Prospecting in wild jackdaws (Coloeus monedula) : effect of breeding success, parental activity and timing

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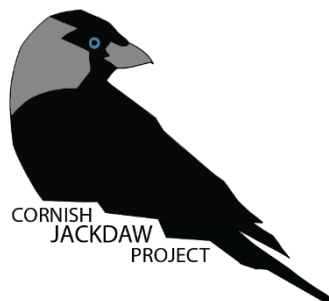
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Abstract (EN)

Gathering information on potential breeding sites, a behaviour known as prospecting, can allow animals to select a breeding habitat of high quality and enhance their breeding success. Prospecting is particularly common in birds, where it can take the form of visits of a conspecific's nest. Despite extensive research on prospecting in birds, there are still uncertainties regarding how breeding success, parental investment, and timing affect both the individual investment in prospecting and the attractiveness of a nest to prospectors. In order to investigate those questions, we conducted a large-scale study on western jackdaws (*Coloeus monedula*) using radio-frequency identification (RFID) technology. I found that prospecting increases over the course of the chick-rearing stage, reaches a peak after the fledgling of the chicks and subsequently decreases over time. Nestboxes where the breeding attempt failed received less prospecting visits during both periods (provisioning and post-fledgling stages). During the provisioning phase, nestboxes with a higher parental activity received more prospecting visits. Accounting for this effect, the number of fledglings did not influence the number of prospecting visits received by the nest. Finally, failed breeders prospected more than successful individuals and no trade-off was observed between parental activity and investment in prospecting (i.e. birds than invested more in parental care did not invest less in prospecting). Those results support the idea that the breeding failure of an individual induces an increased investment in prospecting. Furthermore, they show that parental activity is an important cue for prospectors. Moreover, the finding that jackdaws can discriminate between failed and successful nests even during the post-fledgling stage raises questions about the mechanisms at play (cues in the nest or memory). Overall, this thesis showed that breeding success influences prospecting in jackdaws in multiple ways and highlighted the importance of including the post-fledgling stage when studying prospecting.

Résumé (FR)

Récolter des informations sur des sites de reproduction potentiels, un comportement connu sous le nom de prospection, peut permettre aux animaux de sélectionner in site de reproduction de haute qualité et ainsi d'augmenter leur succès reproducteur. La prospection est particulièrement rependue parmi les oiseaux, où elle peut se manifester par la visite de nids de conspécifiques. Malgré de nombreuses études sur la prospection chez les oiseaux, des incertitudes persistent concernant l'effet du succès reproducteur, de l'activité parentale et de la phénologie à la fois sur le comportement prospectif individuel et sur l'attractivité d'un nid pour les prospecteurs. Pour répondre à ces questions, nous avons mené une étude à large échelle sur les Choucas des tours (*Coloeus monedula*) à l'aide d'équipement de radio-identification (RFID). J'ai trouvé que la prospection augmente en fréquence au cours de la période de nourrissage des poussins, atteint un pic après leur envol puis diminue rapidement, et que la prospection est plus fréquente après l'envol des poussins. Les nichoirs dans lesquels la nichée a échouée reçoivent moins de visites prospectives pendant les deux périodes (pré- et post-envol des poussins). Le nombre de visites prospectives reçues par le nid augmente avec l'activité parentale tant que les poussins sont au nid. En tenant compte de cet effet, le nombre de poussins n'influence pas le nombre de visites prospectives reçues par les nichoirs. Enfin, les individus dont la couvée a échouée ont plus prospecté et aucun effet de l'activité parental n'a été observé sur l'investissement en prospection au niveau individuel. Ces résultats soutiennent l'idée que l'échec de la nichée poussent les oiseaux à augmenter leur investissement dans la prospection. Ils montrent également que l'activité parentale est un signal important pour les prospecteurs. De plus, la

découverte que les choucas peuvent discriminer les nids où la couvée a échouée de ceux où la couvée a réussie même après l'envol des poussins soulève des questions intéressantes concernant les mécanismes en jeu. Dans l'ensemble, ce travail de fin d'étude a montré que le succès reproducteur a un effet sur la prospection chez le choucas à plusieurs niveaux et met en évidence l'importance d'inclure la période après l'envol des poussins dans les études sur la prospection.

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1. State of the art

Animals regularly face decisions that will impact their fitness[1,2]. For example, they must choose their habitat, when to migrate, with whom to mate, where to forage or what to eat. To make the decisions that will maximise their fitness, individuals may need to assess the different options available and the outcomes of each option[3]. However, animals are often faced with uncertainties about the different outcomes[1,3]. Acquiring information allows them to reduce those uncertainties and to increase their fitness through better decision-making[3,4]. Studying how individuals gather and use information is thus essential to understand animal behaviour[5].

There are two ways to acquire information: by personal interaction with the environment (personal information) or by monitoring the interaction of other individuals with the environment (social information)[5–7]. This second type of information can be given voluntarily through traits evolved specifically to this effect, and is then referred to as "signals", or involuntarily, and is then known as inadvertent social information[1,5,8]. Social information can allow individuals to avoid the costs of personal trial-and-error[9,10] but varies in accessibility and reliability compared to privately gathered information[1,10]. Indeed, individuals to copy are not always present and social information can become outdated in a changing environment, leading to maladaptive cultural transmission and error-copying[11,12]. The importance attributed to social and personal information thus depends on the context and on the cost of information gathering[11,13,14]. For example, Webster & Laland (2008)[10] showed that minnows (*Phoxinus phoxinus*) rely on social information only when gathering personal information is costly. However, most of the research in this domain focused on foraging contexts[13] and there is still much to explore regarding the way cost and circumstances affect information gathering in other contexts than foraging-related decisions.

A decision with particularly far-reaching fitness consequences for individuals is selecting a breeding habitat[7,15]. In order to settle in the optimal habitat possible, organisms may need to assess the quality of the different options, which implies gathering information on the different breeding sites[7,16,17]. The behaviour consisting of gathering such information has been defined by Reed et al (1999)[18] as "prospecting". Prospecting is known among several taxa, including mammals[19–21] and fish[22,23], but is most common in birds[18]. This behaviour is central to habitat selection and dispersal decisions,[24,25] has an impact on species expansion[26] and has important fitness implications[27–29]. Indeed, the information gathered through prospecting can allow individuals to select a higher quality breeding site compared to individuals making a less-informed choice[28], which eventually leads to more active prospectors having an increased breeding success during the following breeding season[27,28]. Studying prospecting behaviour is especially relevant in the context of human-induced rapid environmental change, since information gathering behaviour allows animals to keep track of changes in their environment[30,31].

Previous studies on prospecting revealed substantial variation in this behaviour among bird species. Prospecting can happen at different time periods and aim at gathering different information, both personal and social[18]. Many species prospect mostly before the breeding season, in order to choose their breeding habitat for the coming season (e.g. [32–34]). For example, this is the case of the snowy owl (*Bubo scandiacus*), which undertakes exploratory movements in order to find a breeding territory with a suitable density of prey[32,35]. Some species are also known to collect social information, such as conspecific density during pre-breeding prospecting[36–38]. Prospecting can also happen during or after the breeding season, in order to gather information for next year breeding habitat selection[28,39–41]. This

allows birds to gather information from the reproductive success of other individuals[17,28,40–42]. The success of other individuals gives valuable information about the quality of resource[5,43]. This type of information is often referred to as public information[1,5,43,44], although other definitions exist for this term[3,7,8]. Public information (*sensu* Danchin et al., 2004[5]) is a form of social information that can lead to a quicker and more accurate estimate of environmental parameters compared to personal information[5,13]. The reliability of public information is likely to depend on the timing, and to be higher at the end of the chick-rearing season, when the breeding success of others becomes observable[41]. The idea that prospecting towards the end of the chick-rearing seasons allows birds to gather more valuable information is referred as the "optimal-timing hypothesis"[45,46]. Studying the timing of prospecting can thus give us valuable insights on the type of information collected by prospectors.

The optimal-timing hypothesis has first been proposed for the black-legged kittiwake (*Rissa tridactyla*) by Bolinier et al. (1996)[41], and this study found strong empirical support for this hypothesis, with prospecting peaking at the end of the chick rearing stage. Boulinier & Danchin (1997)[17] then created a theoretical model which showed that birds should use public information for habitat selection if two assumptions are met :

1) the environment is patchy, i.e. there is spatial variation in the quality of breeding habitat

2) the environment is predictable, i.e. there is a temporal autocorrelation between years in the quality of a breeding habitat patch

Subsequent theoretical models support the idea that at least some level of public information should be used if the two assumptions are met[44,47] and the use of public information for dispersal decisions has since then been empirically observed in many bird species. Both correlative (e.g.[48–50]) and manipulative[42,51,52] studies have shown that birds immigrate more into patches where the breeding success in the previous year was higher, independently of natal philopatry. It has been established for the black-legged kittiwake that individuals will change breeding patch for next year if two conditions are met simultaneously: their personal breeding attempt failed and the overall breeding success of their patch was low[53,54]. A high breeding success of conspecifics in a habitat patch will override personal information and trigger failed breeders to remain faithful to their nest site. Studies that found no effect of previous breeding success of the patch on habitat selection were performed in environments where at least one of the two assumptions is not met[55,56], except in the case of Serrano et al. (2004)[57]. However, this study on lesser kestrels (*Falco naumanni*) has been contradicted by several articles finding evidence of public information use in this colonial species[42,58–60]. While it thus appears that when the two assumptions are met, birds use public information for habitat selection, the timing of the collection of this information remains poorly studied. Boulinier et al. (1996)[41] is to my knowledge the only study that tested the optimal-timing hypothesis in a satisfying manner, and it studied only non-breeding prospectors. Other studies looked at this hypothesis[45,46,61], but they all stopped the data collection before the post-fledgling stage, which did not allow to test whether prospecting decreases after the fledgling of the chicks, as found by Boulinier et al. (1996)[41]. There is thus a strong need to test the optimal-timing hypothesis in other species and to investigate its applicability for prospecting in active breeders, as they might be constrained by parental care during the late chick-rearing season[46].

While most work on the use of social information for habitat selection has focused on the habitat-patch scale, the nest-site scale has also been subject to some interest[62,63]. For instance, Hoi et al. (2012)[64] showed that if a nest of lesser grey shrikes (*Lanius minor*) produced no fledglings due to

predation, it was avoided in the subsequent year, not only by the previous owners but by all breeders. A series of experiments on tits (*Parus spp.*) and flycatchers (*Ficedula spp.*) used geometric symbols placed on nestboxes to experimentally test habitat copying at the nestbox scale (e.g. [65–67]). Pied and collared flycatchers (*Ficedula hypoleuca* and *Ficedula albicollis*) are migratory birds arriving late in their breeding habitat, compared to the resident great tits (*Parus major*)[65]. This means that they lack time to gather personal information for habitat selection and that social information, even heterospecific social information gathered from great tits, is highly valuable[68,69]. When researchers create an apparent preference of tits for nestboxes displaying a specific geometric symbol, flycatchers have been shown to copy this preference by at least six studies[65–68,70,71]. This copying behaviour is affected by several factors, including breeding date[70], the availability of conspecific cues[66] and cognitive abilities, behavioural traits and age of the copier[65]. Interestingly, flycatchers are more likely to copy tits with higher clutch size[65,67,68,71], which represents another example of nest-scale public information use. Conspecific copying has also been observed for symbol preference in both great tits[66,72] and flycatchers[66].

Exploratory visits at conspecifics' nests or territory can aim at gathering other information than information on habitat or nest site quality. For example, dispersing individuals could prospect to increase their familiarity with the area. Knowledge of the physical and social environment confers a number of advantages, including better foraging ability, reduced predation risk and decreased number of conflicts with conspecifics (reviewed in Piper, 2011)[73]. Increasing familiarity with the future breeding site has thus been proposed as one of the goal of intrusion in conspecifics' territory for the Oystercatchers (*Haematopus ostralegus*)[74]. Prospecting can also include information gathering on the social landscape, in order to be able to fill potential vacancies. A study performed by Kelser & Haig (2007)[75] on the cooperatively breeding Pohnpei Micronesian kingfisher (*Todiramphus cinnamominus reichenbachii*) found that dominant birds visited other territories mostly during nest initiation while juveniles and helpers prospected all year-round and made repeated prospecting visits at the dispersal destination before dispersal. They thus proposed that dominant individuals aimed at extra-pair copulation rather than actual prospection while helpers are prospecting to keep track of potential vacancies and reproduction opportunities. However, alternative hypothesis on the information gathered have received very little interest compared to information gathering on habitat quality and still need to be explored.

