from the table. See Appendix II Table 2 for a description of the behaviours transcribed.

Ethics

Data were collected with permission from the Exeter University Board of Ethics (eCORN000555 v2.1, eCORN002589 v3.3.) Bird ringing was conducted under BTO licenses. The sex of each individual had previously been confirmed through molecular sexing of blood samples (Griffiths et al., 1998) under a UK Home Office licence (project licence 30/3261).

Figure 9. Nest boxes and dominance tables used for prospecting video and dominance hierarchy data collection at a) Stithians Village and b) Pencoose Farm.

3.3.2 Data Analysis

Video data analysis

Between March and July 2019, each nest box was filmed externally for 50 hours with 25 hours in the morning (6:00-9:00am) and 25 hours in the evening (17:00-20:00pm). Across the 20 nest boxes, this totalled 1000 hours of video material. I watched all internal camera footage, but due to only one individual prospecting visit inside a nest box, I decided not to analyse the data. For each prospecting event, I noted the breeding stage it occurred in (Table 5), and recorded the total duration spent at the nest box (the sum of time spent on the perch, on top of the box, and on the side of the box). When analysing the amount of time individuals spent prospecting, I used the mean duration of prospecting visits for each individual.

Calculating Dominance

When calculating dominance, any individuals with 1 or more rings missing were excluded from data analysis. I used the ELO-rating method to calculate dominance scores which uses the outcomes of agonistic dyadic interactions to infer individual dominance scores (Sánchez-Tójar et al., 2018). Using mean randomized ELO rating (hereafter ELO), with 1000 randomisations, dominance was calculated for each individual. The package *AniDom* was used with the elo_scores function (Sánchez-Tójar et al., 2018).

All analyses were conducted in R version 4.0.4 with the package lme4 (R Core Team, 2021). Plots were made in *ggplot2*. Model reduction was not performed on any of these analyses. All data analysed had a non-normal distribution and the statistical tests were chosen to meet that requirement. To evaluate whether dominance was significantly different between prospectors and non-prospectors, a GLM was fitted with prospector (yes/no) as the response variable and ELO score and sex as the explanatory variables. The model was fitted with a Binomial error distribution, using a logit link. To evaluate the relationship between the time an individual spends prospecting and their dominance score, a GLM was fitted with mean time spent prospecting as the response variable and ELO score and sex as the explanatory variable

3.4 Results

In total, 204 individuals (identifiable by their complete ring set) and 1198 interactions were recorded at dominance tables. Of these 204 individuals, 12 individuals prospected 24 times at nest boxes (mean± SE= 2± 0.44). Additionally, 65 individuals seen at the dominance tables were also nest box owners. In total, 152 (11 prospectors and 141 non-prospectors) of the 204 individuals could be sexed. Both analyses were run with the reduced dataset.

Are prospectors less dominant than non-prospectors?

Among the 11 known-sex individuals seen prospecting, 4 were female and 7 were male. Overall, 7.8% of individuals witnessed at dominance tables were prospectors. Prospector individuals had a dominance score of 98.5± 13.3 (mean ELO± SE) compared to 10.2± 3.6 found in non-prospectors (mean ELO± SE). The GLM analysis revealed no sex differences in the probability that an individual would be seen prospecting at other nest sites (model slope estimate ± SE = -0.610 ± 0.710, z=-0.860, P=0.390). Additionally, there was also no effect of dominance on whether an individual prospected (model slope estimate ± SE = 0.002 ± 0.007, z=0.320, P=0.749; Fig 10). The sample size was too small for meaningful examination of any interaction between sex and dominance.

Does dominance affect the amount of time an individual spends prospecting?

