

Spatial, temporal and individual-based differences in nest-site visits and subsequent reproductive success in wild great tits

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ABSTRACT

The behaviour of individual birds before and during the breeding period may be an important factor determining reproductive success. One commonly observed behaviour during the breeding period in many species is the visitation of multiple potential breeding sites. Much research has attempted to determine the function and consequences of this behaviour, but traditionally studies have been limited to not examining individual-level behaviour, or only considering a small number of individuals. We used automated recording of RFID-tagged birds visiting nestboxes to study a population of 80 great tits (*Parus major*) making >3500 daily visits across 74 breeding sites, to quantify the frequency, spatial patterning, and temporal occurrence of this behaviour from the pre-breeding period onwards. We argue that (i) the tight spatial clustering of visits, (ii) juveniles visiting more sites than adults, and (iii) males (but not females) continuing to visit other sites even as egg laying at their own nest occurs, indicate that territoriality and extra-pair mating may underpin visitation behaviour. Further, we find that spatial clustering of female visits relates to increased clutch size and fledging success, while frequently visiting a preferred nesting site increases the likelihood of obtaining a breeding site but reduces subsequent reproductive output for both sexes. Our study offers new insight into the mechanisms potentially driving breeding site visitation behaviour, and demonstrates its relationship to individual fitness. We suggest that although visitation behaviour may be related to different components of fitness, future work should use experiments to fully assess the causal factors and effects of visitation behaviour.

INTRODUCTION

In many bird species, individuals visit multiple potential breeding sites during the settlement and breeding period (Reed et al. 1999, Doligez et al. 2002, Valone and Templeton 2002, Kempenaers et al. 1992). Due to the importance of the breeding period, much research has focused on deciphering the drivers and consequences of this behaviour. Previous studies of breeding site visitations have been limited to either undertaking observations at large spatial scales (i.e. monitoring visits to different colonies or habitat patches) or using small sample

sizes when monitoring individuals' visits to nesting sites at smaller spatial scales (Doligez et al. 2002, Parejo et al. 2007, Kempenaers et al. 1992, Currie et al. 1998, Double and Cockburn 2000, Humbird and Neudorf 2008). However, Radio Frequency Identification (RFID) technology, which allows automated identification of RFID tagged birds as they come within range of fixed RFID readers (Bonter and Bridge 2011), has now enabled a new approach to deciphering breeding site visitation, particularly in regards to the three broad, and overlapping, processes long considered to drive this behaviour, namely *gaining information*, *territoriality*, and *extra-pair mating (EPM)*.

First, visiting a number of sites may allow individuals to *gain information* regarding the suitability of the general area and the specific nesting site for breeding. This may be beneficial for allowing individuals to independently assess the nesting area (Valone and Templeton 2002, Dall et al. 2005), increasing their familiarity with it (Piper 2011), or gaining social cues which indicate the productivity of the area (Doligez et al. 2002, Danchin et al. 2004). Previous studies have found that visits to breeding sites take place throughout the breeding season, and that the social cues appear to shape the future breeding decisions of those obtaining the information (Doligez et al. 2002, Doligez et al. 2004, Boulinier et al. 1996, Schuett et al. 2017, Seppanen et al. 2011). Recent experiments involving RFID monitoring have shown that adult pied flycatchers (*Ficedula hypoleuca*) pay most attention to the most productive nests (Schuett et al. 2017), and tit species (*Paridae*) prospect potential nesting sites with their winter flock members (Firth and Sheldon 2015).

Second, establishing and maintaining a territory is important for the success of birds' breeding attempts (Cody 1985). Thus, *territorial behaviour* and competition for nest sites could cause certain individuals to visit multiple potential breeding sites if they are prohibited from their first choice locations (Hinde 1956, Temeles 1994). Indeed, birds may invest heavily in territorial behaviour and in competing with others when attempting to establish breeding areas (Reed et al. 1999, Bonte et al. 2012). Nevertheless, assessing the fine-scale dynamics of territorial activity and interactions has previously been challenging (Sánchez-Tójar et al. 2017). However, trans-seasonal RFID tracking of house sparrows (*Passer domesticus*) has shed new light on this, and suggested that clear differences may exist in relation to individuals traits as adults appear to hold territories year-round whilst juveniles appear to compete for them up to breeding (Sánchez-Tójar et al. 2017).

Third, individuals may visit other breeding territories to pursue *extra-pair mating* opportunities (Griffith et al. 2002, Akcay and Roughgarden 2007). Movement in relation to EPM opportunities has been suggested for both sexes, and may allow males to gain paternity in other broods or increase females' reproductive success within their own brood (Buitron 1983, Sheldon and Burke 1994). For example, neighbouring males' intrusions onto the territories of female wheatears (*Oenanthe oenanthe*) appears to result in EPMs, and such intrusions subsequently appear to influence territorial behavior of the female's partner male (i.e. the social mate) (Currie et al. 1998). In contrast, female superb fairy wrens (*Malurus cyaneus*) can gain EPMs through visiting neighbouring

males' territories (Double and Cockburn 2000). Recently, RFID monitoring of 69 blue tits (*Cyanistes caeruleus*) over entire breeding seasons across multiple years has demonstrated that larger males visited more nestboxes and were more likely to gain EPMs with the visited females (Schlicht et al. 2015).

Several recent studies have acknowledged that further research examining how individual-level characteristics underpin breeding site visitations and the consequences for reproduction is now needed to advance our understanding of information prospecting, territoriality, and EPMs (Bonter and Bridge 2011, Schlicht et al. 2015, Schuett et al. 2017, Sánchez-Tójar et al. 2017). Thus, we monitored the fine-scale breeding site visitation patterns of 80 wild RFID-tagged great tits. Within our study population, relatively large gregarious winter foraging flocks break down in the spring into mated pairs that have formed throughout the non-breeding period but become highly territorial upon breeding (Hinde 1952, Firth et al. 2015b, Firth and Sheldon 2016), with egg-laying generally taking place from early spring (i.e. April) onwards. Whilst these birds are socially monogamous, they also engage in EPMs, and around 12-13% of young are sired by another male (Patrick et al. 2012, Firth et al. 2015a). Breeding is restricted almost exclusively to nestboxes, which they appear to first begin visiting around 4-6 weeks prior to egg-laying (Hinde 1952, Firth and Sheldon 2015).

We quantified the frequencies, spatial arrangement, and temporal patterning of behaviour of individual great tits when visiting nestboxes that were equipped with continuously recording antennae. We assessed the individual-level characteristics underpinning this variation, and examined the relationships that breeding site visitation behaviour holds with reproductive success. In particular, whilst limited knowledge regarding fine-scale great tit breeding site visitation previously existed, we broadly expected that (i) gaining information would be generally expressed as relatively evenly distributed visits to numerous sites over large spatial areas in a temporally consistent manner, (ii) territoriality would be characterized as visits to a limited number of key sites within a spatially clustered manner during territorial formation period, and (iii) EPM activity would manifest as visits to various neighboring sites (other than their own nestbox) during their own fertile period. Finally, given the observed prevalence of breeding site visits within this species and the expected associations with the above three processes, we also expected that, depending on the underpinning mechanism, the patterning of visitations may be related to subsequent reproductive success.

METHODS

Study site and system

This study took place in Denman's Copses (51°44'35.9"N 1°19'35.7"W and 51°44'38.2"N 1°19'56.8"W - see Fig. S1) which consists of two woodland fragments of 9 and 5 hectares in area, with dominant tree species oak *Quercus* sp. and black alder *Alnus glutinosa*. The study site is approximately 500m south of Wytham Woods, Oxford, UK which is home to a long-term study population of great tits that have been monitored under standard protocols since the 1960s

(Perrins 1965). As the distance between this study site and Wytham is less than the median great tit dispersal distance (males = 558m, females = 879) (Greenwood et al. 1979), the individuals within this study form a sub-part of main Wytham Woods population. We installed 74 woodcrete nestboxes (Schwegler 26mm design) into Denman's Copses ('Denman's A' = 48 nestboxes, 'Denman's B' = 26 nestboxes) on March 1st 2011. The density of boxes in these plots was therefore ~5 per hectare, which compares with ~3 per hectare for Wytham as a whole. Hence, we considered that potential nest sites were provided in considerable excess.

During March-July each year, all nestboxes were visited frequently to record breeding attempts, reproductive data (e.g. lay date, clutch size, fledged young) and to capture adults (Days 7-14 of nestling phase) and nestlings (after Day 15) to mark them with a BTO (British Trust for Ornithology) metal leg ring and record morphometric information. Mist-netting was carried out throughout the winter (September to February) to capture immigrant birds. This protocol, which is also carried out across Wytham as a whole, results in ~70-90% of the great tit population in Wytham being tagged at any one time (Aplin et al. 2013, Matechou et al. 2015). Specifically, within Denman's copses, the tagging that took place prior to this study began at the beginning of the breeding season in 2011 (i.e. capturing at the nestbox) and also took place from September 2011 until March 2012 using mist-netting (with particularly intensive trapping sessions in February 2012 based in close proximity to sunflower seed dispensing feeders placed throughout the area). Again following the standard protocol used across Wytham Woods, the sex of captured birds (including those captured previously) was determined using breeding traits during spring with >95% confidence (presence of brood patch or cloacal protuberance in females and males, respectively) or plumage traits during winter with >90% confidence i.e. wing length/size of black breast patch for great tits (Svensson 1992). The presence/absence of juvenile greater covert feathers was used to determine the age of birds not ringed as nestlings as either 'juvenile' or 'adult' (Svensson 1992) and this binary measure was used throughout the analyses.