Beyond the use of the information gathered, prospecting behaviour itself can be studied, by investigating the factors influencing individual investment in prospecting and prospecting decisions. Knowing what characteristics make a nest more or less attractive for prospectors and studying how individual traits, such as age or personal breeding success, affect prospecting behaviour can give crucial indications on the types of information gathered by prospectors[63]. For instance, several studies have linked the amount of prospecting visits a nest received during the breeding season to different components of the breeding success of the nest (e.g. [27,63,76]). Nests with a higher breeding success being prospected more often is thought to be a clear sign that prospectors are gathering public information[39,76]. Prospecting rate at a nest has been shown to be positively correlated to clutch size for the pied flycatcher[63] and to begging calls in the zebra finch (*Taeniopygia guttata*)[77]. Studies on the effect of nestling number on the attractiveness of a nest to prospectors obtained varying results. Calabuig et al. (2010)[60] found no relation between the number of nestlings and the prospecting rate at the nest scale for the lesser kestrel, while Parejo et al. (2008)[78] found a significant effect for the spotless starling (*Sturnus unicolor*). Two studies on the collared flycatcher[39,76] observed that feeding rate, a

measure correlated to breeding success, was a better explanatory variable than the number of nestlings. This highlights that breeding success can be assessed by different means and that it is not always easy to determine which cues are used by birds when selecting a target for a prospecting visit. While the number of nestlings is a more accurate estimate of breeding success, this cue cannot be assessed from the outside of the nest for cavity nesting birds, and it is thus logical that other cues, such as feeding rate or begging calls, would have a greater effect on the attractiveness of a nest for prospectors[76]. However, feeding rate as a cue for prospector suffers from the same inconsistencies in the results as the number of nestlings, since a study on pied flycatchers[63] obtained the opposite result than Pärt & Doligez (2003)[76] and Doligez et al (2004)[39], i.e. no effect of feeding rate on prospecting rate. Calabuig et al. (2010)[60]'s study on lesser kestrels found that nests with an intermediate feeding rate were the most attractive to prospectors. This can be explained by the fact that prospectors are often violently evicted from the visited nest[57,60,68] and that nests with a high feeding rate are also the best defended nests[60]. There is thus a trade-off between the quality of the prospected nest and the risks for the prospector[60]. For another proxy of reproductive success, nestling condition, the effect on prospecting is also unclear: Schuett et al. (2017)[63]'s study on pied flycatcher observed a correlation between prospecting rate and nestlings condition, but Doligez et al. (2004)[39] found no such significant relation for the collared flycatcher. Overall, the impacts of breeding success and parental activity on prospecting behaviour are still not clearly understood and further studies on those subjects are needed.

Concerning the individual traits of the prospector itself, it is expected that younger birds prospect more[18]. Indeed, older individuals have more experience and personal information to base their choice on, while young birds possess information only on their natal site and would thus need to explore more[18]. A higher investment in prospecting of young birds compared to older ones has been empirically reported for great tits[29], black-browed albatrosses (*Thalassarche melanophris*)[46], domestic sparrows (*Passer domesticus*)[34] and Sandhill cranes (*Antigone canadensis*)[79]. Sex is also known to influence prospecting in several species (e.g. [39,78,80]) but not all species[46]. Kralj et al. (2023)[45] studied prospecting in fourteen seabirds species and found that females prospected more in six species, but the effect was significant for only one of those species due to a relatively small sample size. The authors propose that this difference between sexes might be due to a difference in cost : females of the studied species are usually lighter than males and flying to prospect might thus be less costly in energy for them[45]. Breeding success is also important to consider when studying individual variation in prospecting behaviour. Indeed, failed breeders are more likely to disperse [69,81–83] and would thus be more prone to gathering information on alternative breeding sites[18]. More intense prospecting has been recorded for failed breeders in Audouin's gulls (*Ichthyaetus audouinii*)[84], lesser kestrels[42], Common terns (*Sterna hirundo*)[61], black-legged kittiwakes[81,85] and yellow-headed blackbirds (*Xanthocephalus xanthocephalus*)[48]. However, prospecting is not restricted to young individuals and failed breeders, as active breeders also undertake prospecting[63,84]. A study performed by Schuett et al. (2012)[86] on Eurasian jackdaws (*Coloeus monedula*, hereafter "jackdaws") observed a negative correlation between the graded breeding success (number of fledglings) and the prospecting activity of individuals. Males that fledged fewer chicks prospected significantly more, and the same pattern was observed in females, although not significant, probably due to low sample size. However, the study used a correlative approach which does not allow to disentangle the cause and the consequence. Considering that the authors also found that individual jackdaws are consistent in their investment in prospecting between years[86], they propose that prospecting behaviour might not be completely plastic and might

be influenced by personality. The correlation between breeding success and prospecting could then be due to a trade-off between prospecting and parental activities rather than to an increased interest in prospecting of birds with few fledglings. This hypothesis remains however untested and more evidences are needed to determine whether failures causes an increase in prospecting or whether a high investment in prospecting can increase the probability of failure.

Such a trade-off can be expected since prospecting is time and energy consuming[31], and that the amount of effort spent prospecting is not spent raising off-spring[87]. Moreover, owners often defend their nest or territory against intruding prospectors, which means that prospecting can end up in risky and costly fights[60,68,88]. The trade-off between prospecting and energy consumption has been empirically observed by Kingma et al. (2016)[88] in a study which showed that prospecting Seychelles warblers (*Acrocephalus sechellensis*) have a lower body condition than non-prospectors. The future benefits of this information gathering behaviour might thus be counterbalanced by more short-term fitness costs[86], and the investment in prospecting by individuals is likely to depend on the costs of this behaviour[44]. A recent study on barn owls (*Tyto alba*) showed that females tend to prospect more when the feeding rate of their partner is high[89]. The most likely explanation for this relation is that males with a high provisioning rate allow their female to invest less time in parental activities and more in prospecting[89], which showcases the trade-off between those two activities. However, the cost of prospecting remains very poorly studied, despite being essential to our understanding of the investment decisions of individuals and how they can affect fitness.

Overall, there are still uncertainties regarding how breeding success and parental activities affect both the individual prospecting behaviour and the attractiveness of a nest to prospectors. Traditional methods used to investigate prospecting behaviour include direct observation of colour-banded individuals, radio-telemetry and GPS tracking[31]. However, the two firsts methods limit the observation time and the sample size as they require observers on the field to collect data, while the GPS tracking is not precise enough to collect data on nests-visits within a colony[31,90]. Radio-frequency identification (RFID) technology allows to collect large sample of data regarding prospecting at conspecifics' nests and can help elucidating those questions on prospecting[31,91,92]. To investigate how timing, parental investment and breeding success affect prospecting, we conducted a large-scale study on jackdaws' prospecting behaviour using automated RFID loggers and the populations monitored by the *Cornish Jackdaw Project*.

Jackdaws are the ideal species to conduct such a study on, from both a practical and scientific interest point of view. As a member of the corvid family, they are capable of complex and advanced cognitive skills, which makes them a species of particular interest for behavioural study[93]. Moreover, jackdaws are colonial breeders and prospect at conspecific boxes at a relatively high frequency[86,94]. They have been shown to use social information in various contexts[95–98] and can thus be expected to do so when prospecting. On top of being of high interest, jackdaws are also particularly suitable for this kind of study because they are secondary-cavity nesters[86,94]. This means that they will easily settle in standard nestboxes, which allows close monitoring and some level of control of the effect of the cavity. Jackdaws undertake visits of conspecifics' nestboxes during the entire breeding season, including the post-fledgling phase[86,99–101]. Liebers & Peter (1998)[99] suggested that failed breeders differ in their visits pattern depending on the time of the breeding failure, with pairs losing their brood later in the season focussing on few nestboxes and being more aggressive. However, they provide no statistical evidence and this claim is hard to test due to the relatively small sample size of failed breeders and to the

qualitative analysis of behaviour it would require. In addition to Schuett et al (2012)'s[86] study presented above, two previous Master's theses written with the Cornish Jackdaws Project already investigated the effects of individual characteristics on prospecting behaviour using only the data from the first year of the experiment[100,101]. They found that age had no effect on the prospecting rate if the entire season is considered, but that young jackdaws prospected more in the early breeding season (incubation and early provisioning). Similarly, sex had no effect except during incubation, during which females were limited in their prospecting capacity. Intriguingly, they showed that prospecting is also very frequent after the nestlings have fledged, which contradicts with the optimal-timing hypothesis[41]. This could be due to the fact that the nests are less defended at this stage of the season, which makes prospecting less costly, and it is thus interesting to investigate the effect of parental activity at the nest and timing across the breeding season on prospecting. In addition, the questions raised by to Schuett et al (2012)'s[86] study on the causality of the relation between breeding success and investment prospecting are still open.

Using RFID data collected over two years on three jackdaw colonies, this report will investigate the three following questions:

1) How does parental activity and breeding success interact with the individual investment in prospecting?

In this part of the study, I will try to replicate Schuett et al. (2012)[86]'s finding that individuals with a lower breeding success prospect more with a larger sample size and investigate the causal relationship of this correlation. If individuals that prospect more due to personality see their breeding success diminished due to a trade-off between prospecting and parental investment, a negative correlation between prospecting a parental activity should be observed. In contrast, if the absence of such an observable trade-off between prospecting and parental activity would suggest that individuals with a lower breeding success plastically adapted their prospecting level as a reaction to low breeding success. It is of course impossible to definitely settle a causality relationship without an experimental study, but I hope to bring new evidence supporting either of those two hypothesis.

2) Do prospectors use parental activity or breeding success as cues to decide at which nests they prospect?

If jackdaws are gathering public information, nests with a higher breeding success should receive more prospecting visits[76]. I expect that parental activity will be the more significant explanatory variable since it can be assessed from outside the nestbox, in contrast to the breeding success, and that a positive correlation will be observed. However, nests with a higher parental activity are better defended[60] and a negative correlation is also possible.

3) How does the frequency of prospecting change across the breeding season?

Discovering exactly when the jackdaws are prospecting most actively might help us shed light on the type of information they are looking for. I expect that prospecting will be most frequent at the very end of the chick-rearing stage, as predicted by the optimal-timing hypothesis[41]. I then expect prospecting to slightly decrease compared to the peak, but stay at a relatively high level, since the previous Master's thesis written whiting the project revealed that prospecting is frequent in the post-fledgling stage[100,101].

2. Methods

2.1. Ethical statement

The research conducted in this study received approval from the University of Exeter research ethics committee (512510). The study followed the guidelines of the Association for the Study of Animal Behaviour (ASAB/ABS) for the ethical use of animals in research and the bird ringing process was carried out by trained and licensed ringers from the British Trust for Ornithology. Additionally, blood samples for molecular sexing were collected by experienced individuals under a project licence (P882CF514) issued by the U.K. Home Office.

2.2. Study species

The western jackdaw is a cavity-nesting, semicolonial, omnivorous and monogamous bird[94,102]. Its distribution range extends across Europe, North-Africa and Western-Asia. As secondary cavity-nesters, jackdaws do not excavate their own nests and use pre-existing natural or anthropogenic cavities. Nesting cavities are a limited resource for secondary cavity nesting birds[103,104] and are thus the object of fierce intraspecific competition amongst jackdaws[94]. Breeding pairs defend their nest site aggressively and exhibit strong territorial behaviour, although their territory is limited to the nest site itself[94]. The quality of the nest site secured by a breeding pair has an effect on their breeding output[94,105,106]. The literature identify the following nest site characteristics as having an effect on breeding success : size of the entrance hole[106], nest site density[94], distance to foraging ground[107] and possibilities for the nestlings to go out of the nest[105]. Cavities with a smaller entrance hole are easier to defend[105] and suffer less from predation on the nestlings[106]. The density of nest sites can affect breeding success negatively or positively, due to intraspecific competition and group defence[94]. The distance to foraging ground is also important for the success of the nesting, with nest father away having a lower breeding success[107]. Finally, some types of cavities can present specific risks. For instance, nestlings born in open attics often get lost in the attic and die without being able to find their nest back[105]. In this context, gaining information about the quality of a cavity before committing to its defence can have important fitness implications, especially given the high nest site fidelity exhibited by jackdaw pairs[94].

Jackdaws form long lasting monogamous pairs, with a very low divorce rate, particularly amongst mature individuals[94,102]. Both parents are required to raise the chicks, and the death or departure of the mother or the father will lead to the death of the whole clutch[94]. In England, jackdaws usually initiate clutches in April and lay between one and seven eggs, with a mean clutch size of 4.3 eggs[108–111]. The incubation is performed by the female. During that period, which lasts for an average of 18.5 days, she does not leave the nest to forage and is fed by the male [102,108]. Incubation starts before the completion of the clutch, in order to achieve hatching assynchrony[108,111,112]. Hatching asynchrony reduces parental investment by causing younger chicks that will die anyway due to limited resources to starve early due to competition from older siblings[111,112]. This allows the parents to focus their time and energy on feeding a manageable number of chicks that they can support as they grow older[112]. The male continues to feed the female during the first five days after hatching, and the female redistribute the food to the chicks[102,113]. Following this initial period, both parents are required to feed the clutch and start active provisioning[113].