Overall, the mean time (± SE) an individual spent prospecting other nest sites was 54.3±17.7 seconds. Females prospected for 33±5.4 seconds (mean± SE), whereas males prospected for 21.0±3.8 seconds (mean± SE), nearly two-thirds as long as the females. There was a trend for females to spend more time prospecting than males (model slope estimate ± SE = -0.545 ± 0.285, t=-1.912 P=0.0923, Fig 12a)***.*** Dominant individuals did not spend more time prospecting than subordinate indvididuals (model slope estimate ± SE = 0.005 ± 0.003, t=1.460 P=0.1823; Fig 12b).

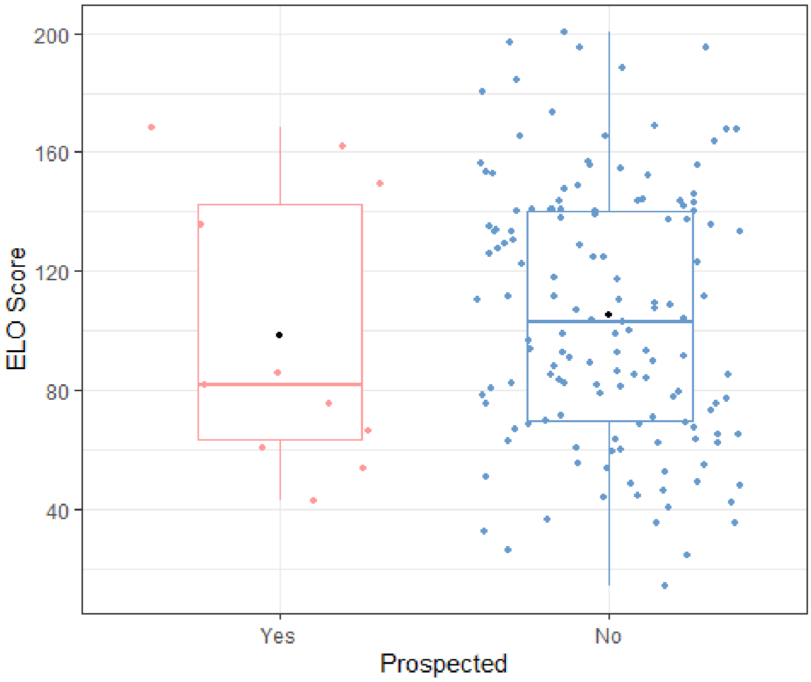

Figure 10. A comparison of dominance (i.e. mean randomized ELO rating) between individuals that were vs. were not prospectors. Mean dominance for each category is labelled with a circle. Boxplots show the median ELO rating with the hinges of the box showing the 25% and 75 quartiles. The whiskers represent the 95% confidence intervals.

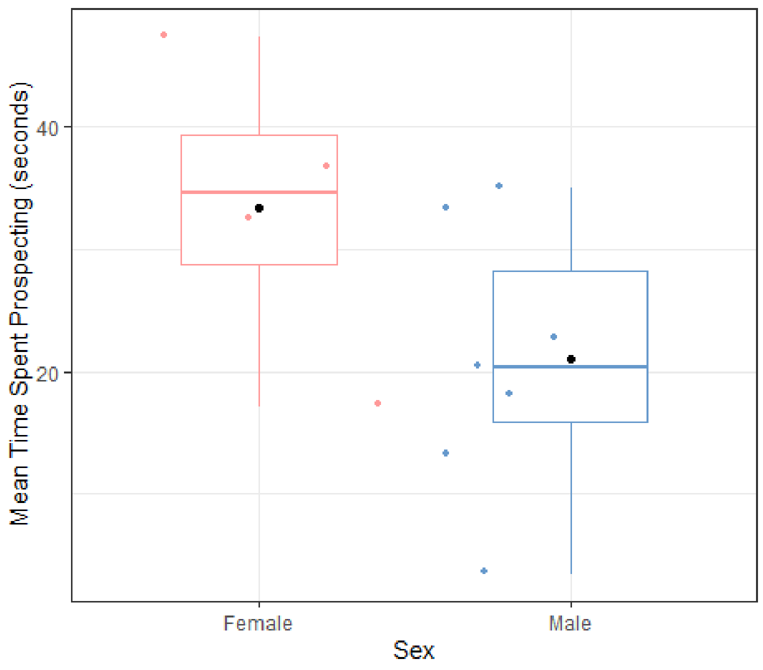

Figure 11a. A comparison of mean time spent prospecting by females and males. Mean time for each category is labelled with a circle. Boxplots show the median time with the hinges of the box showing the 25% and 75 quartiles. The whiskers represent the 95% confidence intervals.