Since 2007, all captured great tits in the Wytham study have also been fitted with an RFID tag, which consists of a unique microchip incorporated into a plastic leg ring (IB technology, Bucks, UK). RFID tags allow the automated recording of individuals when they are in close proximity to an RFID detection system (Bonter and Bridge 2011). In late February 2012, we fitted RFID detection systems (Dorset ID, Aalten, The Netherlands) onto each nestbox in Denman's copses. The antennae were attached to the front of entrance holes with adhesive tape and scanned for RFID tags twice per second from before dawn until after dusk, automatically recording the time and identity of all tagged birds' visits. The antennae were removed on 19th April 2012 except for at nestboxes in which the female was still laying (the final antenna was removed on 24th April). Video recording of the same RFID antennas attached to feeding stations revealed that >99% of visits by RFID tagged birds were successfully recorded. This is similar to reportedly high accuracy and exceptionally low error rates of RFID recording on pied flycatcher and blue tit nestboxes (Schlicht et al. 2015, Schuett et al. 2017). Failure of the RFID recording devices is also exceptionally rare, and we carried

out full checks of each device at least once every three days whilst changing the batteries.

Data analysis

We examined the frequency, spatial arrangement and temporal occurrence of nest box visits and how this related to individual reproductive output. Following previous work, we considered visits at the daily resolution, whereby a 'visit' refers to an individual entering and/or landing on the nestbox entrance at least once during that day (Firth and Sheldon 2015, Sánchez-Tójar et al. 2017). We included all individuals that were known to be present at the study site before March (i.e. that had been detected at a RFID-equipped feeding stations or during trapping sessions). Throughout the analysis, we define 'breeders' as individuals detected breeding in nestboxes (at any point in spring 2012), and 'non-breeders' as those that were not known to breed that year but were known to be present in the study area. It is possible that 'non-breeders' nested in natural cavities or outside the study area. However, no great tits were observed nesting in natural cavities in the study area despite our searches (visual observations and listening for alarm calls) during nest rounds. Further, despite extensive monitoring of surrounding woodland as part of the long-term study, only 1 bird detected on the nestboxes in our study site attempted to breed elsewhere. Therefore, we considered the likely proportion of natural cavity nesting or dispersing breeders to be very small. All statistical analyses were implemented in R (R Core Team 2015) and utilised packages ggplot2 (Wickham 2009), lme4 (Bates et al. 2015) and glmmADMB (Fournier et al. 2012)

Visiting Frequencies

We examined how individual characteristics were related to the frequency of visitations to breeding sites by assessing the relationship between the number of different nestboxes each individual visited prior to the egg-laying period (pre-April) and its age, sex, and breeding status. We used generalised linear models (GLMs) with a negative binomial error structure to account for overdispersion within the standard Poisson modelling of the count-based data (Hardin and Hilbe 2007) to determine the effect of each individual characteristic on the number of nestboxes visited. Second, we assessed how individual characteristics influenced the frequency distribution of birds' visitations to nestboxes: first, we defined each individual's 'preferred nestbox' as their most visited nestbox (i.e. that which was visited on the greatest number of days). For this part of the analysis, we excluded individuals that did not have a clearly defined preferred nestbox (5/73) due to them not having a single nestbox which they visited the most (i.e. two or more nestboxes which they visited their maximum number of times). Following this, we fitted a zero-truncated negative binomial GLM (as only individuals recorded visiting their preferred nestbox on at least one day were included) to assess how the number of visits (over days) each individual made to their preferred nestbox was related to their age, sex and breeding status. We included the total number of nestboxes visited as a fixed effect to control for general breeding site visitation propensity.

Spatial Patterning

We calculated the distance individuals moved from their preferred nestbox (see above) to each of the other nestboxes they were recorded at. We used this to determine the spatial patterning of their visits. For the five individuals that had more than one preferred nestbox, we used the spatial midpoint between their most preferred nestboxes as the position, and we did not include the distances to either nestbox in the analysis. To examine the general spatial pattern of breeding site visitation across individuals, we first compared the distribution of distances to other visited nestboxes (from their preferred nestbox) to those generated using a randomization procedure. In this process, we maintained each individual's preferred nestbox, and randomly reassigned each of the other nestboxes they visited to another nestbox within the same subplot of woodland (Fig. S1), and then recalculated the distances. By running this randomization process 10,000 times and each time calculating the mean distance, we were able to compare the spatial clustering of observed nestbox visits to that expected if individuals maintained the same preferred nestbox and number of other nestboxes visited but randomly visited these other nestboxes within the same small subplots of woodland. We also evaluated how individual characteristics influenced the spatial arrangement of the nestboxes an individual visited. We ran a linear mixed model with the distance of each individual's visited nestboxes (from their 'preferred nestbox') as the response variable (log transformed), and age, sex, breeding status and total number of unique nestboxes visited as the fixed effects, and individual ID as a random factor.

Temporal Trends

Visits to potential breeding sites may also be expected to vary depending on an individual's own breeding stage. Therefore, we assessed how breeders' visits to nestboxes other than their own nestbox changed in relation to the stage of their own reproductive attempt, specifically in relation to egg-laying. We calculated the number of visits each bird made to other nestboxes each day, and included days with no records at any other nestboxes as 0. We scored the start of their own egg laying (i.e. their own nest's 'laydate') as 0, and scored days prior to egg laying as negative values and those following it as positive values. We set 'days to laying' as a fixed effect in a GLMM with a Poisson error structure with 'number of other nestboxes visited that day' as the response variable, and individual ID as a random factor. This simple model allowed us to quantify the general temporal trend in visitations to other nestboxes. To allow us to determine how individual characteristics may influence the temporal trends in breeding site visitations, we created another model which also fit individual age and sex as fixed effects but also included the interaction of each of these with the 'days prior to laying' variable.

Breeding site visits and subsequent reproduction

Finally, we assessed the relationship between breeding site visits and individual reproductive output. We used three models to consider three different reproduction variables: first egg laying date ('laydate'), clutch size, and fledging success. We ran separate models for each of these response variables (see below). Reproductive variables potentially affect one another (Verhulst and Nilsson 2008, Charmantier and Gienapp 2014); therefore we included laydate as a covariate in models considering clutch size and fledging success. Similarly, the

raw number of fledglings produced is partly dependent on clutch size. Therefore, fledgling success (per nest) was modeled as a binomial response variable, specified as the number of fledglings produced given the total clutch size i.e. the number fledged as 'successes' and the number not fledged as 'failures' within this binomial response. The number of fledglings that could have been produced but were not (i.e. 'failures') was due to hatching failure or nestling mortality. As fixed effects of interest within all of the models, we considered three aspects of nestbox visitation behaviour for each individual in the 30 days prior to laying: the total number of nestboxes they visited, the total number of visits they made to their own subsequent breeding site (i.e. the number of days they visited it), and the average distance between their breeding site and other visited nestboxes (log scale). We also controlled for individual age and size by including them as explanatory variables. Size was included in the models as the first principal component (PC1) of a scaled principal component analysis including wing length, tarsus length and the most recent measure of body mass. This measure held a minimum correlation of 0.54 with each body size measurement. As the breeding success (and visitation behaviour) of the male and female at any given nest is non-independent, each of the models was run twice; once considering females and once considering males.

Data deposition

Data available from the Dryad Digital Repository: < <http://dx.doi.org/10.5061/dryad.8nm8r6s> > (Firth et al. 2018).

RESULTS

Automated recording of nestbox visitation patterns during the spring of 2012 resulted in 599,828 RFID detections at 74 nestboxes from 80 great tits, 18 of which had been tagged in the study area the year before, while the remaining 62 were tagged in the months before the start of nestbox recording. This resulted in a dataset of 3,599 'daily visits' i.e. a unique individual detected on a particular box in a given day.

Visitation Frequencies

The majority of birds (70/80) inspected nestboxes in March, and age and breeding status were significantly related to the number of nestboxes visited, with juveniles visiting more nestboxes than adults and breeders visiting more nestboxes than non-breeders (Fig 1a; Table 1a), while sex had no effect. The same results were found when considering the 30 d period before each individual's laydate (instead of March) (Fig. S2a – Table S1a). The distribution of great tits' visits to nestboxes varied between individuals (Fig. 1b;c). On average an individual's 'preferred nestbox' (i.e. their most visited nestbox – see Methods) was visited 4.9 ± 0.9 (mean \pm SE) times more often through March than their second most visited nestbox, and 9.6 ± 1.4 times more often than the third. Most birds which bred in the plot (breeders) generally did so in their most visited (26/37 detected through March) or second or third most visited nestbox (6 and 3 individuals respectively). Subsequent breeders were found to visit their 'preferred nestbox' on more days through March than subsequent non-breeders, whilst age, sex and the total number of nestboxes a bird visited had no significant effect on this (Fig. 1b;1c; Table 1b; Fig. S3). Similarly, the results were again

consistent when considering 30-days before each individual's laydate (Figure S2b;S2c – Table S1b).