The fledgling success of jackdaws depends mostly on chick mortality, with clutch size and hatching rate playing only a marginal role[113]. Chick mortality is caused primarily by starvation and predation[106,107,109,112,114]. The relative importance of those two causes varies from site to site[106,109,112,114], ranging from 80% of deaths caused by starvation[112] to 74% of nest failures due to predation[109]. A recent study by Aastrup et al. (2023)[114] showed that most starvation happened before day 12 after hatching while most of the predation took place after this date. The predation has been reported to be due to goshawks (*Accipiter gentilis*)[114], common ravens (*Corvus corax*)[106], Iberian green woodpeckers (*Picus sharpie*, referred to as *Picus viridis* at the time)[106] and pine marten (*Martes martes*)[109]. Overall, the discrepancies in the relative importance of predation and starvation between sites suggest that chick mortality, and thus breeding success, depends heavily on the types and abundance of predators and on food availability. However, starvation remains one of the most detrimental factors to jackdaws' breeding success and any activity requiring to spent time otherwise than by feeding chicks, such as prospecting, has a potentially high fitness cost.

Raising offspring is an energy-demanding task and parental investment has an effect on breeding success[113,115]. The investment in energy required to breed successfully is visible through body mass change, as both parents lose weight during the breeding season[113]. The cost of parenting seems to be higher for males than females, since their respective average weight loss over the course of the breeding season are of 10% and 5.6% respectively[115]. The parental investment in energy is divided into approximately 5% of nest defence and 95% of provisioning[113]. Henderson et al (1993)[113] showed that the male's feeding rate is positively correlated to the number of fledglings and the chicks' growth. Considering that starvation events usually happen in the early provisioning season[113,114] and that the male is in charge of most of the provisioning at that stage[102,113], it is not surprising that they found no similar correlation for the female provision rate. The fact that male jackdaws rarely attain the full potential breeding output of their nest due to their limiting feeding rate may explain why this species is monogamous[113]. Males would be unable to provision several nests and monogamy is thus the optimal strategy.

While the limiting effect of provisioning rate on breeding output may drive jackdaws to form monogamous pairs, it does not stop individuals from trying to increase their fitness *via* extra-pair mating or intraspecific brood parasitism, and both of those behaviour have been reported[116,117]. There are thus several reasons other than information gathering that can drive jackdaws to enter conspecifics' nests, especially in the early season. Extra-pair mating in particular has been the object of multiple studies on jackdaws[99,116–118], and seems to always be forced by the intruding male[117]. Four genetic studies were performed on different jackdaw colonies in order to assess the frequency of extra-pair offspring. Gill et al. (2020)[117] and Henderson et al. (2000)[118] found no evidence of extra-pair offspring, but Turjman et al (2021)[116] and Liebers & Peter (1998)[99] found a relatively high frequency of extra-pair paternity (respectively one nest out of thirteen and one nest out of fifteen), suggesting that this phenomenon is relatively widespread despite strong rejection of extra-pair mating by the females and their supposed control of cloacal contact during forced-copulation[117]. Indeed, male jackdaws lack a functional intromittent organ and it is thought that females can avoid insemination[117], so that it remains unclear if the extra-pair offspring are conceived through the forced copulation or through, so far unreported, mutually accepted extra-pair copulation. Another case in which jackdaws may deviate from strict monogamy is the follower behaviour[99]. Unpaired jackdaws have been occasionally observed to join an established pair and show strong affiliative behaviour with the two owners of the nest ([99],

personal observation). These additional individuals, known as "followers", are tolerated by the parents and visits the nest at a very high frequency, in addition to exhibiting affiliative behaviour like allopreening with the breeding pair[99]. It is not clear whether they participate in feeding the chicks, but they have been observed to help with parental activities such as removing the faecal sacs[99]. It is currently unknown whether followers are usually males, females or equally likely in both sexes[99]. Liebers & Peter (1998)[99] suggest that followers might be "replacement in waiting" that are hoping to take the place of the current partner, either by ejecting it or by waiting for its death. Jackdaws may thus be constrained to an apparent strict monogamy by the limiting feeding rate, but can deviate from this pattern if this allows them to increase their fitness, which can lead to non-prospecting visits in conspecifics' nests.

2.3. Cornish Jackdaw Project

The complex behaviour of jackdaws, coupled with their secondary-cavity nesters nature and high nest site fidelity, makes them a perfect study species to investigate cognition and behaviour of wild birds. Such is the goal of the *Cornish Jackdaw Project*, one of the largest research groups studying wild jackdaws, as a part of which this study was carried out. This project, running since 2012, has installed standard nestboxes and monitors closely the jackdaws using them every breeding season. All of the 85 nestboxes currently established by the project are constructed with the same standard model and dimensions. More than 3000 individuals, including all the individuals breeding in nestboxes, have been equipped with a unique colour ring combination consisting of three plastic rings and a metal ring. One of those plastic rings contains a passive integrated transponder (PIT) tag that can be read by a logger (see *2.5.1 RFID Data collection*).

At the beginning of every breeding season, the owners of all nestboxes are identified thanks to their colour ring combination. The unmarked owners and owners with a missing or broken ring are trapped and ringed throughout the season, either using a trap-door, night-trapping or a ladder-trap. The trap-door is a remote-controlled door placed on the entrance of the nestbox. The trapper sits in a hide in view of the nestbox and closes the door when the targeted bird enters the nest. Night-trapping consists in blocking the entrance of the nestbox during the night using a pole equipped with a large sponge, and subsequently extracting the trapped individual from the nestbox. The ladder-trap is cage containing food, with small entrance holes at the top, making it easy for the jackdaws to enter but not to leave (Figure 1). This last trapping method also allows to catch birds that do not nest in a nestbox and to monitor the population more broadly. When an individual is caught and ringed, it is weighed and three measures of skeletal size are taken: tarsus length, bill length and total head length. Additionally, the length of the wing is measured, and a blood sample is taken. The blood sample is used to sex the bird according to Griffith et al (1996)[119]'s method.

During the breeding season, the nestboxes are monitored employing the following protocol: every nest is checked every day until all the eggs are laid, using an endoscope attached to a pole. The progress of nestbuilding and the number of eggs are recorded. All the eggs are considered laid if three days have passed without any new eggs or if seven days have passed after the first egg was laid. The nest is then not checked for eight days in order to avoid disturbing the female during incubation. After those eight days, the nest is checked again every day using the endoscope until the first hatch. The chicks are then counted and weighted on day one, two, three, four, eight, fourteen and twenty after first hatch. The chicks are marked with non-toxic marker pen to make individuals distinguishable. On day twenty-six

after first hatch, the chicks are ringed according to the protocol described above for adults. Starting four days after the ringing, the nestbox is checked daily again using an endoscope in order to record the date of fledgling. The chicks are not weighed after the ringing, to avoid provoking early fledgling.

Figure 1 Ladder trap, used to trap and ring jackdaws. Stithians, June 2023.

2.3.1. Study sites

The 85 nestboxes established as part of the *Cornish Jackdaw Project* are spread across three sites: 14 are located at the "C*ampus*" site, 33 at the "*Stithians*" site and 38 at the "*Pencoose*" site (Figure 3). *Campus (50°10'24.0"N 5°07'16.3"W)* is located in a small wood on the Penryn campus of the University of Exeter and is the smallest of the three sites, with an area of 7,500 m². *Stithians* (50°11'22.4"N 5°10'52.9"W) is situated in the village of Stithians and spreads across a churchyard and adjacent fields, covering an area of 40,000 m². Finally, *Pencoose (5*0°11'56.2"N 5°10'11.4"W) is located on the Pencoose farm, including the farm itself and some of its surrounding fields, and is of similar size compared to *Stihians* (45,000 m²). *Campus* exhibits the lowest average breeding success of the three sites (Figure 2), which is explained by its urban location and greater distance to foraging ground[107]. *Stithians* offers close foraging grounds in the form of fields, and possesses a high historic breeding success. However, jackdaws' breeding in *Pencoose* show an even higher breeding success, most likely due to the abondance of available food in the farm itself. Jackdaws notably feed on the anthropogenic food destined to the livestock.
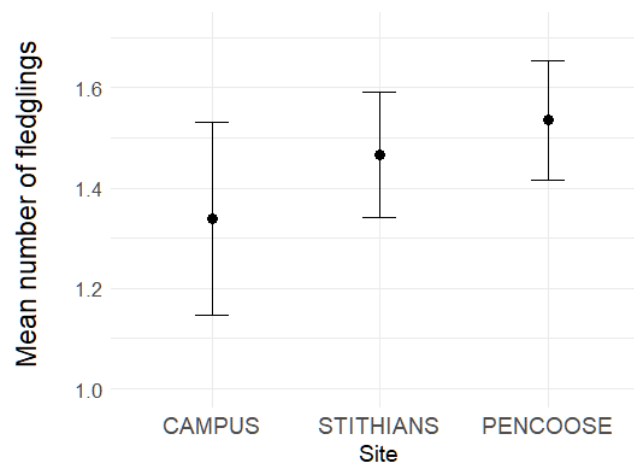
Figure 2 Mean number of fledglings produced per nestbox per year, for every study site, from 2013 to 2023 included. Confidence interval : 95%.
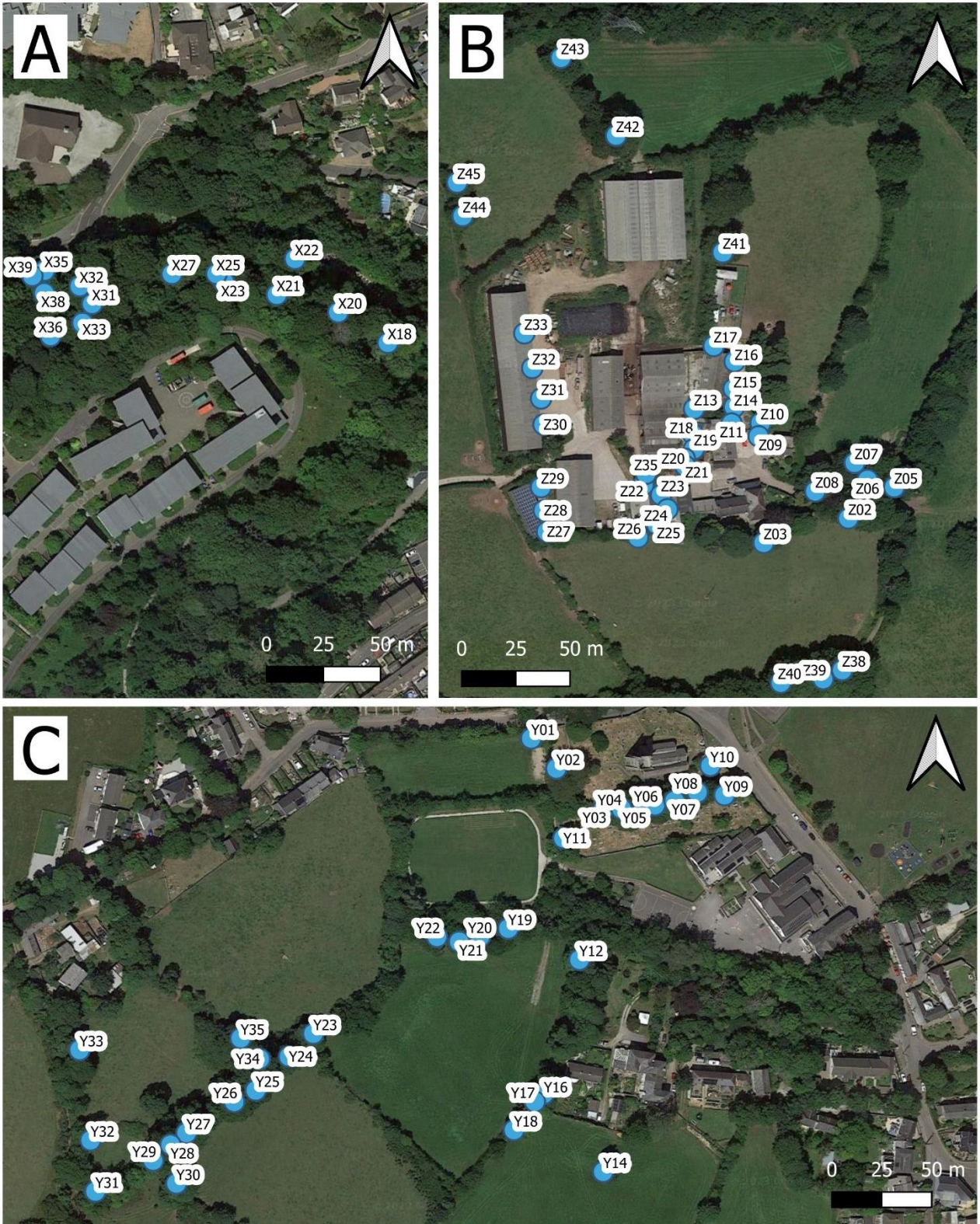
Figure 3 Maps of the three study sites : Campus *(A),* Pencoose *(B) and* Stithians *(C). The blue dots indicate the location of the nestboxes*