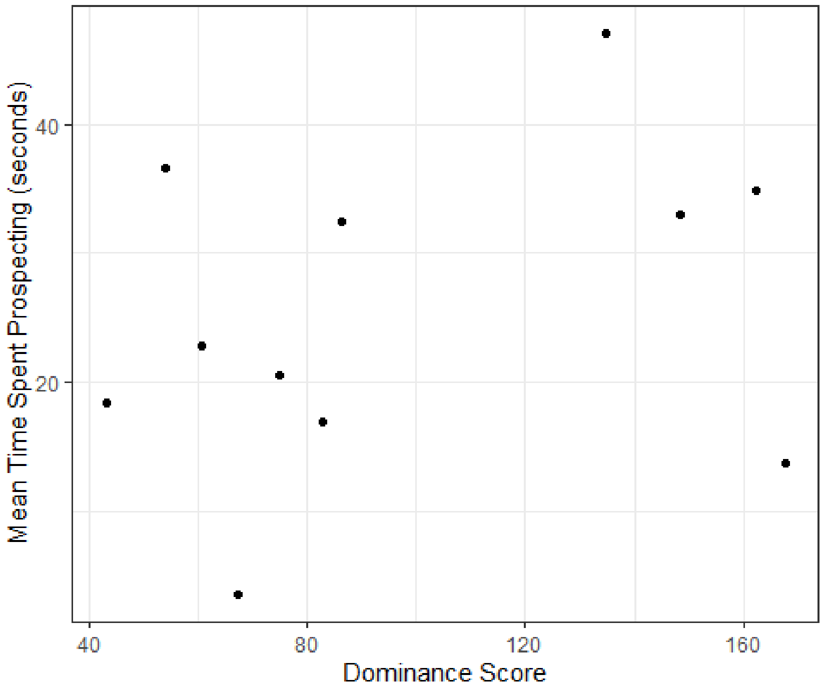

Figure 11b. The relationship between dominance (i.e. mean randomized ELO rating) and the mean time an individual spent prospecting throughout the breeding

3.5 Discussion

This study demonstrates that prospecting behaviour is not affected by the dominance status of an individual. Specifically, dominance score was not significantly different between jackdaws that did and did not prospect, nor was it different for males and females. Additionally, prospecting trip duration did not vary between individuals with higher dominance and those with lower dominance. However, there was a trend for females to prospect for longer than males.