Spatial Patterning

The nestboxes individuals visited were significantly closer to their preferred nestbox than expected under the null model which maintained the number and subplot of the nestboxes each individual visited (randomisation test comparing sample to 10,000 permutations $p < 0.001$). Indeed, the observed average total distance between individuals' preferred nestbox and their other visited nestboxes was around half than that generated in the simulations (observed mean distance = 77m, 95% range of mean distances generated from null model = 145-166m). Therefore, nestbox visitations were generally clustered around a preferred point. As intuitively expected, the total number of nestboxes an individual visited was related to the distances of the nestboxes from their preferred nestbox, with those visiting the most nestboxes also visiting nestboxes furthest away (Table 1c). Controlling for this relationship within the model, non-breeders travelled significantly further than breeders from their most visited nestbox (Fig. 2) but no significant differences were found between sexes or age categories (Table 1c, Fig. S4). Therefore, breeders' nestbox visitations were more spatially clustered around a preferred nestbox than non-breeders.

Temporal Trends

Overall, breeding individuals decreased the number of other nestboxes visited as their own laydate drew closer (GLMM not considering any individual factors: 'days before laying' coef = -0.0354 ± 0.0037 , $z = -9.517$, $p < 0.001$). However this effect differed significantly between males and females (GLMM including individual factors: 'days before laying' and 'sex' interaction coef = -0.058 ± 0.008 , $z = -7.117$, $p < 0.001$ – Table S2). A marked difference between the sexes became apparent particularly from c. 2 weeks before egg-laying: females strongly reduced their visits to other nestboxes up to laying, while males only reduced their visits to other nestboxes after their own female had laid (Fig. 3). There was no significant effect of age on the temporal trend of visitations to other nestboxes ('days before laying' and 'age' interaction coef = -0.015 ± 0.008 , $z = -1.824$, $p = 0.068$ - Fig. S5, Table S2).

Breeding site visits and subsequent reproduction

Across breeding females, nestbox visiting behaviour was significantly related to all three aspects of reproduction. In particular, the distance between their nestbox and other nestboxes visited in the 30 days prior to egg laying was a particularly important factor in relation to reproduction, as it held a significant negative relationship with laydate, clutch size, and relative fledging success (even when controlling for other aspects of nestbox visitation behaviour, age, and size - Table 2a). The proximity between a female's breeding site and the other nestboxes visited before laying was positively related to later egg laying date. Yet, those travelling larger distances between their breeding site and other nestboxes (i.e. reduced proximity) had relatively larger clutch sizes and higher fledgling success given these later laydates (Table 2a). Within these models, laydate was also positively related to the number of nestboxes a female visited (i.e. birds that visit more nestboxes lay later) and clutch size was negatively

related to the number of visits to their own nestbox. No other factors were found to hold significant relationships to the reproductive variables.

Males' nestbox visitation patterns generally only held non-significant relationships with reproduction at their nest, apart from a negative relationship between the number of visitations to their own breeding site before laying and relative fledging success (Table 2b). All the significant relationships (n=6 – Table 2; Table S3) found between female and male nestbox visitation behaviours and reproductive variables remained consistent and statistically significant upon removing age and size separately or both together from the models (with the exception that not controlling for female size reduced the significance of the relationship between laydate and female's spatial distance but maintained a consistent effect - Table S3).

DISCUSSION

We show that great tits visit a large number of breeding sites in a spatially clustered, and temporally-variable manner. Further, this behaviour is related to individual characteristics (breeding status, age and sex) and subsequent reproductive output. Below, we discuss how these results illuminate the mechanisms that may be driving this visitation behaviour, and offer insights into the importance it may hold for individual fitness.

The pattern of breeding site visits and their relationship with individual traits allows further development of the previously proposed hypotheses regarding their function (i.e. gaining information on preferable breeding sites, territorial behaviour, or pursuing EPMs). For example, common terns (*Sterna hirundo*) appear to compare potential future breeding sites and often nest in the area they prospected most (Dittmann and Becker 2003, Dittmann et al. 2005, Becker et al. 2008), and experimental increases in pied flycatcher brood size are correlated with increases in visitors to the nest (Schuett et al. 2017). Our data also show that individuals visit many different nestboxes, and therefore have the potential to gain a lot of information (Fig 1). However, if such visits were to inform future settlement decisions by increasing knowledge of the most suitable habitat for young rearing, then birds may be expected to explore a relatively wide area, in order to overcome the spatial autocorrelation of environmental factors affecting breeding success (Wilkin and Sheldon 2009). Contrary to this expectation, we observed a tight spatial clustering of the visits, which was particularly prominent among those birds that eventually bred (Fig. 2). Further, if visits to breeding sites were aimed at optimizing breeding success through gaining social information on site quality and breeding success at other nests (Doligez et al. 2002, Doligez et al. 2004, Danchin et al. 2004, Schuett et al. 2017), then visits should primarily occur during the time when reproductive success can be assessed (e.g. chick feeding and fledging period). Yet, the majority of visits occurred 30 days before the egg laying period, and this decreased as laying approached (particularly for females - Fig. 3). Indeed, visits to other nestboxes are extremely rare 10-20 days following laying (Fig. 3; Fig. S5). In line with this, observations throughout the Wytham system show it is highly infrequent that a non-parental adult will be recorded at a nestbox over the chick-rearing period (<1% of occasions) when

short-term RFID nestbox monitoring is used to identify adults. Thus, the timing and spatial clustering of nestbox visits we observed does not offer substantial support that breeding site visitations are a way of gaining information for future breeding attempts. Similar results have been found for blue tits, where only 2% of individuals that performed a visit to a particular neighboring nestbox bred in that nestbox in the next year (Schlicht et al. 2015). Thus, it may be the case that non-migratory great tits and blue tits are more familiar with the general breeding area than migratory species and therefore do not rely on gaining social information to inform future breeding settlement decisions.

Territorial behaviours (establishing and maintaining a breeding area) have typically been assessed by drawing comparisons between individuals' observed breeding locations and putatively important variables (Hinde 1956, Greenwood and Dawson 2011). More recent studies have used tracking technologies to link fine-scale breeding site visitations to territorial behaviour (Sánchez-Tójar et al. 2017). We found that, even 30 days before egg laying, birds generally had a strong preference for a particular nestbox (Fig. 1b;1c; Fig. S3). Birds which successfully bred were characterised by significantly higher numbers of visits to their preferred nestbox than non-breeders. They also often subsequently bred in their preferred nestbox, and showed increased spatial clustering of their visits in comparison to non-breeders. Furthermore, our findings of older birds visiting fewer nestboxes than juvenile birds is also suggestive of territorial behaviour, and in line with previous work on house sparrows (Sánchez-Tójar et al. 2017), as younger individuals may struggle to establish territories and obtain nest sites and may have to visit more potential breeding sites due to the territorial behaviour of their older competitors (Jakobsson 1988, Cadiou et al. 1994). In the case of this study, philopatry (maintaining a territory from year-to-year) was rare, as not a single nestbox was occupied by the same pair from the previous year (2011), and only 3 individuals (but with different partners) were recorded in the same nestbox from year-to-year. Indeed, the majority of breeding birds (>72%) in 2012 had not been recorded breeding in any of the site's 74 nestboxes in the previous year. Therefore, our results suggest active territoriality each year may at least partly explain the age and breeding status related differences in breeding site visitation patterns.

A large proportion of socially monogamous species engage in EPMs (Griffith et al. 2002), and this has previously been proposed as an explanation as to why individuals visit various breeding sites (Kempnaers et al. 1992, Schlicht et al. 2015). Past research has suggested that male birds visit other breeding sites to pursue EPMs, with larger, older, more competitive individuals doing this most frequently (Buitron 1983, Westneat 1988, Stutchbury 1998). Supporting this, larger male blue tits visit other nesting sites more often than smaller individuals, and visits usually occur when the occupying female is present and also correlate with gaining extra-pair paternity at the visited nest (Schlicht et al. 2015). Our data also suggest that visits may be linked with EPMs as the concentration of visits around the preferred nestbox corresponds to the commonly observed pattern of individuals engaging in EPMs with close neighbours due to their proximity (Griffith et al. 2002). Further, the temporal patterning of male and female visitations differed strikingly (Fig. 3). Whilst females show a gradual

reduction in the number of visits they make to other nestboxes in the 30-days before laying, males maintained their visitation rates until laying commenced. The timing of these visitations could facilitate obtaining paternities at neighbouring nests. Indeed, a large sex difference in visits to other nestboxes is evident during the period immediately prior to laying (5 days before), when great tits (and other tit species) are expected to be most fertile (Mace 1987, Kempenaers et al. 1995, Hoi 1997, Magrath et al. 2009). Thus, if a male's own fertility is correlated with his partner's fertility, or if neighbouring females' fertility is correlated, this time period would present the best opportunity to seek EPMs. Interestingly, this temporal pattern contrasts with that found in blue tits, where male visit rates were unrelated to their female's own laying date (Schlicht et al. 2015).