2.4. Data collection

2.4.1. RFID Data

Automated RFID loggers designed to read the PIT-tag contained in jackdaws' rings were fitted on the front of nestboxes (Figure 4). Those loggers are equipped with two coils able to energized the PIT-tag: one on a perch in front of the entrance and the other on the entrance hole. Once energized, the PIT-tag will transmit a unique tag ID to the logger[91]. The ID will then be stored by the logger on an external SD card, along with the time and place of the read (perch or entrance hole). In order to avoid draining the batteries powering each logger too quickly, each coil is activated only when a bird is detected. The perches contain a scale and trigger the coil when a weight similar to the one of a jackdaw is detected. The entrance hole is equipped with two infrared light beams with a matching sensor. The entrance hole's coil triggers when at least one of those light beams is broken. The batteries of each logger were changed based on a three-day rotation. The data was taken out of the SD card during the battery change and the scale of the perch was systematically recalibrated.
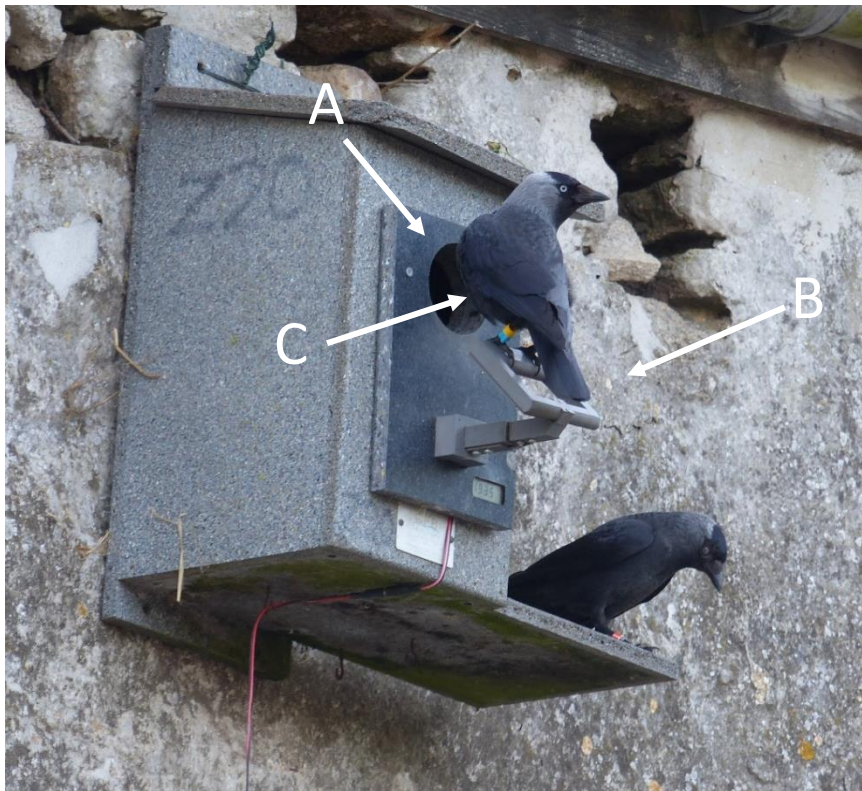
Figure 4 Nestbox equipped with an automated RFID logger. A : RFID logger, B : perch containing a coil and C : entrance hole containing a coil. Since a ringed bird is currently using the perch, its PIT-tag's ID is being recorded by the RFID logger, along with the time of the event and the reading coil (perch in this case). Pencoose, June 2023

A total of 61 boxes were equipped with a logger in 2023 (9 on *Campus*, 23 at *Stithians* and 29 at *Pencoose*) and 49 boxes in 2022 (22 at *Stithians* and 27 at *Pencoose*). The RFID data was collected for several studies rather than just for this thesis, some of which required to equip specific nestboxes with loggers. The placement of the loggers was thus not randomized. The time the loggers were left on each nestbox varied due to technical issues, and ranged between 7 and 101 days with a mean of 71.3 ± 21.9 (mean ± SD) days of data collection per nestbox. The data collection spanned from the 28th of March 2022 to the 30rd of June 2022 and from the 25th of March 2023 to the 4th of July 2023.

2.4.2. Validation

Due to the fast and unpredictable nature of birds, the RFID loggers were sometimes unable to detect a visit to a nestbox. To test the reliability of the loggers, we recorded 20 hours of videos of nestboxes equipped with loggers from outside and compared them with the RFID data. When coding the videos, we defined three types of events: "perch" when a jackdaw lands on the perch of the logger, "in" when a jackdaw enters the nestbox and "out" when a jackdaw exits the nestbox. Occurrences of jackdaws landing on the perch and peeking inside the nestbox without fully entering it were coded as "perch" for the purpose of this analysis, since the PIT-tag could not be detected by the entrance hole. This allowed to separately test the reliability of the two coils of the loggers (the perch and the entrance hole). We recorded every occurrence of those events and paired them with a Boolean variable that was set as true if the logger detected the bird correctly and false if no PIT-tag was detected by the logger.

2.5. Data analysis

The raw RFID data consists of a list of events during which a PIT-tag was read by a logger. However, a bird visiting a nestbox will usually generate several reading events. For example, a typical visit consists in landing on the perch, going in the box through the entrance hole's coil, going out of the box and landing on the perch again. Each of those steps will generate a different reading event. Moreover, if a bird sits on the perch or in the entrance hole for more than a few seconds, the PIT-tag will be read several times. In order to avoid data inflation, the reading events were thus converted in visits. A visit was defined as a group of RFID reads with the same ID, separated from the next visit by at least five minutes. A visit was assigned as a prospecting visit if the visitor was not an owner of the nestbox and as a parental visit if it was. The visits from the chicks at their own nestboxes, which happened during fledgling, were removed from the analysis. One nestbox was owned by a trio (a pair with a follower) and the visits of the follower at that nestbox were not counted as prospecting visits or parental visits.

The visits were assigned to a breeding stage, based on the nest of the visiting bird for the analysis of individual prospecting and based on the visited nestbox for the analysis of nestbox attractiveness. Five breeding stages were defined: pre-lay, incubation, provisioning, post-fledgling and failure. The pre-lay period spans from the beginning of the data collection to the laying of the first egg. The incubation period spans from the laying of the first egg to the first hatching. The provisioning period spans from the first hatching to the date of last fledgling. Finally, the post-fledgling period spans from the date of the last fledgling to the end of the data collection season. For nestboxes where the breeding season failed, a failure period was assigned from the date of failure to the end of the data collection. The date of failure was determined differently depending on the cause of the failure. If none of the eggs hatched, the date of failure was set to 22 days after laying, since eggs should have hatched by the 21st day[108]. If all the chicks died, the date of failure was set as the date the last chick was found dead or missing in the nest. For two nestboxes, the failure date was decided on the case by case. One of the nestboxes fell from the tree during the incubation period and its failure date was thus set on the date of the falling. Another box saw the female die during incubation, and the failure date was assigned as the date of death of the female.

The visits happening during the pre-lay and incubation periods were excluded from this analysis, because the reasons that may drive an individual to enter a conspecific's nestbox other than

prospecting are too numerous at this stage of the breeding season to consider those visits as prospecting visits with enough certainty. For example, those early visits could aim at forced copulation[117], intraspecific brood parasitism[116] or stealing nest material (Luca Hahn (2021)[110] : unpublished data) and our data does not allow us to disentangle the different type of visits.

The data was subsequently grouped in order to get the total number of prospecting and parental visits undertaken by every bird or received by every nestbox for the period of interest, according to the research question. A **prospecting rate** and **parental activity** were calculated by dividing the total number of prospecting and parental visits respectively by the number of hours of effective data collection, to account for the difference in study period length and observation effort. The rate was then multiplied by 24 to obtain the number of visits per day. Note that for simplicity, the number of visits from a box owner to their own nestbox per day will be referred to as parental activity during both the provisioning and post-fledgling phase, even if visits of nestbox owners during the post-fledgling phase do not aim at parental care (as they are no nestlings in the nest).

As a mean to avoid variability induced by the changing activity of jackdaw with daytime, only the days were 95% of the 24 hours (22.8 hours) were covered by a functional logger were used to calculate the number of visits received by the nestboxes and the parental activity of individual birds. The threshold of 95% was used instead of keeping only the days for which the full 24 hours were covered because the battery change and data downloading required to disconnect the board for at least 5 minutes every 3 days. The procedure of discarding the days with 22.8 or more hours of data collection was not applied when calculating the prospecting rate of individual birds, since this variable doesn't depend on a specific logger. The number of prospecting visits recorded for individual birds were thus divided by the number of hours in the studied period to get the prospecting rate, instead of dividing in by a duration for which a specific logger was functional. Finally, to ensure the reliability of the measure of prospecting rate and parental activity, only the individuals or nestboxes with at least 50% of the study period covered by a functional logger were considered in the different analysis.

2.6. Statistical analysis

All the analysis were run using R 4.1.2[120]. I analysed the data with linear mixed models (LMM) using the lme4 package[121] and with generalized linear mixed models (GLMM) using the *glmmTMB* package[122]. For every model, the respect of the assumptions were checked using the *DHARMa* package[123] and the variance inflation factor (VIF) was calculated using the *car* package[124] to verify the absence of multicollinearity. When a significant interaction was encountered, the model was divided by factor according to the interaction. In addition to the outlier test proposed by the *DHARMa* package[123], the distribution of the data was manually inspected for every models using scatterplots, and potential outliers are discussed in the *Results* section.

2.6.1. Validation videos

The reliability of the two antennas of the RFID loggers (entrance hole and perch) was estimated by calculating a percentage of the events that were correctly recorded. In addition, the number of visits was calculated following the method as described above (a visit is a group of events of the same bird at the same box separated by less than 5 minutes) using first all the events observed on the video and in a second time only the events recorded by the loggers. The results obtained with the two datasets were then compared.

2.6.2. Effect of breeding success and parental activity on individual prospecting

To investigate the effect of breeding success and the potential trade-off between prospecting and parental activity, two LMMs were fitted: one for the breeding phase and one for the post-fledgling phase. The response variable was the prospecting rate of the individual for the whole study phase and was log-transformed to ensure the normality of the residuals. The fixed factors used were the parental activity, the number of fledglings successfully raised by the bird, the site and the year and the random factors were the ID of the bird and the breeding attempt (shared by the male and the female). The site and year, although not the focus of this analysis, were added as fixed factors instead of random factors because of the low number of levels of those factors (two and three). The age and sex were not added into the model since the two previous Master's thesis written within the *Cornish Jackdaw Project* showed that those two variable had no effect for the studied period[100,101]. The two breeding phases (provisioning and post-fledgling) were separated into two models because the parental activity should not be interpreted the same way for both periods. During the provisioning, parental activity is very high and almost entirely explained by the feeding rate[118], while the parents have by definition no chicks to feed inside the nestbox during the post-fledgling phase, and visit their nestbox for other reasons (*e.g.* nest defence or nest cleaning). The number of fledglings was used as a factor for both breeding periods since it is the most direct measure of breeding success and because its effect on prospecting has been shown in previous studies[86]. Only the prospectors (birds that prospected at least once during the breeding phase) were considered in this analysis to avoid zero-inflation, and only the successful birds were considered to avoid the strong confound effect between failure and parental activity. Indeed, birds with no chicks do not need to provision and come less frequently at their nest, which means that failed breeders have a lower parental activity.

A third LMM was thus fitted to compare the prospecting rate of failed and successful breeders. Since most of the failures happened during the provisioning phase, only the late provisioning and post-fledgling phase could be analysed with a large enough sample of failed nests. The study period chosen for the provisioning phase thus covered the last nine days before the first fledgling date of the site. This period allowed the best compromise between the number of days of data collection and sample size of failed nests, and will be refereed as "late provisioning". For the post-fledgling phase, the study period spanned from the last fledgling date of the site to the end of the data collection. The parental activity was not tested in the model, meaning that the two phases (provisioning and post-fledgling) could be grouped in a single model, with the prospecting rate (after a Box-Cox transformation) as a response variable, the Boolean breeding success, the breeding period, the year, the site as fixed effects and the ID of the bird and the breeding attempt as a random factors. The interaction between the Boolean breeding success and the breeding period was also tested, as we can hypothesise that the effect of failure is different for the late-provisioning phase and for the post-fledgling phase.