Although there is much historic research on dominance hierarchies in birds (Francis et al., 2018; Pravosudov et al., 1999; Umphress et al., 2007), to my knowledge this study is the first to assess the relationship between prospecting behaviour and dominance status. Previous studies have shown that dominant individuals often secure better quality nest sites and territories (Lambrechts & Dhondt, 1986; Yasukawa, 1979). Possessing a high-quality nesting site may create less need for dominant individuals to use time and energy searching for potentially better alternatives. Yet, this study found no difference in dominance scores between prospectors and non-prospectors. Additionally, dominance scores were not significantly different between males and females. This finding is striking and is contrary to previous research which has found males to be typically dominant over females, and in breeding pairs, for female dominance to be closely linked to that of the male (Röell, 1978; Wechsler, 1988). Wechsler reported that individuals were more likely to win a contest over an individual with higher dominance if their own partner was present. However, it is unlikely that pairs visited the dominance table together due to the low instances of pairs prospecting together (Cuff, Chapter 2). If jackdaws are commonly prospecting alone, then feeding behaviour is likely to follow the same trend, due to both behaviours being affected by other demands an individual needs to meet, such as incubating, provisioning and protecting their nest. An important point to make is the very low sample size of individuals that both prospected a nest box and interacted on a dominance table. Whilst my study only found a small number of individuals to visit both the dominance tables and prospect at other nest boxes, it is likely that many more individuals did. This will have likely limited the power of my analyses. Additionally, the dominance table methodology may have induced more conflict than naturally occurs, potentially disrupting any normal patterns of dominance that would otherwise have been seen. Jackdaws have been shown to exhibit transitive inference, whereby they are able to deduce the dominance of individuals with which they themselves had only observed interacting (Mikolasch et al., 2013). This knowledge on conspecifics could have a great impact on dominance detailed at the dominance tables as many interactions that may otherwise would have happened, in this instance did not because of fear; even more so when dominance was potentially artificially increased. More detailed analysis is required to further assess the role of dominance status in individuals and breeding pairs to truly understand how this effects prospecting behaviour.

The dominance of an individual did not predict the amount of time they spent prospecting potential nest sites. One potential explanation for this finding is that dominance may be less beneficial for jackdaws, and other group-living species, than previously thought. The study sites in this study system It is also important to consider that jackdaws are a long-lived species who establish not only breeding pair bonds, but who also maintain relationships with other members of the community, supporting group cohesion and integration (Jungwirth et al., 2015; Schjørring et al., n.d.).

This study found a trend that suggests females prospect for longer than males. A possible reason for this is the division of labour between the pair-bonded pairs. Females may more closely inspect potential nest sites, whilst males, often the larger of the two, may stand guard and watch for danger or returning nest site owners. Equally, males may more frequently stay near their own nest box to defend it, whilst the female gathers information. This result highlights the parallels between prospecting behaviour, and another behaviour important for reproductive success; nest-building (Hahn et al., 2021). Female jackdaws have been found to spend more time nest-building, and in return, males have increased levels of vigilance (Hahn et al., 2021). This may be because the female is better informed about her own requirements and will be responsible for incubation. Prospecting nests sites around the colony may therefore be multifaceted and provide information above and beyond nest site suitability. Previous research has focused primarily on the dominance of males and its influence on the societal structure of jackdaw groups (Verhulst et al., 2014; Verhulst & Salomons, 2004). However, female interactions and the dominance resulting from thus, may play more of an influential role in the society of semi-colonial species than previously realised (Jonart et al, 2007). However, because this result failed to reach significance, and because of the low sample size, the results must be interpreted with caution. More research should be conducted to further asses the role of dominance on prospecting behaviour and to further investigate what prospectors are doing; the time spent vigilant, time spent inspecting the nest and their risk of being attacked by nest box owners.

In summary, the relationship between prospecting behaviour and dominance status is integral for the establishment and maintenance of jackdaw societies (Henderson & Hart, 1995; R. D. Smith et al., 2001). An individual's understanding of local dominance and reproductive success will often rely on the social information gathered about neighbours and other members of the community (Morand-Ferron et al., 2009). Social information has not only pervasive impacts on how and when interactions take place between different individuals, but it can influence dispersal and the social transmission of culture (Morand-Ferron et al., 2009). Due to my small sample size, my results must remain tentative. We need further research to be conducted to establish whether male and female dominance is more similar than previously thought and how much longer females prospect than male, and what consequences these have on decision making in jackdaws. Therefore, understanding more about the interaction of dominance hierarchies and prospecting behaviour will not only increase our knowledge of decision making at an individual level, but will also help our understanding of dynamics at the group level.