Although extra-pair paternity may contribute to reproductive output for great tits, success within their own brood is likely to be the primary component (Patrick et al. 2012, Firth et al. 2015a, Griffith et al. 2002). Earlier studies have considered the relationship between breeding site visitations and productivity at the patch level (rather than between individuals within patches) and found that higher rates of prospecting generally relate to increased reproductive output (Bollinger and Gavin 1989, Cadiou 1999, Danchin et al. 1998, Brown et al. 2000, Calabuig et al. 2008, Calabuig et al. 2010). Recent studies have concluded that RFID tracking offers a new opportunity to examine how breeding site visitations relate to individual-level reproductive success (Schlicht et al. 2015, Sánchez-Tójar et al. 2017, Schuett et al. 2017). We consistently found that the spatial clustering of females' visits to other nestboxes was related to reproduction. Tight spatial clustering was associated with later laydates, yet positively correlated with clutch size and fledging success (Table 2a). This either suggests that concentrating breeding site visitations around their own breeding site may afford females benefits in terms of reproductive output (e.g. a well-established territory) or is correlated to another aspect of female/site quality which increases fitness (e.g. if more territorial females also have higher success).

Another aspect of breeding site visitation behaviour related to reproduction was the number of visits an individual made to their breeding nestbox prior to laying. Interestingly, while frequently visiting their future breeding nestbox is related to lower reproductive output for breeders in terms of reduced clutch size for females and lowered fledging success for males (Table 2), the number of visits to a preferred breeding site appears to initially increase the likelihood of breeding at all (Table 1; Fig. 1b-c). This suggests a possible trade-off, whereby focusing attention onto a particular site heightens the chances of gaining residence and being able to breed but also inhibits the chances of maximizing reproductive output upon breeding (potentially due to increased prior energy expenditure, or through early dedication to a particular nestbox limiting future options).

Our findings also indicate various areas for investigation in future work. Firstly, combining RFID tracking of visitation behaviour with manipulative experiments (Firth and Sheldon 2015) will also allow further advances in uncovering the causal relationships within breeding site visitations, such as through utilizing brood-size manipulations to examine social information usage (Schuett et al.

2017). Further, while this study takes an individual-based approach (examining each individual's own behaviour in relation to their own state), future work could also examine the interactive effects of not only the traits and state of the visiting bird, but also the traits of the individual whose nest-site they are visiting. This could, for example, shed light on how much information individuals store regarding the characteristics of others, or elucidate how the traits of a subsequent breeder influence the territorial interactions with other individuals visiting their chosen breeding site, or whether males assess the reproductive state of surrounding females and if this determines their own activity. Indeed, considering how dyadic-level properties shape breeding site visitations would also enable the examination of the social drivers of this behaviour. For instance, previous work within our system monitored flocking behaviour during winter and subsequent breeding behaviour during spring and demonstrated that birds which form winter flocks together subsequently prospect nesting sites together, and ultimately form mated pairs or breed close to one another as territory neighbours (Firth and Sheldon 2015, Firth and Sheldon 2016, Firth et al. 2015b). Thus, such an approach, combined with examining the interactive effects of the characteristics of the visitor and the individual whose nestbox they are visiting, would help identify how prior social associations and familiarity directly shape breeding site visits.

In conclusion, we demonstrate that great tits frequently visit a relatively large number of potential breeding sites in structured spatio-temporal patterns. The frequencies, spatial clustering and temporal patterning of visitations, and the relationship these hold with individual characteristics, suggest that territorial behaviour and extra-pair mating opportunities may be the primary underlying drivers of this behaviour. Although we demonstrate that aspects of visitation behaviour may be related to fitness, and that this may differ depending on sex, further work considering the interactions between individuals, along with experiments, is now needed to clearly elucidate the causal effects of breeding site visitations.

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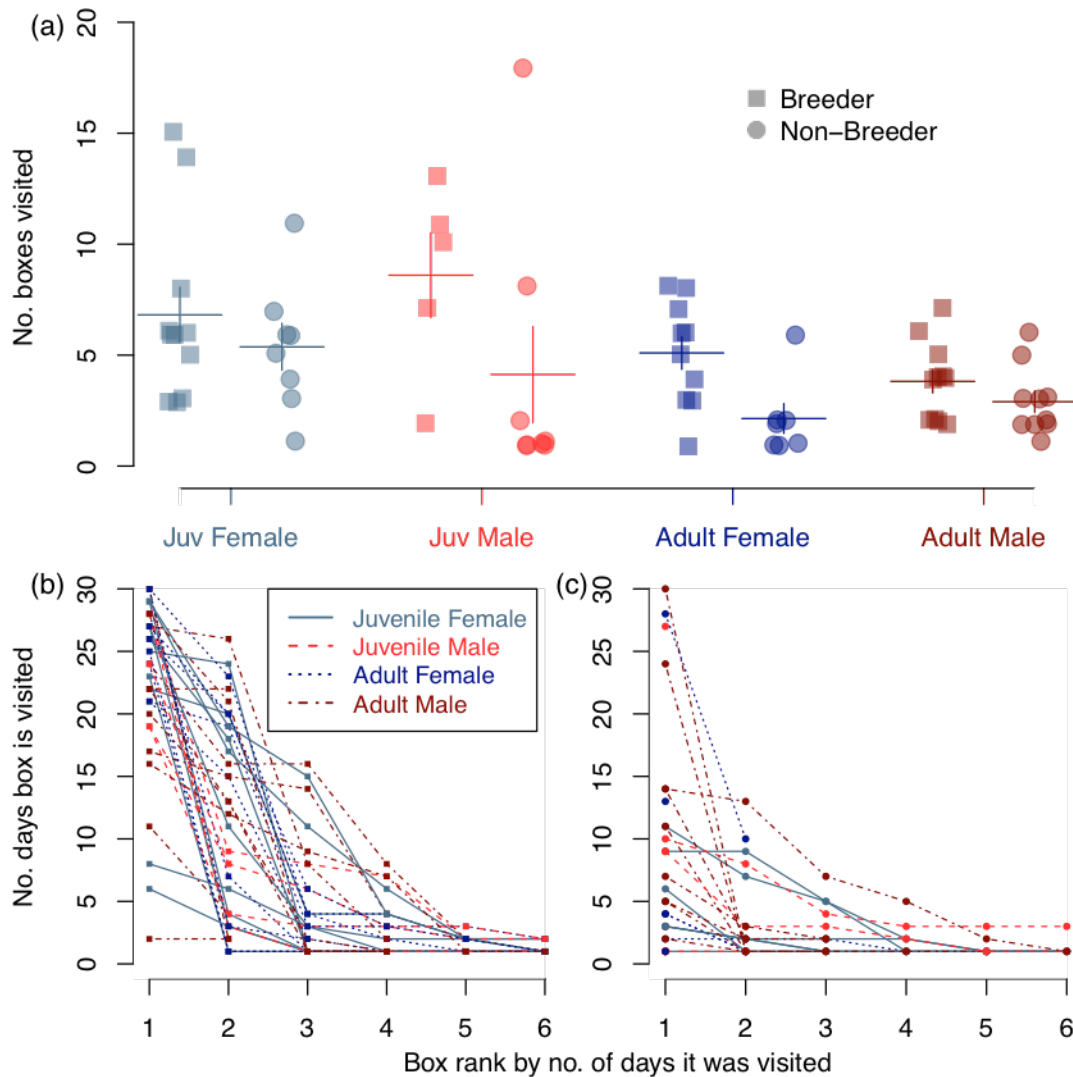
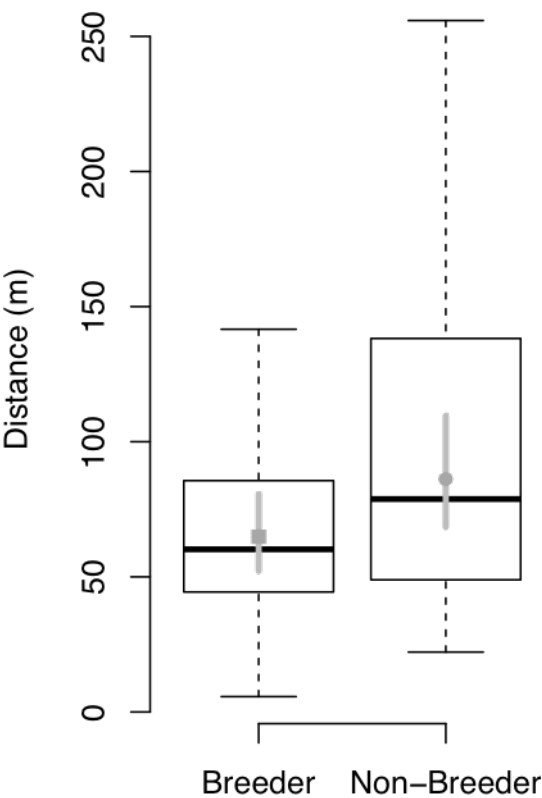


Figure 1. (a) Total number of boxes visited through March per individual by age and sex (as denoted by colour). Breeders are shown as squares (left) and non-breeders as circles (right). Points are semi-transparent and slightly jittered to show overlap. Horizontal lines show the mean of the raw data and the vertical lines show standard error around this. (b) Distribution of daily visits over the boxes visited by birds recorded breeding and (c) non-breeders (i.e. birds not recorded breeding in 2012). A steep decline in visits indicates that a bird's visits are particularly concentrated over a few boxes while making only occasional visits to others. Conversely, a slow decline reflects a rather even distribution of visits across boxes.