2.6.3. Effect of parental activity and breeding success on attractiveness of nestboxes for prospectors

A comparable approach was used to test the effect of breeding success and parental activity on the attractiveness of a nestbox to prospectors. Two LMMs were fitted, one for the provisioning phase and one for the post-fledgling phase. The response variable used was the prospecting rate for the whole study phase. The fixed factors are the parental activity of the pair, the number of fledglings successfully raised by the pair, the site and the year. In addition, the nestbox ID was added as a random factor to

account for nestbox-level repeatability across years. A Box-Cox transformation was applied to the response variable to ensure the normality of the residuals. The nestboxes where the breeding attempted failed (no fledglings) were excluded of those two models because of the confound effect between parental activity and Boolean breeding success.

A third LMM was thus fitted to test whether the failure of the nesting influences the attractiveness of the nest for prospectors, using the same periods as described above for the analysis comparing the failed breeders to the successful ones (late provisioning and post-fledgling). This model used the prospecting rate, after a Box-Cox transformation, as a response variable, with the phase, success or failure, site and year as fixed factors and the ID of the box as a random effect. The model also incorporated the interaction between the Boolean breeding success and the breeding period, as it is possible that the effect of failure is different for the late-provisioning phase and for the post-fledgling phase. For example, the failure of the nest might not be as visible for prospectors during the post-fledgling season, when all the nests are empty.

2.6.4. Effect of parental activity on chick growth

To check if my proxy for parental activity impacted breeding success, I tested whether there is an effect of the parental activity, as measured in this study, on the growth of the chicks. Jackdaw chicks' growth follows a sigmoidal curve with an initial lag phase followed by a phase of high growth rate before the weight stabilises[125]. The phase of high growth rate can be approximated as a linear growth and takes place approximately during the second week after hatching. Since the nestlings were weighted on day eight and thirteen after the first hatching, the linear growth of every chick was calculated by taking the difference between those two measures and the total growth of every nest was calculated by summing the linear growth of all the chicks in the nests. A LMM was run with the total nestbox linear chicks' growth as a response variable, the parental activity at the nestbox during the study period, the number of chicks at the beginning of the study period (day eight), the year and the site as fixed effects and the breeding pair as random factor. The initial number of chicks was added to the model because it ensured the homoscedasticity of an otherwise heteroscedastic model. A Box-Cox transformation was applied to the response variable to reach the normality of the residuals.

2.6.5. Phenology of prospecting

In order to better understand how the prospecting behaviour changes across the breeding season, I tested the effect of the time of the breeding season on the number of prospecting visits received by nestboxes each day. The time of the breeding season (relative day) was calculated for every day by counting the number of days since the median hatching date of the site in which the box of interest is established. Two GLMMs with a negative binomial distribution of type II were conducted, one for the provisioning phase and one for the post-fledgling phase. The number of prospecting visits a nestbox received on that day was used a response variable, with the relative day, the site and the year as fixed effects and the nestbox as a random factor. The two phases (provisioning and post-fledgling) were separated in two models because of the strong interaction and confound effect between the phase and the relative day. The comparison between the two periods is provided by the previous models (models analysing the prospecting rate based on the Boolean breeding success and the period).

3. Results

3.1. General descriptive results

A total of 177,109 hours of data were collected by the automated RFID loggers on 70 different nestboxes over the course of the two years of the study: 67,214 hours in 2022 and 109,895 hours in 2023. 582,595 visits (230,123 in 2022 and 352,472 in 2023) from 659 different birds were recorded, out of which 62,552 were prospecting visits. For nestbox owners, the average distance of a prospecting visit was 32.4 ± 43.7 (mean ± SD) m, not accounting for the 228 cross-site visits recorded between *Stithians* and *Pencoose*.

3.2. Validation videos

The loggers correctly detected 94.5% of the visits recorded on video, with no false positives (Table 1). The reliability was lower when considering each event independently, but the fact that a visit usually comprises several events (typically, the bird lands on the perch, enters the nestbox, exits the nestbox and lands on the perch again, for a total of 4 events per classical visits) mitigated the number of missed visits. Additionally, visits during which the bird only lands on the perch and peeks inside the nestbox last longer than a quick entrance, making it easier for the perch to detect the PIT-tag. Indeed, the undetected visits were usually missed because the jackdaw was too fast. Based on those results, only the loggers with both working perch and entrance coils were considered as working when calculating prospecting rate and parental activity.

Table 1: summary of the results of the test of the reliability of the automated RFID loggers using validation videos.

		Recorded on video	True positives	False negatives	False positives	Reliability
Visits		146	138	8	-	94.5%
Events	Perch	241	209	32	-	86.7%
	Entrance	289	232	57	-	80.3%
	Total	530	441	89	-	83.2%

3.7. Effect of breeding success and parental activity on individual prospecting

3.7.1. Successful parents

82 out of 145 box-owners (56.6%) prospected at least once during their provisioning phase, and those birds did so on average 0.39 ± 0.77 (mean ± SD) times per day. This proportion was of 110 out of 135 (81.4%) for the post-fledgling season and the average prospecting rate of active prospector was 1.87 ± 3.58 (mean ± SD) visits per day for that period. The mean parental activity of prospectors was of 57.9 ± 6.5 (mean ± SD) visits per day during the provisioning phase and 23.5 ± 10.4 (mean ± SD) visits per day during the post-fledgling period. The LMMs revealed no significant associations between parental activity or the number of fledglings and prospecting rate, no matter the period considered (Table 2; Figure 5). The effect of site was significant (Table 2), but an ad-hoc Tukey test revealed no differences in prospecting rate amongst sites (Figure 6). Only one couple included in the analysis successfully raised four fledglings and one couple undertook a remarkably high number of prospecting visits during the post-fledgling phase (>20 visits/day), but removing those potentially influential points did not change the significance of the results (*Appendix* table A2) and they were retained in the analysis.
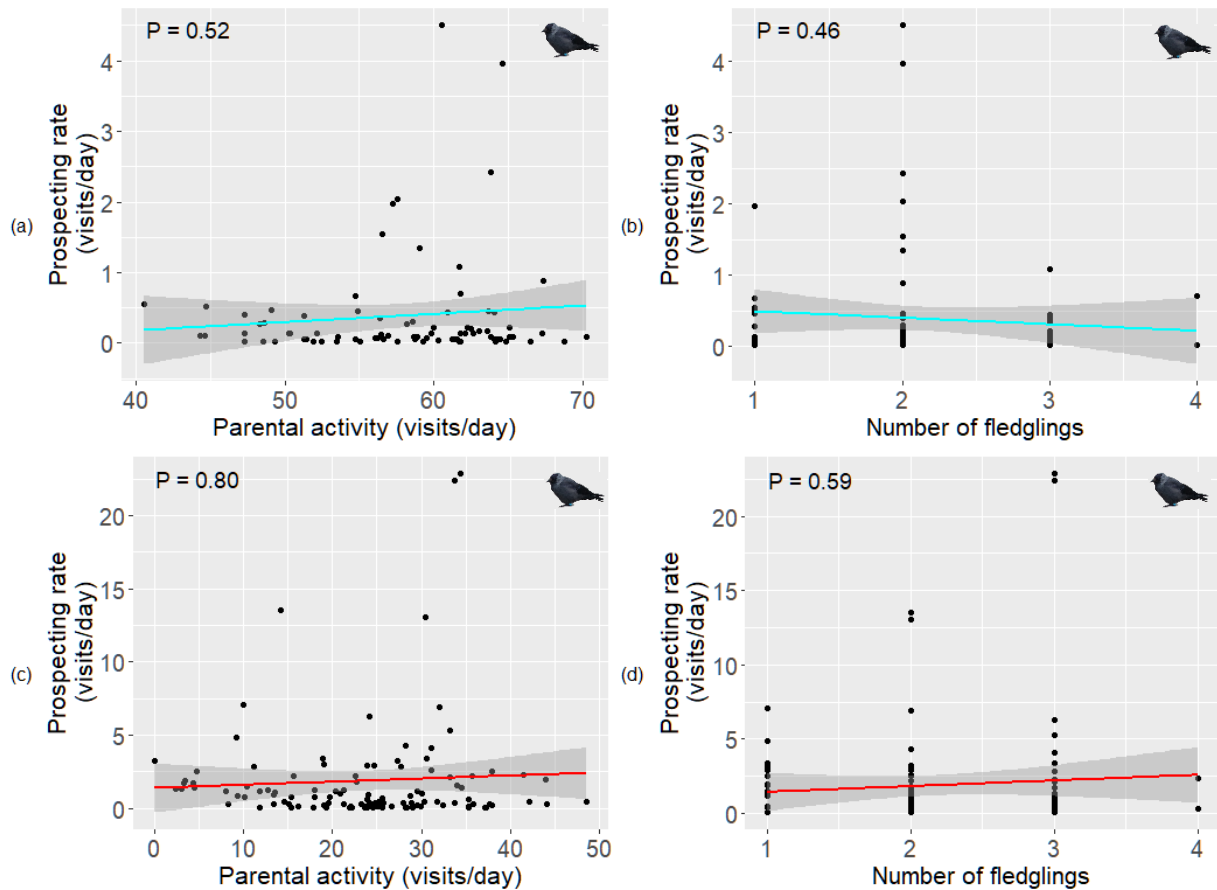
Figure 5 Prospecting rate (mean number of prospecting visits per days) of individual birds during the provisioning phase (blue) and post-fledgling phase (red) depending on the parental activity (a & c) and the number of nestlings successfully fledged (b & d). One data point represents a bird during a breeding season phase. The p-values presented were obtained with the 2 LMMs testing those factors.

*Table 2 Summary of the results from the 2 LMMs assessing the effect of parental activity and breeding success on prospecting for the provisoning phase and post-fledgling phase. *P < 0.05*

Response: prospecting rate (visits/day)								
Provisioning phase (N = 82 datapoints across 69 unique birds)					Post-fledgling phase (N = 110 datapoints across 85 unique birds)			
Explanatory variable	Estimate	SE	P		Explanatory variable	Estimate	SE	P
Parental activity	0.016	0.025	0.52		Parental activity	-0.002	0.010	0.80
No. Fledglings	-0.165	0.220	0.46		No. Fledglings	-0.150	0.278	0.59
site Y	-1.74	0.671	0.012	*	site Y	-1.34	0.772	0.087
site Z	-1.07	0.657	0.11		site Z	-0.354	0.773	0.65
Year	-0.290	0.292	0.33		Year	0.087	0.390	0.82
Random factor	Variance	SD			Random factor	Variance	SD	
Bird ID	0.839	0.916			Bird ID	0.398	0.631	
Breeding attempt	0.496	0.503			Breeding attempt	1.94	1.39	

Figure 6 Prospecting rate of individual birds by study site. The p-values were calculated with a Tukey-test. N : sample size (number of birds studied in 2022 and 2023 combined)

3.7.2. Failed breeders

The analysis comparing failed nests to successful ones for the late-provisioning and post-fledgling phases showed a significant interaction between the Boolean success and the period (Table 3). This LMM was thus separated in two distinct models according to the period. This revealed that birds that failed their breeding attempt prospected more than successful parents (Figure 7), but that this effect was significant only during the provisioning phase (Table 3).
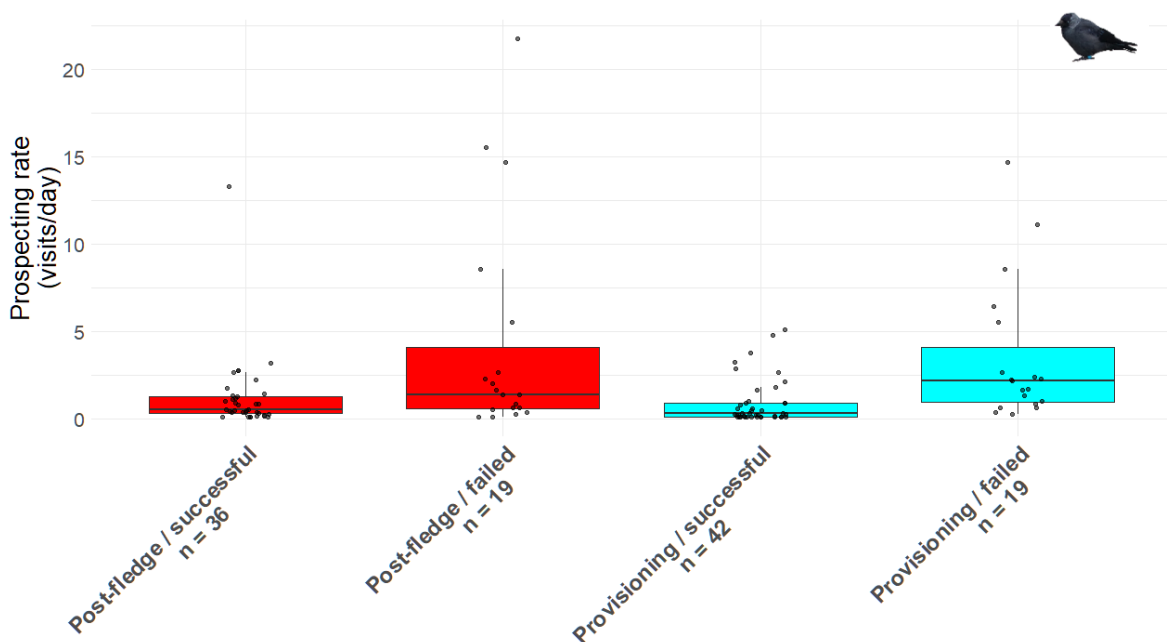
Figure 7 Prospecting rate (total number of prospecting visits/days of data collection) of individual birds during the late provisioning phase (blue) and post-fledgling phase (red), based on the Boolean breeding success (failed: no fledglings; successful: at least one fledgling). N : sample size (combined number of birds studied in 2022 and 2023)

