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Winter territory prospecting is associated with life-history stage but not activity in a passerine

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Finding a high quality territory is essential for many animals to reproduce successfully. Despite its importance for fitness, we know little about the process of territory prospecting in wild birds, and whether individual traits and behaviours, such as personality, co-vary with territory prospecting. Here, we use long-term data from a wild, insular house sparrow *Passer domesticus* population to test three hypotheses about territory fidelity and prospecting: 1) house sparrows show high territory fidelity between years and also during winter. 2) Individuals will prospect for a breeding territory during their first winter whereas older, more experienced individuals will keep a territory from previous years and will, therefore, show no or reduced winter territory prospecting. 3) More active behavioural types will prospect more than less active behavioural types. We use data from four winters from automatically, daily recorded nest-box visits of 188 birds of known age. The number of nest-boxes that each individual visited within each winter was used as a proxy of winter territory prospecting. We show that house sparrows visit multiple nest-boxes during their first winter, whereas older individuals keep territories year-round and, potentially because of this, indeed show reduced winter territory prospecting. Activity was not associated with the number of nest-boxes visited. Further research is needed to investigate whether time of territory and mate acquisition differs among individuals and the possible effect on lifetime fitness.

A territory is commonly defined as a defended area (Noble 1939, Maher and Lott 1995). Many animals need a territory to raise their offspring, and thus an individual's fitness strongly depends on choosing and obtaining a good territory (e.g. birds: Cody 1985; and mammals: Groenendijk et al. 2015). Territory selection has traditionally been studied by comparing individuals' territory locations during one breeding season and any associated, potentially correlated variables (Verdolin and Slobodchikoff 2010, Greenwood and Dawson 2011, Harrison et al. 2011). Although territoriality is observed in a variety of taxa such as fish (Armstrong et al. 1997), mammals (Woollard and Harris 1990), and of course birds (Reed and Oring 1992), the actual process of territory prospecting – how animals search and gather information to ultimately obtain a territory (Reed et al. 1999, Calabuig et al. 2010) and what traits co-vary with it –, is not well described in wild populations. This is surprising since the process of prospecting for different territories is assumed to be costly in terms of time, risk taking, and other resources; a cost that is intensified by competition with other prospectors (Reed et al. 1999, Bonte et al. 2012). Furthermore, territories are often held over several years, thus the choice of which territory to settle in may have long-term fitness consequences across years (i.e. carry-over effects, O'Connor et al. 2014). Therefore, investigating territory fidelity and prospecting during one reproductive season alone is insufficient; a better approach would be to study territorial behaviours throughout the year and over multiple years (Marra et al. 2015).

Both early territory acquisition and holding one during breeding are usually associated with greater reproductive success in birds (Perrins 1970, Verhulst and Nilsson 2008, Matechou et al. 2015). It is expected that territory prospecting takes place early in the season (Ponchon et al. 2015), during which, inter- and intra-specific competition for nest sites is common, especially in birds (Semel and Sherman 2001, Kokko et al. 2004, Haynes et al. 2014). This competition is expected to promote individual variation in nest site (territory) prospecting behaviour and acquisition. Furthermore, as the capability to defend and keep a territory is likely to change during an individual's lifetime, territory prospecting can be expected to co-vary with age (Cadiou et al. 1994). For example, young individuals have greater

difficulties obtaining nest sites (Jakobsson 1988, Eikenaar et al. 2009), mates (Bayne and Hobson 2001) and extra-pair paternities (Cleasby and Nakagawa 2012), and have, possibly as a result of this, lower breeding success (Sasvári and Hegyi 2011) than older individuals. These differences might be explained by increasing experience with age, but they might also reflect different needs or different cost/benefit ratios at different life-history stages (Harts et al. 2016). Thus, in species that hold territories year-round and show high territory fidelity, first-time breeders, who need to acquire a territory for the first time, are expected to show more frequent territory prospecting than older, established territory owners.

Individual behavioural consistency or animal personality has been shown in many taxa ranging from spiders (Keiser et al. 2014) to lizards (Bajer et al. 2015) and birds (Hollander et al. 2008). Different individuals show different personalities and these differences are maintained over time and across contexts (Dingemanse and Réale 2005). Personality influences how individuals cope with life challenges, which in turn can affect survival and fitness (Santos et al. 2015). For example, differences in personality between individuals can be associated with differences in foraging (Amy et al. 2012, Kurvers et al. 2012), predation risk (Réale and Festa-Bianchet 2003), dispersal (Dingemanse et al. 2003, Cote et al. 2010), singing behaviour (Naguib et al. 2016) and nest site selection (Seltmann et al. 2014). Personality traits are often measured in captive single-individual (i.e. non-social) behavioural assays (Dingemanse et al. 2002, Quinn and Cresswell 2005). Although captivity allows the standardizing of environmental conditions, it excludes both the natural abiotic and social environment, which may impede assessing the ecological and behavioural relevance of the traits measured (Niemelä and Dingemanse 2014). Thus, if personality traits measured in captivity are ecologically relevant and maintained across contexts, we can expect that, for example, individuals that are highly active in captivity would show increased territory prospecting in the wild, and vice versa.