775
776 Figure 2. Distance between individuals' most visited nestbox (their i.e. 'preferred
777 nestbox') and the other nestboxes they visited for breeders (left) and non-
778 breeders (right). Boxplots show the raw data where the box shows interquartile
779 range (IQR), whiskers shows range (with values outside 1.5 times IQR excluded)
780 and mid horizontal lines show median. Grey points with vertical grey line show
781 the LMM estimate and standard error (where plotted points denote the
782 estimated 'average' individual visiting the mean number of boxes – Table 1 for
783 model details).
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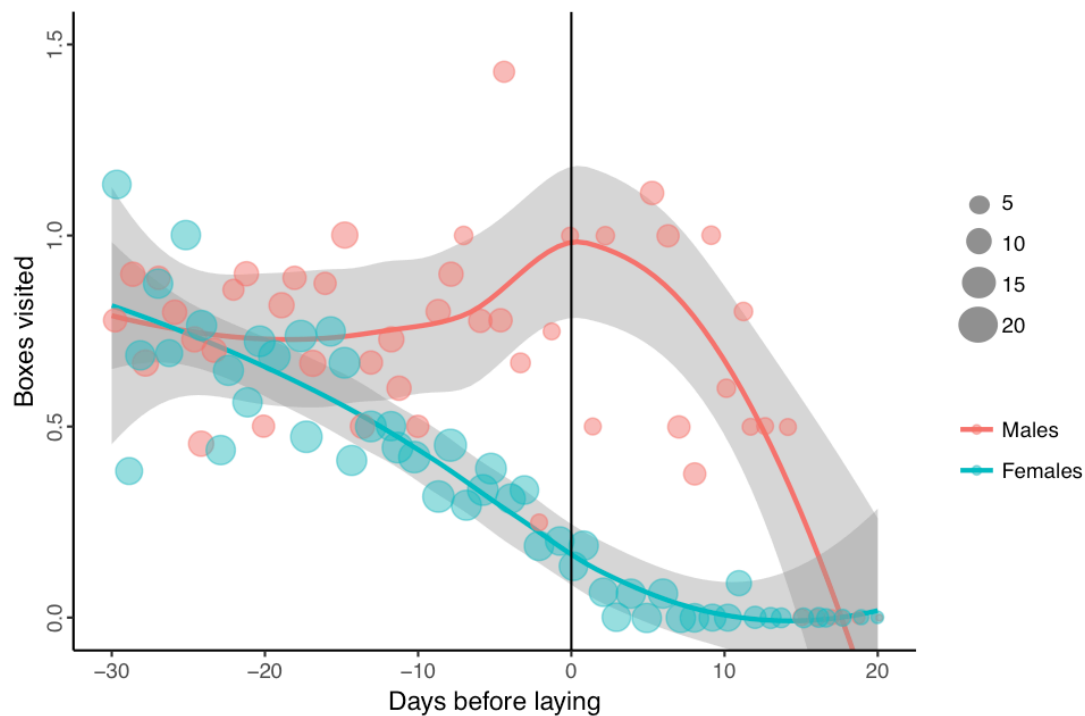


Figure 3. Temporal trends in visits by great tits to nestboxes; red indicates males and blue indicates females. The y-axis shows the mean number of boxes (excluding its own box) visited by individuals of a given sex each day. Day is relative to the lay date at its own nest box (shown as the vertical black line), and includes days when the bird was not recorded on any box during the logging period. Points show the data as the mean value for each sex on each day and the size of the point represents sample size (i.e. number of individuals the mean was calculated over). To illustrate the temporal trend, smoothing lines (based on the raw data points) show local polynomial regression fit smoothing (by least squares) and associated standard error, with degree of smoothing and polynomials set as 0.75 and 2 respectively using ggplot2 (Wickham 2009).

Table 1. Individual characteristics and nest-site visiting behavior. Model outputs for each of the three responses considered are given, with the estimate (\pm standard error), associated t (or z) value, and the p value for each factor. The breeding status estimate is shown in relation to non-breeders compared to breeders, the sex estimate for males compared to females, and the age estimate for adults compared to juveniles.

<i>Response</i>	<i>Factor</i>	<i>Estimate (\pmSE)</i>	<i>t/z</i>	<i>p</i>
<i>(a) No. boxes visited</i>	<i>Intercept</i>	1.943 \pm 0.134	14.472	<0.001
	<i>Breeding Status</i>	-0.579 \pm 0.165	-3.516	<0.001
	<i>Age</i>	-0.417 \pm 0.162	-2.580	0.010
	<i>Sex</i>	0.027 \pm 0.160	0.166	0.868
<i>(b) No. visits to preferred box</i>	<i>Intercept</i>	3.069 \pm 0.191	16.029	<0.001
	<i>Breeding Status</i>	-1.166 \pm 0.164	-7.122	<0.001
	<i>Age</i>	0.113 \pm 0.144	0.782	0.434
	<i>Sex</i>	-0.059 \pm 0.131	-0.451	0.652
	<i>No. boxes</i>	0.009 \pm 0.020	0.438	0.662
<i>(c) Distance (log metre)</i>	<i>Intercept</i>	3.703 \pm 0.157	23.512	<0.001
	<i>Breeding Status</i>	0.283 \pm 0.104	2.720	0.008
	<i>Age</i>	-0.035 \pm 0.122	-0.284	0.777
	<i>Sex</i>	-0.084 \pm 0.103	-0.814	0.419
	<i>No. boxes</i>	0.056 \pm 0.014	4.146	<0.001

Table 2: Results of models relating breeding birds' reproduction (laydate, clutch size, fledging success) to their nestbox visitation behaviours (Number of unique boxes visited ('No. Boxes'), number of visits to their breeding site ('Site Visits'), log distance of other boxes visited from their breeding site (Distance) 30 days before laying. Age estimate is shown for adults compared to juveniles. Size refers to a composite size measure considering wing and tarsus length and weight (see Methods). Table columns (a) gives results for females and table columns (b) gives results for males.

<i>Response</i>	<i>Factor</i>	<i>(a) Female</i>			<i>(b) Male</i>		
		<i>Estimate</i>	<i>t/z</i>	<i>p</i>	<i>Estimate</i>	<i>t/z</i>	<i>p</i>
<i>Lay-date</i>	<i>Intercept</i>	74.8±25.5	2.93	0.01	104.9±77.3	1.36	0.22
	<i>No. boxes</i>	1.41±0.52	2.7	0.02	2.56±2.04	1.25	0.26
	<i>Own box visits</i>	-0.48±0.29	-1.68	0.12	-1.25±0.52	-2.39	0.05
	<i>Distance</i>	-13.75±5.94	-2.31	0.04	-16.31±19.6	-0.83	0.44
	<i>Age</i>	-3.7±3.24	-1.14	0.28	-7.55±7.51	-1.01	0.35
	<i>Size</i>	1.37±1.38	0.99	0.34	-5.54±3.44	-1.61	0.16
<i>Clutch Size</i>	<i>Intercept</i>	29.6±8.8	3.35	0.01	-1.83±12.4	-0.15	0.89
	<i>No. boxes</i>	0.27±0.17	1.52	0.16	-0.45±0.32	-1.39	0.22
	<i>Own box visits</i>	-0.19±0.08	-2.27	0.05	0.11±0.1	1.11	0.32
	<i>Distance</i>	-4.41±1.88	-2.35	0.04	2.14±2.91	0.73	0.5
	<i>Age</i>	0.11±0.89	0.12	0.91	-0.17±1.14	-0.15	0.89
	<i>Size</i>	-0.27±0.37	-0.72	0.49	0.52±0.58	0.89	0.41
	<i>Lay-date</i>	-0.15±0.08	-1.96	0.08	-0.01±0.06	-0.09	0.93
<i>Fledging Success</i>	<i>Intercept</i>	15.8±6.9	2.29	0.02	13.5±6.8	1.99	0.05
	<i>No. boxes</i>	0.05±0.14	0.37	0.71	0.06±0.18	0.32	0.75
	<i>Own box visits</i>	-0.08±0.07	-1.14	0.26	-	-	-
	<i>Distance</i>	-3.37±1.44	-2.34	0.02	0.3±0.65	0.47	0.64
	<i>Age</i>	-0.18±0.53	-0.33	0.74	-2.67±1.55	-1.72	0.08
	<i>Size</i>	-0.14±0.21	-0.69	0.49	-0.07±0.35	-0.19	0.85
	<i>Lay-date</i>	-0.09±0.05	-1.66	0.10	-0.04±0.03	-1.25	0.21