*Table 3 Summary of the results from three variants of the LMMs assessing the effect of the Boolean breeding success and breeding season phase (late provisioning or post-fledgling) on the number of prospecting visits per day undertaken by individual birds. * P < 0.05, ** P < 0.01, *** P < 0.001*

		Response : prospecting rate (visits / day)						
Model	Fixed effect	Estimate	SE	P		Random factor	Variance	SD
Both periods N = 116 data points across 75 unique birds	Failure	0.204	0.072	0.006	**	Bird ID	0.009	0.096
	Period	-0.120	0.048	0.014	*	Breeding attempt	0.032	0.178
	Site Y	-0.306	0.103	0.004	**			
	Site Z	-0.226	0.101	0.029	*			
	Year	-0.070	0.058	0.24				
	Failure * period	0.146	0.068	0.037	*			
Late Prov. N = 61 data points across 52 unique birds	Failure	0.296	0.082	<0.001	***	Bird ID	0.009	0.094
	Site Y	-0.245	0.137	0.079		Breeding attempt	0.026	0.160
	Site Z	-0.248	0.121	0.047	*			
	Year	-0.141	0.077	0.072				
Post-Fledg. N = 55 data points across 50 unique birds	Failure	0.174	0.091	0.067		Bird ID	0.00	0.00
	Site Y	-0.293	0.130	0.033	*	Breeding attempt	0.042	0.207
	Site Z	-0.227	0.143	0.12				
	Year	-0.018	0.093	0.85				

3.5. Effect of parental activity and breeding success on attractiveness of nestboxes for prospectors

3.5.1. Successful breeding attempts

Nestboxes received on average 6.0 ± 4.7 (mean ± SD) prospecting visits per day during the provisioning phase and 19.2 ± 14.4 (mean ± SD) prospecting visits per day during the post-fledgling phase. The average parental activity at a nestbox was of 111.6 ± 11.8 (mean ± SD) visits from the owners per day for the provisioning phase and 44.9 ± 19.6 (mean ± SD) visits from the owners per day for the post-fledgling phase. The model fitted for the provisioning phase showed that parental activity had a significant effect on the number of prospecting visits received by a nestbox, with nests that had higher levels of parental activity receiving more prospecting visits (LMM: N = 71 breeding attempts; $\beta \pm SE$ = 0.019 ± 0.009, P = 0.033; Figure 8.a). The number of fledglings had a non-significant positive effect on the attractiveness of a nestbox for prospectors (LMM: N = 71 breeding attempts; $\beta \pm SE$ = 0.235 ± 0.134, P = 0.084; Figure 8.b). None of the tested factors had a significant effect on the prospecting rate during the post-fledgling period (LMM: N = 70 breeding attempts; $\beta \pm SE$ = -0.002 ± 0.009, P = 0.77 for parental activity; Figure 8.c; and $\beta \pm SE$ = -0.187 ± 0.207, P = 0.37 for the number of fledgling; Figure 8.d). There was a correlation between the parental activity and the number of fledglings for the provisioning phase (LM: N = 71 breeding attempts; $\beta \pm SE$ = 6.90 ± 1.94, P < 0.001), but this did not generate collinearity problems in the models (VIF < 1.25). The dataset contained a single nestbox with 4 fledglings, but removing this data point did not change the significance of the results (*Appendix* table A5) and it was thus retained into the analysis.
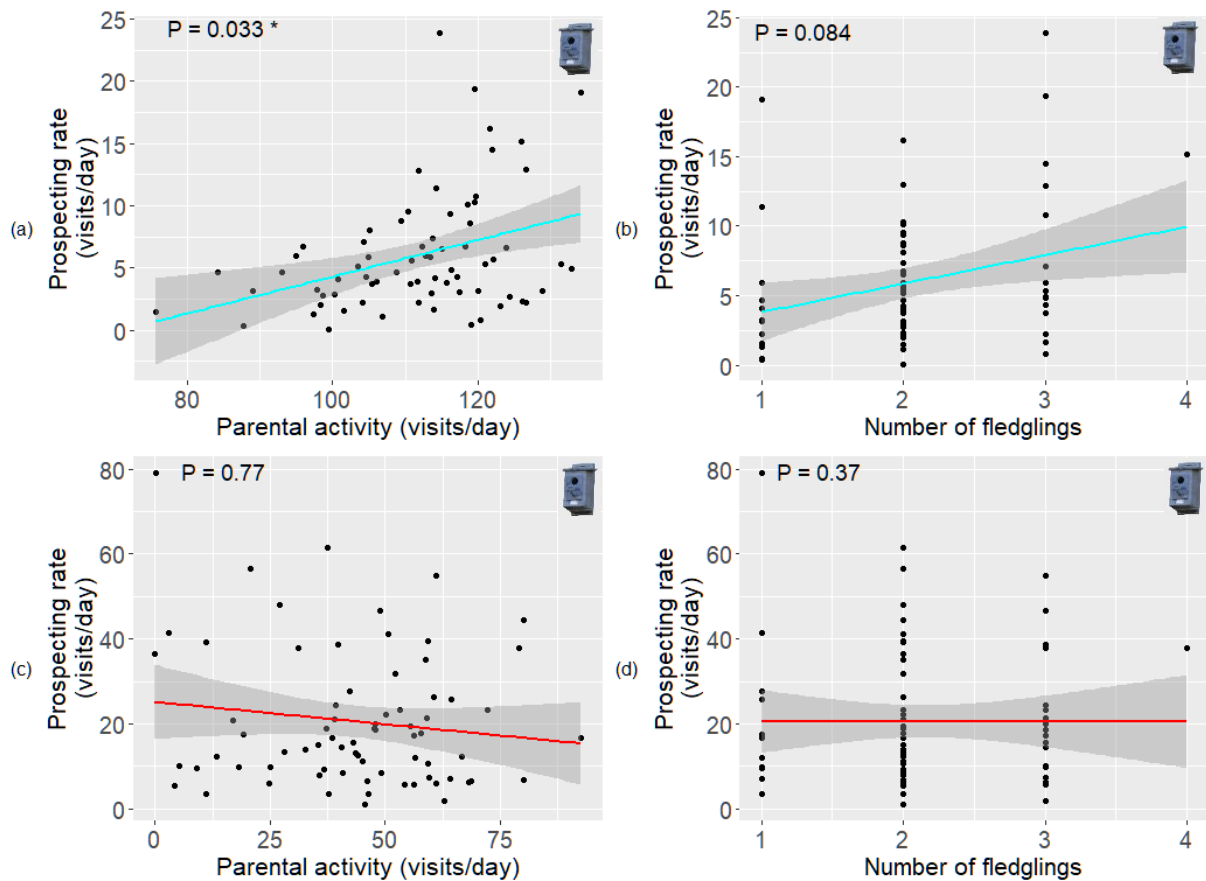
*Figure 8 Prospecting rate at nestboxes (mean number of prospecting visits received by the nestbox per days) during the provisioning phase (blue) and post-fledgling phase (red), depending on the parental activity (a & c) and the number of nestlings successfully fledged at the nestbox (b & d). One data point represents a nestbox during a breeding phase. The p-values presented were obtained with the 2 LMMs testing those factors. *P < 0.05*

3.5.2. Failure of the breeding attempt

The analysis comparing the nestboxes where the breeding attempt was successful to the ones where the owners failed their breeding attempt revealed that failed boxes received fewer prospecting visits (LMM: N = 131; β ± SE = -0.468 ± 0.196, P = 0.019; Figure 9) and that nestboxes received more prospecting visits during the post-fledgling phase than during the provisioning phase (LMM: N = 131 breeding attempts; β ± SE = -0.414 ± 0.113, P < 0.001; Figure 9). The interaction between those factors was not significant (LMM: N = 131 breeding attempts; β ± SE = 0.422 ± 0.229, P = 0.070).
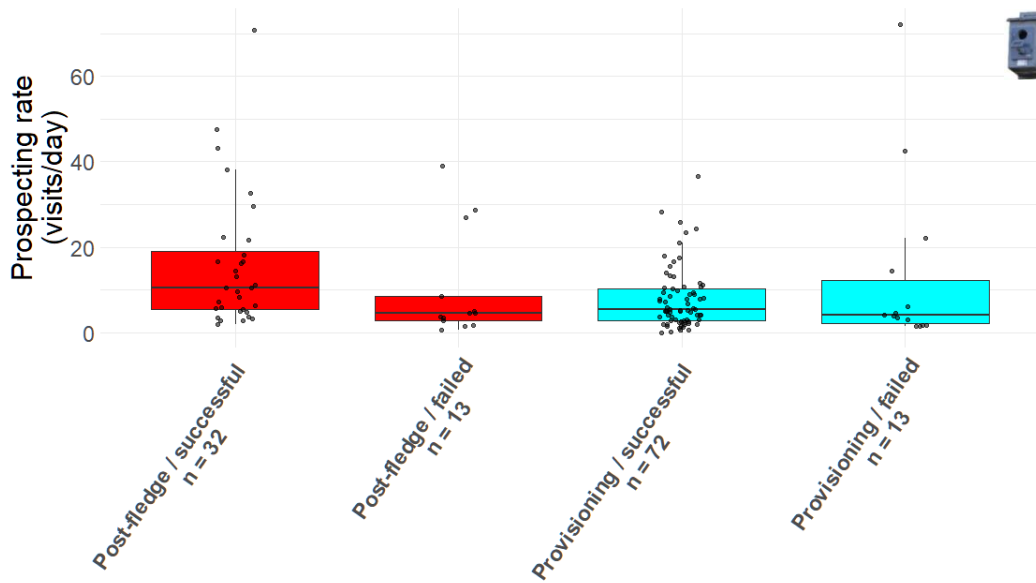
Figure 9 Number of prospecting visits per day received by nestboxes, based on the breeding season phase (late provisioning: blue; post-fledgling : red) and on the Boolean breeding success (failed : no fledgling, successful ; at least one fledgling). N : sample size (number of breeding attempts)

3.4. Effect of parental activity on chick growth

During the studied period (linear growth phase), the growth rate in chick weigth per brood was of 168.3 ± 64.3 (mean ± SD) g and the mean parental activity was of 118.3 ± 14.2 (mean ± SD) visits per day, combining the visits from the male and the female. Larger broods showed a higher increase in total chick weigth (LMM: N = 70 breeding attempts; β ± SE = 6.26 ± 1.77, P < 0.001). Accounting for this effect, parental activity had a significant positive effect on the chick growth (LMM: N = 70 breeding attemps: β ± SE = 8.12 ± 2.91, P = 0.007; Figure 10).
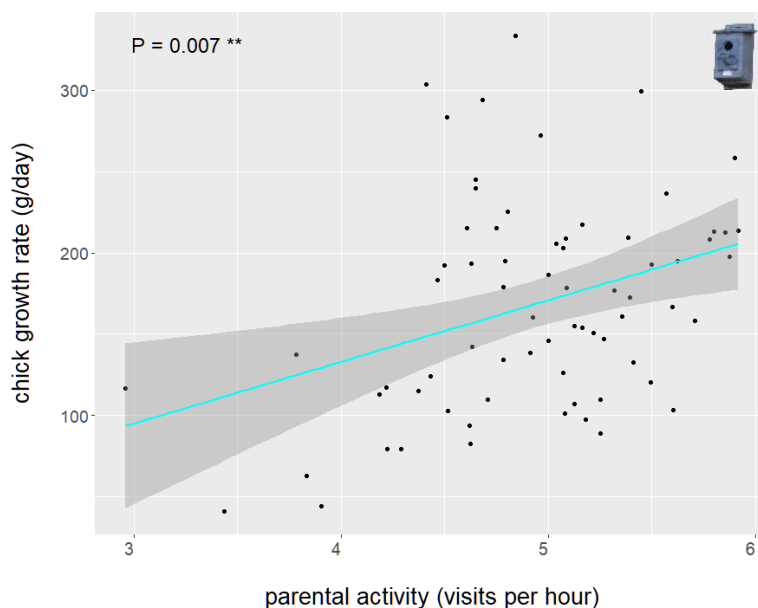
Figure 10 Total increase in chick weight per day for each nest during the linear growth phase, depending on the combined parental activity of the parents.