Chapter 4 - General Discussion

4.1. General Discussion

Information is essential for animals living in fluctuating environmental conditions (Dall et al., 2005). Gathering information reduces an individual's uncertainty and may allow more accurate decisions to be made (Valone, 2007). Increasing our understanding of the drivers behind essential life history choices, not least breeding habitat selection, will advance our knowledge on the dispersal of individuals, communities and ultimately the cultural evolution of a species (Danchin et al., 2004). Investing time and energy into gathering information about potential future breeding sites will reward individuals with not only nesting site information, but also mating opportunities and knowledge of the dominance structure of the animals living in that habitat (Moody et al., 2005; Schjørring et al., n.d.; Sherry & Holmes, 1989). Both prospecting behaviour and social dominance can be key in attaining higher breeding success (Henderson & Hart, 1993; Schuett et al., 2012). Yet prospecting behaviour in wild birds has received little attention, with the relationship between prospecting and dominance not having yet been studied. To understand these behaviours in more detail, this thesis investigated prospecting behaviour in wild jackdaws, assessing the effect dominance status has on individual prospecting behaviour. I found that pair-bonded individuals were more likely to prospect alone than with their partner, but when they did prospect together, prospecting events were longer. Prospecting frequency did not differ significantly between each stage of the breeding season and nest boxes with greater breeding success did not receive higher numbers of prospecting visits, however, there was a positive relationship between the amount of times an individual prospected and the total duration of prospecting. When investigating the relationship between prospecting behaviour and dominance status, I found that dominance was not lower in prospecting individuals and the amount of time an individual spent prospecting did not depend on their dominance. However, there was a trend for females to spend more time prospecting than males.

In monogamous species that establish long-term pair-bonds, such as jackdaws, breeding success is often reliant on the participation of both the male and the female (Kubitza et al., 2015). How and when information is gathered will influence the success of breeding pairs. (Brandl et al., 2018; Van Bergen et al., 2004). This thesis found that prospecting events were longer when conducted with a partner. Not only may it afford individuals greater protection from aggressive interactions with conspecifics (Mainwaring & Griffith, 2013), but prospecting in pairs may also provide males and females the opportunity to act more boldly and preferentially focus on different cues. For instance, Hahn et al (2021) found that when jackdaws are nest-building, females invested more time in nest construction and males invested more time in standing vigilant outside of the nest. Such a division of labour that is often associated with bi-parental care, may be linked to, and influence, the cue preferences of males and females in not only jackdaws, but other pair-bonded species too.

Yet, contrary to this, this thesis also found that individuals were more likely to prospect alone than with their partner. One possible explanation for this finding is that the ability for both the male and female to leave their nest simultaneously relies on the experience of the pair and pair-bond strength. For many species who exhibit long-term partnerships, pair-bond strength develops over time, increasing with age and experience, and positively effects breeding success (Firth, Cole, et al., 2018). A study by Royer and Anderson (2014) on captive Caribbean flamingos found that pair-bond strength was associated with the dominance of the pair. Pairs with greater dominance and higher pair-bond strength may be fitter (Royer & Anderson, 2014), allowing them to leave their nest unattended for longer and commit more time to other essential behaviours. Gathering information together may additionally allow for joint decision making to occur on where the pair will breed. Alternatively, increased pair-bond strength may facilitate not only the male and female leaving simultaneously, but also allow them to travel alone to other locations. For instance, when we consider monogamous species, like jackdaws, who share the cost of raising offspring, a fair division of labour ought would help to reduce the sexual conflict between the male and the female (Griffith, 2019; Mariette & Griffith, 2015). A study on socially monogamous long-tailed tits (*Aegithalus cordatus*), for example, demonstrated that parents alternated the provisioning of food to their offspring (Bebbington & Hatchwell, 2016). By alternating their foraging trips, they were better able to synchronously provide food for their chicks. Nests whose parents alternated provisioning also received less predation, likely as a result of the synchronised feeding reducing the noise at the nest, which would draw less attention to predators. Such benefits of foraging trips may be paralleled in prospecting behaviour when partners prospect singularly, leaving their mate to watch over the nest. If correct, this scenario would potentially maximise the amount of information that could be collected whilst helping to reduce the energy expended in prospecting behaviour, thus addressing a trade-off faced by many animals. However, it remains unknown whether the ability for both male and female jackdaws to leave the nest simultaneously to prospect other nest sites is reflective of pair-bond strength or dominance. To truly understand why only some breeding pairs prospect together, future studies on wild birds should assess the characteristics of pair-bonded individuals that prospect together, and the benefits of doing so. Do these pairs have higher breeding success, and is this behaviour influenced by their dominance or pair-bond strength?