SUPPLEMENTARY INFORMATION: Spatial, temporal and individual based differences in nest-site visits and subsequent reproductive success in wild great tits

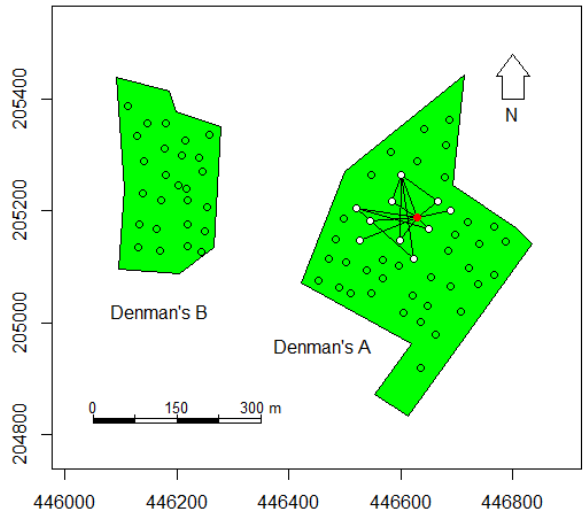


Figure S1. The study area 500m south of the main Wytham woodland. Denman's Copses comprises of (i) a 5 hectare site containing 26 nestboxes at coordinates 51°44'38.2"N 1°19'56.8"W (left-hand side) and 9 hectare site containing 48 nestboxes at coordinates 51°44'35.9"N 1°19'35.7"W (right-hand side). A example visitation pattern of a single bird (juvenile male) is shown. The red dot shows the individual's 'most visited box' and the lines indicate movement between boxes (in the order in which they were observed).

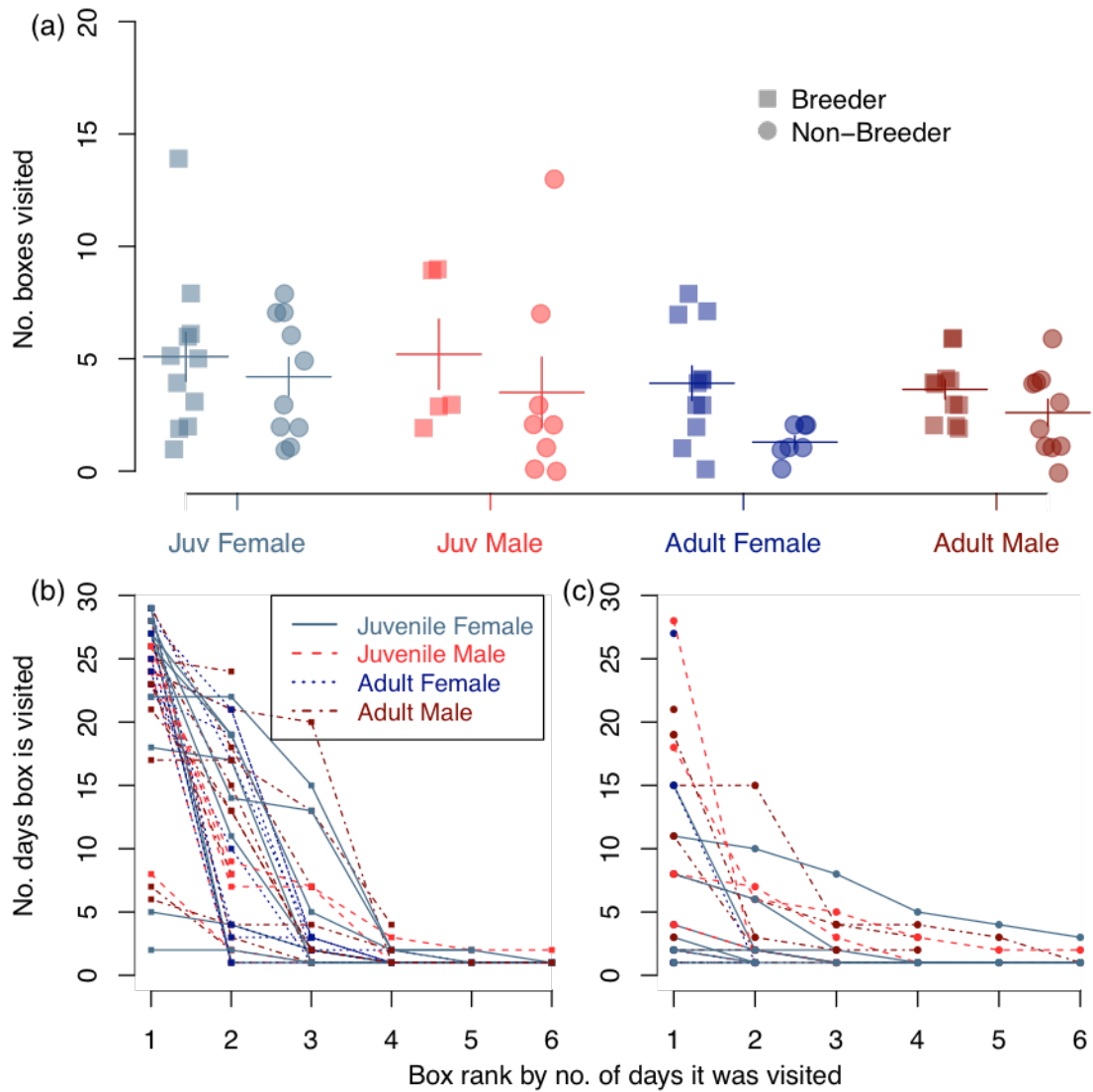


Figure S2. (a) Total number of boxes visited per individual by age and sex (also denoted by colour). Data only includes boxes visited 30 days before the individuals laydate, where individuals not recorded laying were assigned the mean laydate. Breeders are shown as squares (left) and non-breeders as circles (right). Points are semi-transparent and slightly jittered to show overlap. Horizontal lines show the mean of the raw data and the vertical lines show standard error around this. (b) Distribution of daily visits over the boxes visited by birds recorded breeding and (c) birds not recorded breeding. A steep decline in visits indicates that a bird's visits are particularly concentrated over a few boxes while making only occasional visits to others. Conversely, a slow decline reflects a rather even distribution of visits across boxes.