3.3. Phenology of prospecting

Nestboxes received on average 6.43 ± 8.03 (mean ± SD) visits per day during the provisioning phase and 19.6 ± 19.9 (mean ± SD) visits per day during the post-fledgling phase. The number of prospecting visits received by nestboxes steadily increases over the course the provisioning phase before reaching a peak just after the fledgling of the nestlings (Figure 11). It then decreases over time, until the end of the data collection. The moment a nestbox is most attractive for prospectors is right after fledgling. The positive trend of the provisioning phase and the negative trend of the post-fledgling phase were both significant (GLMM: N = 2245 days across 65 nestboxes; β ± SE. = 0.048 ± 0.002, P < 0.001 and GLMM: N = 1300 days over 59 nestboxes; β ± SE = -0.050 ± 0.003, P < 0.001, respectively).
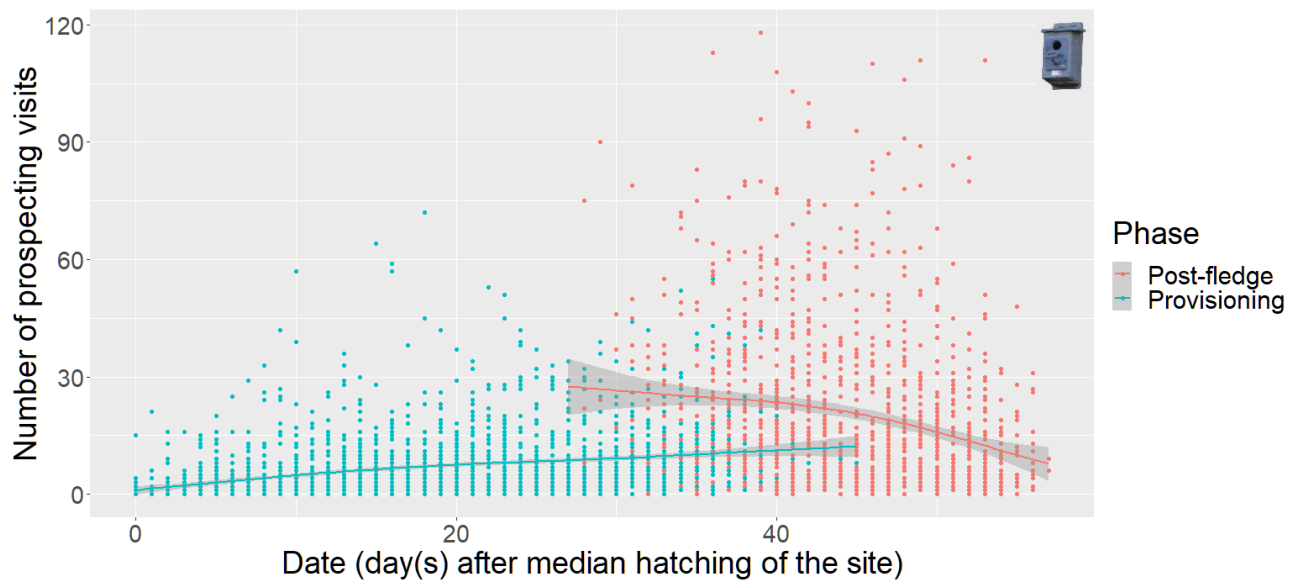
Figure 11 Daily nestbox prospecting visitation pattern, based on the breeding phase of the nestbox : provisioning (blue) or post-fledgling (red). One data point represents a nestbox during one day. The X-axis represents the number of days after the median hatching day of the site for the year, while the Y-axis depicts the number of prospecting visits received by the nestbox during the study day. The two phases overlap because the fledgling day varies from nestbox to nestbox.

4. Discussion

In this study, automated RFID loggers were used to investigate the prospecting behaviour of jackdaws throughout their breeding season. The accuracy of the loggers in recording the prospecting visits was high, with a reliability rate of 94.5%. 5.5% of the visits remained undetected, but the loggers still provided a good estimate of the number of prospecting and parental visits at every nestbox. Moreover, all nestboxes were equipped with the same logger model, ensuring a consistent proportion of missed visits across all nests and mitigating any impact of the missed visits on the results of the statistical tests conducted. Using this RFID data, this study revealed that failed breeders prospected more than successful birds, although this effect was significant only during late provisioning and not during the post-fledgling phase. The parental activity of individual prospectors did not correlate with their prospecting rate, meaning that no significant trade-off between parental activity and prospecting was found. I also observed that nestboxes with a higher parental activity received more prospecting visits during the provisioning period and that nests where the breeding attempt had failed were less attractive to prospectors during the provisioning and post-fledgling phase. Finally, the findings concerning the phenology of prospecting are that that prospecting in jackdaws increases throughout the provisioning phase of the breeding season, reaches a peak just after post-fledgling and subsequently declining, with a higher total frequency of prospecting during the post-fledgling phase. Overall, this shows that failed breeders prospect more, that prospectors use public information including during the post-fledgling phase and that prospecting is more frequent after the fledgling of the chicks.

Concerning the finding that failed breeders prospected more than successful ones, the fact that the effect was below the significance threshold only during the provisioning phase and not during the post-fledgling phase can most likely be attributed to the low sample size of failed breeders. This number was not extremely low (N = 19), but the effect was close to being significant. Considering this, it is reasonable to expect that the impact of failure during the provisioning stage may still carry over to the post-fledging period. The result that failed breeders invest more in prospecting is consistent with previous studies on several species[42,61,81,84,85]. This is traditionally explained either with the increased amount of available time for prospecting due to absence of feeding duty[81] or with the idea that the information gathered through prospecting is more valuable for failed breeders[84], for example because they are more likely to change nest site on the following year[48,55,69,84]. However, a study by Schuett (2012)[86] on jackdaws showed that jackdaws are consistent in their investment in prospecting across years and that this investment may thus be driven by personality and not be as plastic as thought before. There is thus another possible explanation for the negative correlation between breeding success and prospecting: birds that invest more in prospecting due to personality see their breeding success decrease because of a trade-off between prospecting and parental activity. The present study tested the presence of such a trade-off and found no significant link between parental activity and prospecting rate of individuals. This result supports the traditional hypothesis that failing breeding causes birds to prospect more and did not find evidence supporting the alternative causality.

The absence of a significant trade-off between parental activity and prospecting does not mean that information gathering doesn't have a cost, but probably rather that the variation in prospecting amongst individuals is not high enough to explain variation in parental investment. Indeed, there is no denying that gathering information through prospecting takes time and has a high cost in energy,

especially when it leads to a fight with the nest owners[60]. The time and energy spent prospecting are not spent in raising the chicks and a trade-off is in theory inevitable. However, the investment in prospecting amongst successful parents was negligeable in comparison to the parental investment, with prospectors making on average less than one prospecting visit every two days and more than 55 parental visits per day. The resources spent in prospecting are thus negligeable compared to other factors and the trade-off could not be detected. In other words, jackdaws probably limit their prospecting to a minimal number of visits that will not significantly affect their parental investment due to the trade-off between those two activities, and thus suppress any variability high enough to detect said trade-off.

While this study found that failed breeders prospect more and brought new evidences to support the view that this increase in prospecting is due to the failure rather than the reverse, it did not find any effect of the number of chicks fledged by successful breeders on their investment in prospecting. This result is in stark contrast with Schuett et al. (2012)[86] study, which found that jackdaws that fledged fewer fledglings prospected more (effect significant only for males, perhaps due to small sample size). This difference in results could be explained by a difference in methodology. Schuett et al. (2012)[86] collected data only during late provisioning (late March- early June), while I used data starting from the hatching of the chicks. Considering that the number of fledglings cannot be known before later in the season, it is possible that including data from the early provisioning season diminished the effect of the number of fledglings. However, I also found no effect of the number of fledglings during the post-fledgling phase, a period during which the number of chicks they managed to fledged was known to the birds. This period was not studied by Schuett et al. (2012)[86] and no study of my knowledge investigated the effect of the graded breeding success on prospecting during that period. Despite the difference in results concerning the effect of the number of fledglings, the present study and Schuett et al. (2012)[86] both found that more successful breeders prospect less, even if they investigated only the number of fledglings while I found this effect only for the Boolean breeding success. The general conclusion that breeding success overall has a negative effect on the investment in prospecting is thus shared by both studies.

While failed breeders prospected more, their nests received less prospecting visits than nestboxes where the nesting was successful. This shows that jackdaws use public information (*sensu* Danchin et al. (2004)[5], i.e. information on the breeding success of other individuals), and focus their prospecting visits on successful nests, which is consistent with previous findings on the northern wheatear (*Oenanthe Oenanthe*)[27]. The correlation between the parental activity at a nestbox and the number of prospecting visits received by the nest also supports the idea that jackdaws use public information, since feeding rate is known to correlate with breeding success[113,126,127] and the result of the corresponding LMM showed that this was true for my measure of parental activity. However, the effect of the final number of fledglings on the attractiveness of the nests could also tested thanks to the absence of collinearity problem with parental activity and was found to be positive, but non-significant. This seems to indicate that prospectors cue on parental activity rather than on direct breeding success when choosing a target for a prospecting visit, which can be explained by the fact that parental activity can be assessed from a distance while direct breeding success can be assessed only once the prospector is already visiting the cavity[39]. The parental care being the most explanatory variable for the attractiveness of a nest is consistent with the results of several studies on flycatchers[39,76,128], although one other study on the pied flycatcher found that breeding success explained the variation

better than parental activity[63] and a study on the lesser kestrel showed that intermediate feeding rate were more attractive due to the trade-off between the quality of the information (visiting more successful nests) and the risk of a costly fight with the owners[60]. My results show that jackdaws are ready to face higher risks of being attacked by the owners in order to gather information from more successful nests, and that they can choose a successful nest to prospect at by cueing on the parental activity, as a proxy for breeding success.

Since jackdaws seem to gather public information, we can expect, according to the optimal-time hypothesis, that they will prospect more when the breeding success of others is most observable, which should be at the end of the provisioning period[17,41]. In accordance with this hypothesis, I indeed found that prospecting increases steadily over the course of the provisioning season. However, the RFID data also revealed that the number of visits received by nestboxes is much higher just after the nestlings fledged. This finding does not support the idea that the optimal time to gather information from the nest sites of other individuals is at the end of the provisioning stage. One potential explanation for this jump in prospecting visits after fledgling is that parents have more time to spend in prospecting after their nestling fledge, but this explanation would neglect some key elements. First, jackdaws continue to feed and guard their offspring for some time after fledgling (juveniles start independent foraging at 6 weeks old[129]) and are thus unlikely to have such a massive rapid increase in free-time just after their chicks' fledgling. Secondly, nestboxes in which the chicks fledged earlier received more visits than the average nestbox (Figure 11), despite most of the other breeders being still in the provisioning phase. The increase in prospecting at nestboxes just after fledgling cannot be explained by an increase in free time of prospectors for the first nests to see their chicks fledge. Another explanation could be that post-fledgling nestboxes are less defended and thus less costly to prospect. This is plausible since prospecting can end up in costly fights if the prospector meets the owners[60]. The risks of encountering the owners is however not the only factor considered by prospectors when choosing which nest they will visits, since the prospecting rate was higher at nestboxes with a parental activity during the provisioning phase. Moreover, if the low parental activity was the explanation of the popularity of post-fledged nestboxes amongst prospectors, we could expect failed nests (which also had a low parental activity) to receive many prospecting visits. Instead, the opposite was observed, with failed nests receiving fewer prospecting visits during both periods. I thus argue that, in combination with their low parental activity, post-fledgling nestboxes are most attractive because they allowed a completely successful breeding attempt to take place, and are thus considered even more successful than nestboxes with nestlings. The optimal time to gather public information would thus not be just before fledgling but just after, when prospectors can be sure that the breeding attempt was successful.