Most bird species need a territory to build a nest and lay their eggs. Secondary cavity nesters that accept nest-boxes, such as the house sparrow *Passer domesticus*, are a good model species to study territory fidelity and prospecting because their breeding attempts can be easily monitored and nest-box owners and prospectors can be identified by colour rings and transponders. House sparrows tend to breed in loose colonies and limit their territory to the immediate vicinity of their nest (-box) (Anderson 2006). This relatively small size of their territories further facilitates the study of territory prospecting in this species by allowing easy, automatic recording of territory (nest-box) visits made by prospectors. Additionally, the study of territoriality in the house sparrow may help us to better understand the potential mechanisms of its dramatic decline over the last decades (BirdLife-International 2015).

This study aims to test three hypotheses about territory fidelity and prospecting. 1) Individual birds show high territory fidelity between years and also during winter. 2) Individuals will prospect for a breeding territory during their first winter whereas older, more experienced individuals will keep a territory from previous years and will, therefore, show no or reduced winter territory prospecting. 3) More active behavioural types will prospect more than less active behavioural types. We test these hypotheses using four years of data from a wild, insular house sparrow population. We expect older, more experienced sparrows to preferentially visit their previous and/or future breeding nest-box during the winter (i.e. winter territory fidelity). Furthermore, we predict that individuals in their first winter will visit (prospect) more nest-boxes than older, more experienced birds. Lastly, we also expect that the number of nest-boxes visited during winter will correlate positively with two behavioural traits, nestling and post-fledging activity.

Material and methods

Study species and population

The house sparrow is a non-migratory, multi-brooded, socially monogamous passerine that shows high between-year nest site fidelity (Summers-Smith 1963, Anderson 2006). This study was carried out on Lundy Island, 19 km off the coast in the south west of England (51°10′N, 4°40′W). The relatively remote location of the island together with the sedentary nature of house sparrows (Bengtson et al. 2004), and our intensive monitoring since 2000 have made it possible to fit virtually all sparrows living on Lundy with a British Trust for Ornithology metal ring, a unique combination of colour rings and a passive integrated transponder (TROVANID100: 12 × 2 mm and 0.1 g; hereafter transponder; details in Simons et al. 2015). The transponder is inserted subcutaneously on the chest and contains a unique combination of 10 alphanumeric digits that can be read with an electromagnetic field such as the one produced by a Radio Frequency Identification (RFID) antenna. Carrying a transponder does not negatively affect fitness in this population (Schroeder et al. 2011), nor in other passerines (Nicolaus et al. 2008).

Winter territory fidelity and prospecting

Most house sparrows in this population breed in nest-boxes (n = 110). Our nest-boxes have a base and roof surface of 11.5 × 11.5 cm, a height of 20 cm and a circular opening of 3.2 cm in diameter. Inter-specific competition for nest-boxes is non-existent in this population because no other bird species of a size that could utilize the nest-boxes breeds on Lundy (Davis and Jones 2007). We analysed nest-box use in four consecutive non-breeding seasons (hereafter referred to as 'winter') between 1 October 2011 and 20 February 2015. Eighteen nest-boxes had an RFID antenna fixed to the entrance that recorded all birds visiting the nest-box. These nest-boxes were restricted to the most popular breeding area on the island (Supplementary material Appendix 1, Fig. A1). The RFID equipment recorded the date, the time and the individual transponder identity of birds that visited the nest-boxes every day from 6:00 am to 00:00 (electricity on the island is off between midnight and 6:00 am, Schroeder et al. 2011). Therefore, not only birds roosting in the nest-boxes but also those visiting at any time during the day were recorded. Additionally, to gain information about individuals' presence, survival and transponder loss, a square RFID antenna (20 × 20 cm) recorded birds visiting an automatic feeder regularly filled with sunflower seeds.

For the purpose of this study, we defined winter as the period between 1 October and 9 February each year (i.e. 132 d per winter), because no reproductive attempts have been recorded within this period in this population, and most individuals go through a complete post-nuptial moult before 1 October, including juveniles (our unpubl. data). To study winter territory fidelity we extracted the identity of the nest-boxes visited per day for each individual after their first breeding season (hereafter referred to as adults). Winter territory fidelity was only studied for the adults that bred in at least one of the eighteen RFID-equipped nest-boxes in the previous or subsequent summer. Prospecting movements are commonly defined as the individuals' visits to breeding sites others than its current breeding site (Reed et al. 1999). Therefore, to study differences in territory prospecting between individuals searching for a territory for the first time and those who had held a territory before, we calculated the total number of different nest-boxes an individual visited each winter as a proxy for individual winter territory prospecting.