When prospecting, it is often thought that individuals use reliable cues at a time when gathering information will provide the greatest increase to their fitness in accordance with the ‘optimal timing hypothesis’ (McNamara et al., 2011). However, contrary to previous research, which found that prospectors used cues like brood size and begging calls as the focus of their prospecting trips, both of which are only available during the nestling stage (Brandl et al., 2019; Schuett et al., 2017), I found that jackdaws were not more likely to gather information in the nestling stage of the breeding season. To understand why jackdaws use time and energy visiting other nest boxes when information regarding breeding success is not at its most reliable, we must consider the social dynamics of jackdaw colonies and how important good relationships are, for not just pair-bonded individuals, but between many other individuals within a colony. Research by von Bayern et al (2007), suggests that jackdaw social bonds are established in the post-fledging months. Creating and maintaining strong relationships within a colony can be helpful in social species who rely on one another for flock cohesion and predator avoidance (Woods et al., 2018). It has been found that jackdaws are able to discriminate between alarm calls made from a member of their colony and a bird outside of their colony as they have unique calls. By visiting other breeding sites regularly, birds can keep up-to-date on the unique characteristics of colony members, including the recognition of colony members' calls which may positively affect colony responses to danger and alarm calls (Woods et al., 2018). Additionally, a study by Braun and Bugnyar (2012) showed that ravens (*Corvus corax*), a close relative of the jackdaw, use social bonds to access resources, with nonbreeding ravens involved in affiliative relationships having more success when competing with conspecifics for food. As well as this, a long-term study on nonbreeding captive rooks (*Corvus frugilegus*) found that nonbreeders not only form social bonds, but use the social knowledge acquired about their colony to inform their social decision-making and are aware of not only their own relationships, but those of conspecifics in the colony. Therefore, the ability to uphold stable relationships beyond pair-bonds is not only important for increasing breeding success, but is also integral for maintaining good relationships and the transmission of information in group-living birds. Understanding more about the information collected when visiting other nest boxes, will help not only in our understanding of prospecting behaviour and the information gathered when deciding on a good breeding site, but it can also support social bonds essential for group cohesion in colonial-living species.

There was, however, a trend for birds who had successfully bred, to visit other nest sites once their own chicks had fledged. Whilst this might be explained by the increased capacity of parents whose chicks had fledged to conduct prospecting forays to other nest sites, it may also represent the complex social dynamics at play in group-living species (Brandl et al., 2021). Creating and maintaining relationships outside of the pair-bond may help contribute to successful group living, which could increase group coordination year-round. Group cohesion can facilitate not only improved social foraging and protection from predators, but can also improve synchronized reproduction (Brandl et al., 2021). A study on wild zebra finches showed that birds with greater group cohesion and great synchronization in their reproduction have stronger social ties both during breeding and post-breeding (Brandl et al., 2021). The benefits of greater accuracy in breeding synchrony may be multifaceted. This suggests that prospecting trips conducted by jackdaws at a time when information about nesting sites is not at its most reliable, may instead be as a way to reinforce social bonds and help to gather information on the breeding synchrony of the colony. Further research into the effects of breeding synchrony on group cohesion in jackdaws would help to understand why jackdaws prospect year-round, including in the post-fledging stage of the breeding season.