What remains unclear, however, is how jackdaws manage to discriminate between successful and failed nests once the chicks have fledged. Empty nests can still provide information[130–132]. For example, jackdaws tend to empty their nestbox over the course of the season while nests that got fully abandoned remain intact (personal observation). The smell of the nest can also be informative and could be a potential cue[133–135]. Prospectors might thus be able to determine whether a nest was successful or not by peeking inside the nestbox, and return to prospect more often at successful nestboxes. It is also possible that long-term memory is an important mechanism in explaining this difference in prospecting visits rates. Jackdaws could remember that a specific nest was abandoned since the early provisioning phase and is thus failed, and use this information to avoid prospecting it

during the post-fledgling phase. This is very plausible considering that the entire concept of birds prospecting during and after the provisioning season in order to choose a better breeding site the following year[18] implies that they are capable of holding information for a long time. Another possible cue allowing jackdaws to know which empty nests are post-fledged and which are failed could be the fledglings themselves. Jackdaws are capable of recognising specific individuals[136] and likely knows who owns which nest, at least in the close neighbourhood. Seeing the owners of a nestbox feeding their fledglings, even away from their nests, would thus be a clear cue that their breeding attempt was successful and we can hypothesise that prospectors could link this information to the nestbox. None of those possible mechanisms have been tested so far and the way prospectors discriminate between successful and unsuccessful empty nests could be the subject of future research.

Jackdaws thus use public information to decide where they will prospect, and this even during the post-fledge period, but this does not necessarily mean that the prospecting visits aims at gathering said public information. Indeed, the fact that they prospect more often at nestboxes with a higher breeding success shows that they are already aware of the breeding success of said nestbox before visiting it, or that they prospect repeatedly at the same nestbox after having already assessed the breeding success. Doligez et al. (2004)[39] suggested that prospectors could get an estimate of the breeding success *via* some indirect cues, such as parental activity, and use it to decide where to prospect. They would then enter the nest to gather a more precise, direct and non-falsifiable measure of breeding success by counting the nestlings or assessing their body condition. However, this hypothesis cannot apply to post-fledgling prospecting, since those cues (number or body condition of nestlings) are not available anymore. Jackdaws use public information when deciding where to prospect, but the prospecting visits during the post-fledgling period are unlikely to aim at gathering more public information. Prospecting visits could aim at gathering other information, such as personal information on the nest (how wide is the cavity, how large is the entrance, how clean or dry is the nest, …), or have a completely different role. For instance, jackdaws could visit a nest to show an intention of taking over the ownership of the nestbox. Indeed, jackdaws often defend their cavities during the whole year[94], and it is thus not unreasonable to think that fights over the ownership of a nestbox can happen during the post-fledgling stage. Overall, this study suggests that public information is used for prospecting decisions during a stage during which the prospecting visits are unlikely to aim at gathering more public information. This highlights that using public information during prospecting does not mean that prospecting aims at gathering public information. The specific information gathered during a prospecting visit and the potential other roles of such visits is outside of the scope of this thesis and should be explored in further researches.

5. Conclusion

Overall, this thesis showed that jackdaws use public information when prospecting, including during the post-fledgling phase, that prospecting in jackdaws reaches a peak just after the fledglings of the chicks and that failed breeders prospect more, with some evidence supporting the idea that the failure causes them to prospect more. The link between public information gathering and prospecting behaviour in birds was already well established[27,48,54,76,78], but this had never been tested for jackdaws before. This study also brought new evidence that prospectors cue on parental activity when choosing a target for a prospecting visit. The fact that failed breeders prospect more is also in accordance with the current literature[48,81,84] and the lack of correlation between investment in prospecting and parental activity amongst successful breeders supports the traditional causality view, i.e. lower breeding success causes birds to prospect more. However, the peak in prospecting after fledgling contrasts with previous research. Indeed, the optimal-time hypothesis states that prospecting should peak just before fledgling rather than just after[41]. I showed that this assumption is wrong in jackdaws, as this species prospect mostly after fledgling, and this results most likely extends in other species of similar biology. Future studies on the prospecting behaviour of similar birds should thus include the post-fledgling phase. Furthermore, the study's observation that jackdaws can differentiate between successful and unsuccessful breeding attempts even after the chicks have fledged opens up interesting questions about the mechanisms underlying this discrimination. Whether it is due to cues left in empty nests or involves memory-related processes remains uncertain. Exploring these possibilities could yield important implications, shedding light on the significance of old nests to birds or on the depth of jackdaws' knowledge of their social environment. In conclusion, this thesis helped expanding our understanding of jackdaw prospecting behaviour and emphasized the importance of considering the post-fledgling phase in future studies on prospecting behaviour.

5. Contribution of the student

All the statistical analysis, literature review and writing are my own work. The data collection was a team effort of the *Cornish Jackdaw Project*, which I joined for the field season of 2023 (March-June). During this period, I installed RFID loggers, repaired them when needed and routinely changed their batteries. I also took part in the nest monitoring, by identifying the owners of the nests, performing nest-checks using the endoscope and weighting the chicks. Furthermore, I assisted the ringing of the nestlings and several ladder trapping sessions. I did not take part in the data collection of 2022. The writing of the code for the data extraction and the coding of the validation videos was shared amongst the three Masters' student of the project.

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7. Appendix

7.1. LMMs and GLMM results

7.1.1. effect of breeding success and parental activity on individual prospecting

7.1.1.1. Successful breeders

*Table A1 summary of the results from the 2 LMMs assessing the effect of parental activity and breeding success on prospecting for the provisoning phase and post-fledgling phase. *P < 0.05*

Response: prospecting rate (visits/day)								
Provisioning phase (N = 82 datapoints across 69 unique birds)					Post-fledgling phase (N = 110 datapoints across 85 unique birds)			
Explanatory variable	Estimate	SE	P		Explanatory variable	Estimate	SE	P
Parental activity	0.016	0.025	0.52		Parental activity	-0.002	0.010	0.80
No. Fledglings	-0.165	0.220	0.46		No. Fledglings	-0.150	0.278	0.59
site Y	-1.74	0.671	0.012	*	site Y	-1.34	0.772	0.087
site Z	-1.07	0.657	0.11		site Z	-0.354	0.773	0.65
Year	-0.290	0.292	0.33		Year	0.087	0.390	0.82
Random factor	Variance	SD			Random factor	Variance	SD	
Bird ID	0.839	0.916			Bird ID	0.398	0.631	
Breeding attempt	0.496	0.503			Breeding attempt	1.94	1.39	

Without potential highly influential points

*Table A2 summary of the results from the 2 LMMs assessing the effect of parental activity and breeding success on prospecting for the provisoning phase and post-fledgling phase, after removing the potentially highly influential points. *P < 0.05*

Response: prospecting rate (visits/day)								
Provisioning phase (N = 80 datapoints across 67 unique birds)					Post-fledgling phase (N = 106 datapoints across 81 unique birds)			
Explanatory variable	Estimate	SE	P		Explanatory variable	Estimate	SE	P
Parental activity	0.020	0.024	0.416		Parental activity	-0.005	0.010	0.61
No. Fledglings	-0.192	0.237	0.421		No. Fledglings	-0.263	0.284	0.36
site Y	-1.76	0.674	0.012	*	site Y	-1.17	0.744	0.12
site Z	-1.11	0.659	0.098		site Z	-0.309	0.741	0.68
Year	-0.310	0.302	0.31		Year	0.230	0.382	0.55
Random factor	Variance	SD			Random factor	Variance	SD	
Bird ID	0.722	0.850			Bird ID	0.354	0.600	
Breeding attempt	0.475	0.765			Breeding attempt	1.79	1.34	

7.1.1.2. Failed breeders

Table 4 Summary of the results from three variants of the LMMs assessing the effect of the Boolean breeding success and breeding season phase (late provisioning or post-fledgling) on the number of prospecting visits per day undertaken by individual birds. * P < 0.05, ** P < 0.01, *** P < 0.001

				Response : prospecting (visits / day)				
Model	Fixed effect	Estimate	SE	P		Random factor	Variance	SD
Both periods N = 116 data points across 75 unique birds	Failure	0.204	0.072	0.006	**	Bird ID	0.009	0.096
	Period	-0.120	0.048	0.014	*	Breeding attempt	0.032	0.178
	Site Y	-0.306	0.103	0.004	**			
	Site Z	-0.226	0.101	0.029	*			
	Year	-0.070	0.058	0.24				
	Failure * period	0.146	0.068	0.037	*			
Late Prov. N = 61 data points across 52 unique birds	Failure	0.296	0.082	<0.001	***	Bird ID	0.009	0.094
	Site Y	-0.245	0.137	0.079		Breeding attempt	0.026	0.160
	Site Z	-0.248	0.121	0.047	*			
	Year	-0.141	0.077	0.072				
Post-Fledg. N = 55 data points across 50 unique birds	Failure	0.174	0.091	0.067		Bird ID	0.00	0.00
	Site Y	-0.293	0.130	0.033	*	Breeding attempt	0.042	0.207
	Site Z	-0.227	0.143	0.12				
	Year	-0.018	0.093	0.85				

7.1.2. Effect of parental activity and breeding success on attractiveness of nestboxes for prospectors

7.1.2.1. Successful breeding attempts

Table A4 summary of the results from the 2 LMMs assessing the effect of parental activity and breeding success the number of prospecting visits receuved by nestboxes for the provisoning phase and post-fledgling phase. *P < 0.05

Response: prospecting rate (visits/day)								
Provisioning phase N = 71 breeding attempts across 55 nestboxes					Post-fledgling phase N = 70 breeding attempts across 50 nestboxes			
Explanatory variable	Estimate	SE	P		Explanatory variable	Estimate	SE	P
Parental activity	0.019	0.009	0.033	*	Parental activity	-0.002	0.009	0.77
No. Fledglings	0.235	0.134	0.084		No. Fledglings	-0.187	0.207	0.37
site Y	-0.262	0.360	0.47		site Y	-0.345	0.208	0.11
site Z	-0.219	0.379	0.57		site Z	0.099	0.717	0.89
Year	-0.037	0.157	0.81		Year	0.940	0.747	0.21
Random factor	Variance	SD			Random factor	Variance	SD	
Bird ID	0.133	0.365			Bird ID	1.33	1.15	
Breeding attempt	0.339	0.583			Breeding attempt	0.470	0.685	

Without potential highly influential points

*Table A5 summary of the results from the 2 LMMs assessing the effect of parental activity and breeding success the number of prospecting visits receeved by nestboxes for the provisoning phase and post-fledgling phase, after removing the potentially highly influential points. *P < 0.05, **P<0.01*

Response: prospecting rate									
Provisioning phase N = 70 breeding attempts across 54 nestboxes					Post-fledgling phase N = 69 breeding attempts across 49 nestboxes				
Explanatory variable	Estimate	SE	P		Explanatory variable	Estimate	SE	P	
Parental activity	0.019	0.009	0.033	*	Parental activity	-0.005	0.009	0.55	
No. Fledglings	0.199	0.142	0.17		No. Fledglings	-0.275	0.215	0.21	
site Y	-0.050	0.159	0.76		site Y	-0.383	0.209	0.079	
site Z	-0.246	0.362	0.50		site Z	0.215	0.715	0.770	
Year	-0.212	0.380	0.58		Year	1.02	0.743	0.17	
Random factor	Variance	SD			Random factor	Variance	SD		
Bird ID	0.128	0.358			Bird ID	1.31	1.14		
Breeding attempt	0.347	0.589			Breeding attempt	0.465	0.682		

7.1.2.2. Failure of the breeding attempt

*Table A6 summary of the results from the 2 LMMs assessing the effect of parental activity and breeding success the number of prospecting visits receeved by nestboxes for the provisoning phase and post-fledgling phase, after removing the potentially highly influential points. *P < 0.05, **P<0.01*

Response : prospecting rate N = 131 breeding attempts across 64 nestboxes							
Fixed effect	Estimate	SE	P		Random factor	Variance	SD
Failure	-0.468	0.196	0.019	*	Bird ID	0.175	0.419
Period	-0.414	0.113	<0.001	***	Breeding attempt	0.234	0.484
Site Y	-0.144	0.233	0.54				
Site Z	0.065	0.230	0.78				
Year	0.083	0.098	0.40				
Failure * period	0.422	0.229	0.070				

7.1.3. Effect of parental activity on chick growth

*Table A7 summary of the results from the LMM assessing the effect of parental activity on the growth rate of the total chick weight inside the nestbox during the linear growth phase. * P < 0.05, ** P < 0.01, *** P < 0.001*

Response : total growth in chick weight of the nest N = 70 breeding attempts across 55 nestboxes				
Explanatory variable	Estimate	SE	P	
Parental activity	8.12	2.91	0.007	**
Initial no. nestlings	6.26	1.77	<0.001	***
site Y	1.98	6.14	0.75	
site Z	3.74	6.41	0.56	
Year	-2.73	2.60	0.31	
Random factor	Variance	SD		
Breeding attempt	96.6	9.8		