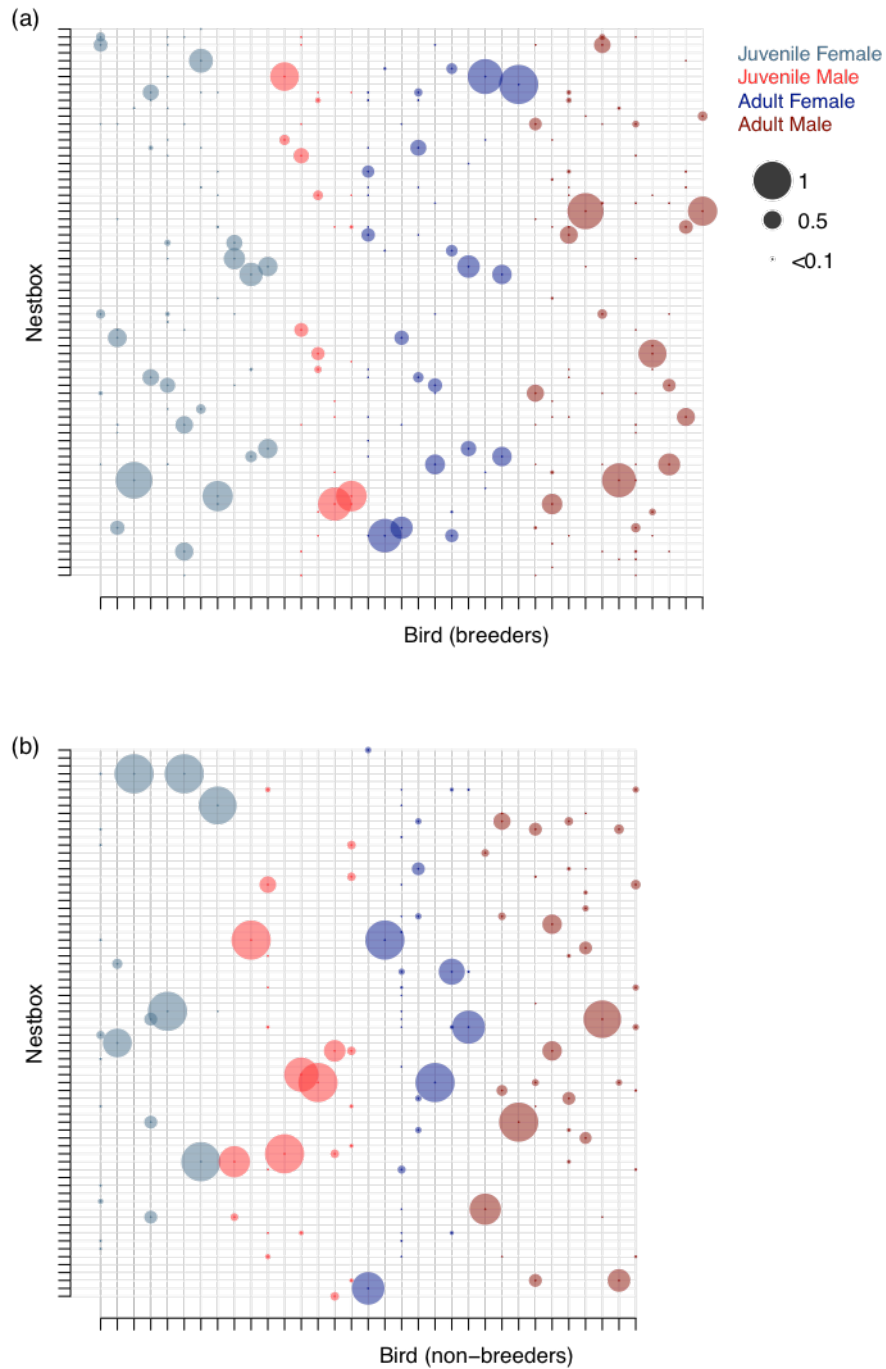


Figure S3. Distribution of proportions of each bird's (grid columns) daily visits to each of the 70 nestboxes (grid rows) through March 2012. Circle size represents the proportion of visits and circle colour shows the individual age and sex (see legend). Birds subsequently recorded breeding are shown in panel (a) and non-breeders are shown in panel (b). The nestboxes (grid row order) are consistent across both panels. Nestbox figure structure taken from Sánchez-Tójar et al. (2017).

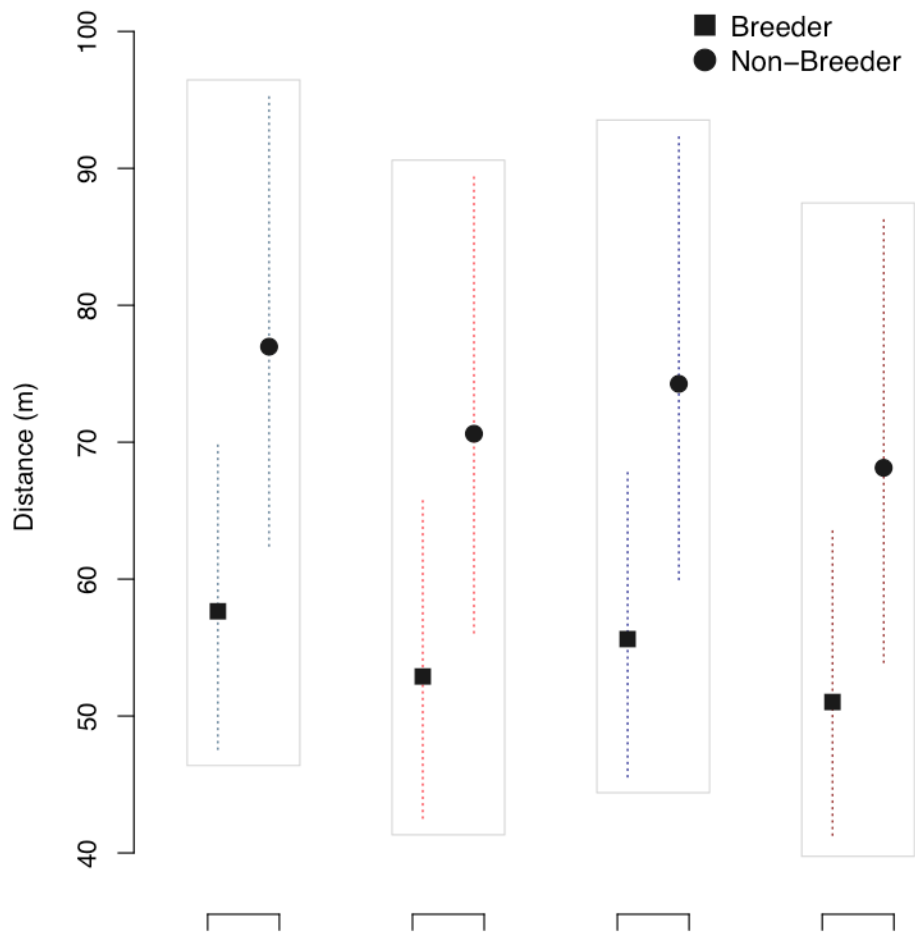
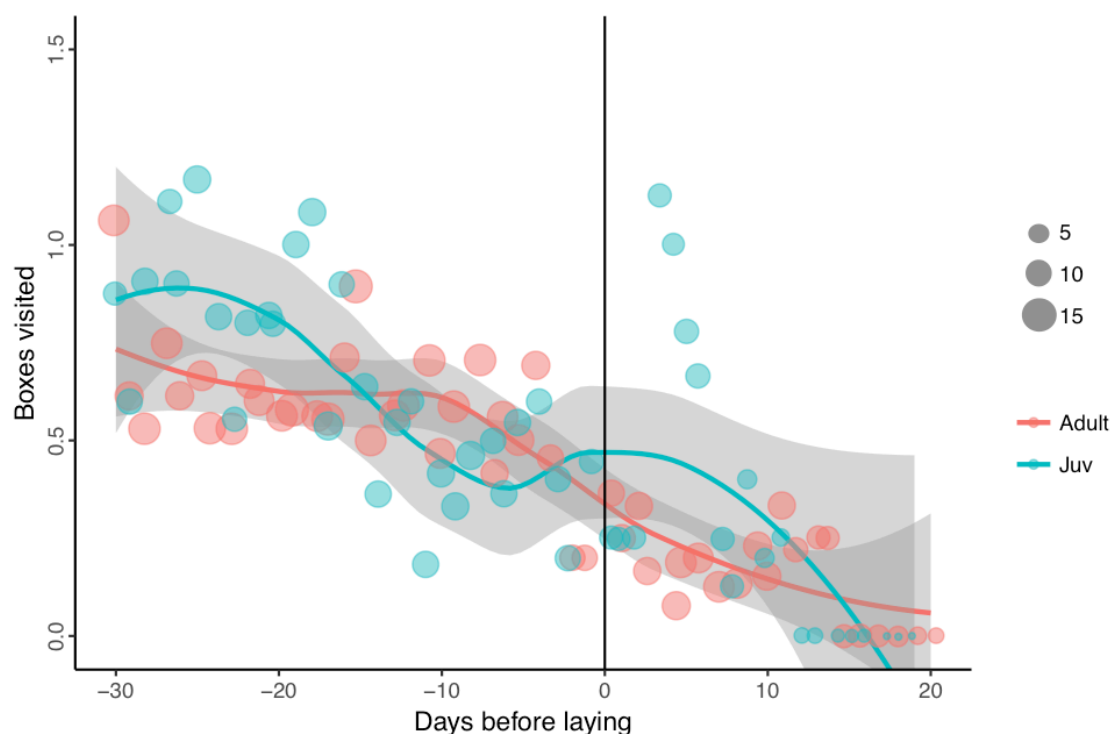


Figure S4. Distance between individuals' most visited nestbox (their i.e. 'preferred nestbox') and their other visited boxes per individual by age and sex (as denoted by line colour) and breeding status (as denoted by point shape). Points show LMM estimate controlling for number of boxes visited (Table 1) (where plotted points denote the estimated 'average' individual visiting the mean number of boxes) and dotted lines show standard error around this estimate.

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880 Figure S5. Temporal trends in visits from great tits to nestboxes, red indicates
881 adult birds and blue indicates juveniles (first-year birds). The y-axis shows the
882 mean number of boxes (excluding its own box) visited by individuals of each age
883 group each day. Day is relative to the lay date at its own nest box (shown as the
884 vertical black line), and includes days when the bird was not recorded on any
885 box during the logging period. Points show the data as the mean value for each
886 sex on each day and the size of the point represents sample size (i.e. number of
887 individuals the mean was calculated over). To illustrate the temporal trend,
888 smoothing lines (based on the raw data points) show local polynomial
889 regression fit smoothing (by least squares) and associated standard error, with
890 degree of smoothing and polynomials set as 0.75 and 2 respectively using
891 ggplot2 (Wickham 2009).

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Table S1. Full model results in relation to Figure S2. The relationship between individual characteristics and nestbox visiting behaviour for the 30 days prior to laying. Model outputs with the estimate (\pm standard error), and associated t (or z) value, and the p value for each factor. The breeding status estimate is shown in relation to non-breeders compared to breeders, the sex estimate for males compared to females, and the age estimate for adults compared to juveniles.