Achieving greater dominance is often associated with increasing an individual’s access to, and monopolization of, key resources such as breeding sites. Monopolizing resources may allow individuals to spend less time prospecting for breeding sites and allocate more time on other essential behaviours, such as foraging and nest defence (Clutton-Brock et al., 1984; Haley et al., 1994; Majolo et al., 2012). However, I found no difference in the dominance status between prospectors and non-prospectors, nor was there a difference in dominance status between males and females. This apparent equality in levels of dominance contradicts previous research (Röell, 1978; Wechsler, 1988) which suggests that female dominance relies on that of her partner, and that females typically have lower dominance than males. However, females jackdaws in this study appear to spend more time prospecting nest sites than males, which may be representative of the division of labour required to maximise breeding success (Henson & Cooper, 1992; H. G. Smith et al., 1988). In order to collect the information they need when prospecting, having dominance similar to that of their pair-bonded male may allow females a better opportunity to gather information and travel around the colony alone, without being dominated by opposing males. To truly understand the effect dominance status has on prospecting behaviour in jackdaws, research should further investigate what information is being gathered when dominant individuals prospect other breeding sites, and if their movements are correlated with group cohesion as well as gathering information on breeding sites. Further research should study the benefits of dominance hierarchies in jackdaw societies, and to what extent it increases breeding success, above and beyond that of prospecting behaviour.

When thinking about the patterns of prospecting behaviour seen, and how representative this is of jackdaw populations, it is important to consider the study system itself. Jackdaws are long-lived birds whose societies are built around the establishment of not only strong pair-bonds, but also dominance hierarchies. Individuals within a colony may come into contact with one another frequently, especially since nest locations are fairly close together and foraging is often performed collectively and is non-territorial. The study sites within the study system are very similar; sites Y and Z are both in similar locations, have similar habitats and similar proximities to food sources. At both sites, due to the location of nest boxes being on trees and buildings, it is possible for prospectors to watch many of the boxes and assess the provisioning rate and potential breeding success of the pair without visiting the box. This may have impacted the amount of prospecting behaviour that was detected, with prospecting events in jackdaw societies potentially being much higher. In other bird species, nest site quality has been found to be influential in the decision-making process on where to breed. Orange-crowned warblers, for example, respond to the presence of predators in potential habitats. When a predator in seen whilst prospecting, warblers will switch their nest site preference and begin looking for other viable nest site options with reduced proximity to danger (Taper et al., 1995) Investigating what constitutes a ‘high-quality’ nest site and why prospecting behaviour occurs, is therefore important in increasing our understanding of the evolution of jackdaw communities. In other Beyond this, we can investigate what other benefits might be afforded those who visit other nest sites and members of the colony outside of the breeding pair. Creating and maintaining relationships outside of the pair-bond may help contribute to successful group living and help to increase group coordination year-round. Group cohesion can facilitate not only improved social foraging and protection from predators, but can also improve synchronized reproduction (Brandl et al., 2021).

4.2. Conclusion

In conclusion, this thesis shows that prospecting behaviour in wild jackdaws may be an important component of pair-bonded pair behaviour, effecting how long they gather information for, as well as showing that females are likely to commit more time to prospecting than males. Additionally, jackdaws don’t preferentially gather information in the nestling stage, but instead gather information throughout the whole breeding season, even whilst in some cases, still rearing chicks. It is unclear the effect prospecting has on future breeding success, and if there is a trade-off between provisioning chicks whilst simultaneously allocating energy to prospect potential breeding sites. When investigating the relationship between social dominance and prospecting behaviour, I found that prospecting behaviour was not influenced by the dominance of an individual. Additionally, the amount of time an individual allocated to prospecting behaviour was not influenced by their dominance but may be influenced by their sex. Future studies should consider the effect pair bonds have on the dominance and prospecting behaviour of jackdaws, and further what impact these have on breeding success. Pair bonds, which are a key component of jackdaw societal structure, are thought to influence dominance and may also determine the need for an individual or a pair to prospect. To truly understand prospecting behaviour in wild birds, we must consider the types of information being collected, and the division of labour between breeding pairs. This will not only increase our knowledge on how individuals make habitat decisions, but it will also help our understanding of group-level dynamics and how this contributes to the dispersal of a species.

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Appendix I.

Appendix 1 Table 1. Breeding success and 2019 nest box location of nest box owners randomly chosen for video data collection.

Box Owners		2018 Breeding Success (g)	2019 Location
F	M		
J1315	J515	195.6	Y05
J2403	J2965	167.4	Y07
J250	J290	268.2	Y09
J510	J516	226.3	Y11
J1903	J469	195.6	Y12
J2409	J2402	229.6	Y21
J1915	J1507	189.7	Y22
J505	J1480	237.4	Y23
J1318	J494	205.4	Y24
J1317	J1602	259.3	Y34
J793	1352	192.7	Y35
J2951	2966	237.5	Z05
J41	J323	196.5	Z06
J2375	J837	229.3	Z13
J243	J145	240.8	Z14
J164	J831	209.1	Z15
J1375	J1898	257.1	Z22
J692	J899	231.5	Z27
J1916	J1903	197.2	Z32
J995	J1376	200.5	Z38

Appendix I Table 2. Ethogram of behaviours transcribed from video data.

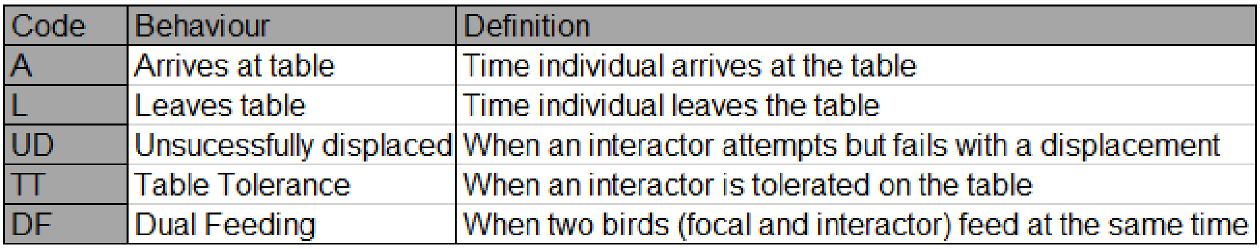
Behaviour code	Behaviour type	Description	Modifiers
In Frame	State event	In frame	In frame, On perch, On roof, On side
PEEK	State event	(Out) Subject looks outside of the nest box for more than 1s; (In) Subject looks inside the nest box for more than 1s	In, Out
IN	State event	Start IN when bird enters box, and stop IN when bird leaves box	N/A
ATTACK	State event	Subject attacking another individual	Flying at, Touching Intentionally
OTHER	State event	Unlisted behaviour, describe this as a comment	N/A

Appendix II

Appendix II Table 1. Behaviours transcribed from prospecting video data.

Behaviour code	**Behaviour type**	**Description**	**Modifiers**
In Frame	State event	In frame	In frame, On perch, On roof, On side
PEEK	State event	(Out) Subject looks outside of the nest box for more than 1s; (In) Subject looks inside the nest box for more than 1s	In, Out
IN	State event	Start IN when bird enters box, and stop IN when bird leaves box	N/A
ATTACK	State event	Subject attacking another individual	Flying at, Touching Intentionally
OTHER	State event	Unlisted behaviour, describe this as a comment	N/A

Appendix II Table 2. Behaviours transcribed from dominance table videos.



Code	Behaviour	Definition
A	Arrives at table	Time individual arrives at the table
L	Leaves table	Time individual leaves the table
UD	Unsucessfully displaced	When an interactor attempts but fails with a displacement
TT	Table Tolerance	When an interactor is tolerated on the table
DF	Dual Feeding	When two birds (focal and interactor) feed at the same time

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