<i>Response</i>	<i>Factor</i>	<i>Estimate (\pmSE)</i>	<i>t/z</i>	<i>p</i>
<i>(a) No. boxes visited</i>	<i>Intercept</i>	1.67 \pm 0.141	11.86	<0.001
	<i>Breeding Status</i>	-0.446 \pm 0.167	-2.673	0.008
	<i>Age</i>	-0.353 \pm 0.165	-2.142	0.032
	<i>Sex</i>	0.008 \pm 0.164	0.048	0.962
<i>(b) No. visits to preferred box</i>	<i>Intercept</i>	2.948 \pm 0.201	14.66	<0.001
	<i>Breeding Status</i>	-1.074 \pm 0.171	-6.286	<0.001
	<i>Age</i>	0.14 \pm 0.148	0.946	0.344
	<i>Sex</i>	0.047 \pm 0.141	0.334	0.739
	<i>No. boxes</i>	0.021 \pm 0.028	0.752	0.452

Table S2. Full model results examining the temporal trends in breeders' visits to other nestboxes. Output shown for full GLMM (Poisson error structure) with individual as random effect. The sex estimate is shown in relation to males compared to females, and the age estimate is shown for adults compared to juveniles.

<i>Factor</i>	<i>Estimate</i>	<i>t/z</i>	<i>p</i>
<i>Intercept</i>	-0.086 \pm 0.373	-0.229	0.819
<i>Days before lay</i>	0.001 \pm 0.008	-0.066	0.947
<i>Sex</i>	-1.779 \pm 0.379	-4.700	<0.001
<i>Age</i>	-0.717 \pm 0.378	-1.895	0.058
<i>Days*Sex</i>	-0.058 \pm 0.008	-7.117	<0.001
<i>Days*Age</i>	-0.015 \pm 0.008	-1.824	0.068

Table S3. Additional supplementary models relating breeding birds' reproduction and nestbox visitation excluding (i) age, (ii) size and (iii) age and size. Following Table 2, models use laydate, clutch size, fledging success as response variables, each which includes all measures of nestbox visitation behaviours: Number of unique boxes visited ('No. Boxes'), number of visits to their breeding site ('Site Visits'), distance of other boxes visited from their breeding site 30 days before laying. Age estimate is shown for adults compared to juveniles. Size refers to a composite size measure considering wing and tarsus length and weight (see Methods). Table columns (a) gives results for females and table columns (b) gives results for males.

(i)		<i>(a) Female</i>			<i>(b) Male</i>		
<i>Response</i>	<i>Factor</i>	<i>Estimate</i>	<i>t/z</i>	<i>p</i>	<i>Estimate</i>	<i>t/z</i>	<i>p</i>
<i>Lay-date</i>	<i>Intercept</i>	73.56±25.81	2.85	0.01	133.57±71.95	1.86	0.11
	<i>No. boxes</i>	1.44±0.53	2.73	0.02	3.56±1.78	2	0.09
	<i>Own box visits</i>	-0.63±0.26	-2.42	0.03	-1.4±0.5	-2.79	0.03
	<i>Distance</i>	-13.2±6	-2.2	0.05	-25.39±17.41	-1.46	0.19
	<i>Size</i>	0.67±1.26	0.54	0.6	-4.71±3.34	-1.41	0.2
<i>Clutch Size</i>	<i>Intercept</i>	29.86±8.16	3.66	<0.001	-1.62±11.3	-0.14	0.89
	<i>No. boxes</i>	0.27±0.16	1.64	0.13	-0.44±0.29	-1.53	0.18
	<i>Own box visits</i>	-0.19±0.08	-2.42	0.03	0.11±0.09	1.22	0.27
	<i>Distance</i>	-4.47±1.74	-2.57	0.03	2.02±2.56	0.79	0.46
	<i>Size</i>	-0.25±0.31	-0.8	0.44	0.55±0.49	1.13	0.3
	<i>Lay-date</i>	-0.16±0.07	-2.22	0.05	0±0.05	-0.04	0.97
<i>Fledging Success</i>	<i>Intercept</i>	16.12±7.03	2.29	0.02	13.13±6.74	1.95	0.05
	<i>No. boxes</i>	0.06±0.14	0.42	0.67	0.04±0.18	0.24	0.81
	<i>Own box visits</i>	-0.09±0.06	-1.45	0.15	-0.13±0.06	-2.25	0.02
	<i>Distance</i>	-3.42±1.47	-2.33	0.02	-0.12±0.34	-0.36	0.72
	<i>Size</i>	-0.18±0.18	-1	0.32	-2.47±1.49	-1.66	0.1
	<i>Lay-date</i>	-0.09±0.05	-1.66	0.1	-0.05±0.03	-1.44	0.15

(ii)		<i>(a) Female</i>			<i>(b) Male</i>		
<i>Response</i>	<i>Factor</i>	<i>Estimate</i>	<i>t/z</i>	<i>p</i>	<i>Estimate</i>	<i>t/z</i>	<i>p</i>
<i>Lay-date</i>	<i>Intercept</i>	60.41±23.95	2.52	0.03	42.07±42.24	1	0.34
	<i>No. boxes</i>	1.16±0.5	2.3	0.04	1.7±1.78	0.96	0.36
	<i>Own box visits</i>	-0.45±0.25	-1.8	0.1	-0.53±0.34	-1.55	0.15
	<i>Distance</i>	-10.18±5.54	-1.84	0.09	-5.36±10.94	-0.49	0.63
	<i>Age</i>	-3.43±2.78	-1.23	0.24	-1.9±6.55	-0.29	0.78
<i>Clutch Size</i>	<i>Intercept</i>	26.3±7.65	3.44	<0.001	5.46±6.27	0.87	0.41
	<i>No. boxes</i>	0.22±0.16	1.4	0.19	-0.3±0.22	-1.37	0.21
	<i>Own box visits</i>	-0.12±0.07	-1.67	0.12	0.04±0.05	0.72	0.49
	<i>Distance</i>	-3.84±1.63	-2.36	0.04	0.82±1.56	0.53	0.61
	<i>Age</i>	-0.47±0.77	-0.61	0.56	-0.49±0.96	-0.51	0.63
	<i>Lay-date</i>	-0.14±0.07	-1.87	0.09	-0.04±0.04	-1.02	0.34
<i>Fledging Success</i>	<i>Intercept</i>	20.78±6.24	3.33	<0.001	9.4±4.17	2.25	0.02
	<i>No. boxes</i>	0.14±0.13	1.04	0.3	-0.02±0.15	-0.14	0.89
	<i>Own box visits</i>	-0.11±0.06	-1.88	0.06	-0.1±0.04	-2.65	0.01
	<i>Distance</i>	-4.42±1.31	-3.37	<0.001	0.27±0.61	0.45	0.65
	<i>Age</i>	-0.21±0.44	-0.47	0.64	-1.77±1.02	-1.74	0.08
	<i>Lay-date</i>	-0.12±0.05	-2.44	0.01	-0.03±0.03	-1.14	0.25

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(iii)		<i>(a) Female</i>			<i>(b) Male</i>		
<i>Response</i>	<i>Factor</i>	<i>Estimate</i>	<i>t/z</i>	<i>p</i>	<i>Estimate</i>	<i>t/z</i>	<i>p</i>
<i>Lay-date</i>	<i>Intercept</i>	58.12±24.31	2.39	0.03	43.01±40.32	1.07	0.31
	<i>No. boxes</i>	1.21±0.51	2.37	0.03	1.94±1.51	1.28	0.23
	<i>Own box visits</i>	-0.54±0.25	-2.16	0.05	-0.56±0.31	-1.78	0.1
	<i>Distance</i>	-9.62±5.62	-1.71	0.11	-6.01±10.25	-0.59	0.57
<i>Clutch Size</i>	<i>Intercept</i>	25.16±7.23	3.48	<0.001	5.98±5.89	1.02	0.34
	<i>No. boxes</i>	0.21±0.15	1.37	0.19	-0.27±0.2	-1.34	0.22
	<i>Own box visits</i>	-0.13±0.07	-1.77	0.1	0.04±0.05	0.76	0.47
	<i>Distance</i>	-3.62±1.55	-2.34	0.04	0.54±1.39	0.39	0.71
	<i>Lay-date</i>	-0.12±0.07	-1.81	0.09	-0.04±0.04	-0.95	0.37
<i>Fledging Success</i>	<i>Intercept</i>	21.15±6.44	3.29	<0.001	9.08±4.1	2.21	0.03
	<i>No. boxes</i>	0.14±0.13	1.08	0.28	-0.04±0.14	-0.27	0.79
	<i>Own box visits</i>	-0.12±0.06	-2.12	0.03	-0.1±0.04	-2.66	0.01
	<i>Distance</i>	-4.49±1.35	-3.33	<0.001	-1.61±0.95	-1.69	0.09
	<i>Lay-date</i>	-0.12±0.05	-2.4	0.02	-0.03±0.03	-1.27	0.2

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