We used only data from individuals that did not die and/or lose their transponder during a winter in which they were recorded. We therefore excluded individuals that: a) had lost a transponder when re-captured during the winter when they were recorded, b) were not re-captured or recorded by our RFID antennae (either a nest-box or the feeder antenna) after a winter in which they were recorded, and/or c) had lost a transponder when re-captured and were not recorded by our RFID antennae after a winter in which they were recorded. These criteria are highly conservative, and strictly ensure that our data is not biased by transponder loss or by premature death of an individual.

Activity measurements

Nestling activity was measured during the breeding seasons of 2012 and 2013. Every 12-d old nestling was subjected to an adapted version of the open field test used in rodents (Hall and Ballachey 1932). A circular plastic surface (diameter = 33.5 cm, the 'arena'), with cardboard walls (height = 22 cm) to prevent escape, was gridded up into 5 cm squares that were numbered anticlockwise from 1 to 16 around the circumference to record the nestlings' position. Tests were recorded with a camera placed always at the same reference point. Each test started by placing the nestling in the centre of the arena. Nestling activity was defined as the total number of squares entered with half or more of the body by the nestling during the first 30 s. Nestlings that did not move were given a score of one (Winney 2015).

Post-fledging activity (i.e. activity measured from after fledging onwards) was measured from 2011 to 2015. We captured individuals during two non-consecutive weeks from mid-October to mid-March (i.e. right before the start of the breeding season), with about two to three months (range: 59–96 d) between both capture events. The main method was mist-netting but we also captured some birds inside nest-boxes and with funnel walk-in traps. Our population shows very limited, close to no resighting bias (Simons et al. 2015); using this information we can exclude possible trapping biases (Archard and Braithwaite 2010, Michelangeli et al. 2015). After capture, each bird was introduced into a 2 m high dome-shaped camping tent with five sides (each side measuring 2.74 m width at the floor) that contained two artificial trees made of plastic and bamboo. All tests were performed at the same sheltered location to standardize environmental conditions. Each test started by placing the bird inside the tent. Post-fledging activity was defined as the total sum of flights and runs carried out by the bird during the first 5 min (details in Winney 2015). We only included post-fledging activity scores obtained during the same winter in which territory prospecting was recorded. If a bird was tested twice or more within the same winter, we only used the score of the first test to avoid including any potential biases derived from heterogeneity between birds in the precision of the estimate and, also, to avoid any potential effect of short-term habituation. Nestling and post-fledging activity show repeatability and heritability in this population but do not constitute a behavioural syndrome, i.e. they are not correlated (Winney 2015). Here we use the term 'activity' to define the behaviour measured. However, estimating exploration behaviour involves measuring the individual's activity in a novel environment. Therefore, separating activity from exploration is technically not possible in this context.

Data analyses

Winter territory fidelity was studied by counting the number of days that each adult visited a given nest-box during each winter (hereafter number of visits). Then, we calculated the proportion of visits per nest-box per individual out of the total number of visits per individual during each specific winter. For example, a bird that visited two nest-boxes for 50 d each in a specific winter, will show a total number of visits of 100 and a proportion of visits of 0.5 for each nest-box. Each breeding season, the identity of the individuals breeding in each nest-box was obtained from video recordings, transponder readings and captures (Schroeder et al. 2011). The individual proportions of visits per nest-box and the individual's breeding nest-box(es) in the previous and subsequent breeding season were then plotted separately for each winter (Fig. 1; Supplementary material Appendix 1, Fig. A2–A4).

With regards to winter territory prospecting, we ran generalized linear models and generalized linear mixed effects models both with a zero-truncated Poisson distribution (zt-GLMs and zt-GLMMs, respectively) and a log link function using Markov chain Monte Carlo simulations as implemented in the package 'MCMCglmm' (Hadfield 2010) in R 3.0.2 (R Core Team). Zero-truncation was used because the birds visited at least one of the RFID equipped nest-boxes, hence the dataset did not contain zeros for the response variable. The number of different nest-boxes that an individual visited during each winter was the response variable in all models.

Our main interest was to compare individuals searching for a territory for the first time with older, more experienced individuals. Therefore, age group was fitted as a categorical independent variable with two levels ('juvenile' and 'adult'; but see below). Juveniles were defined as birds in their first winter, before their first breeding season, and adults were any

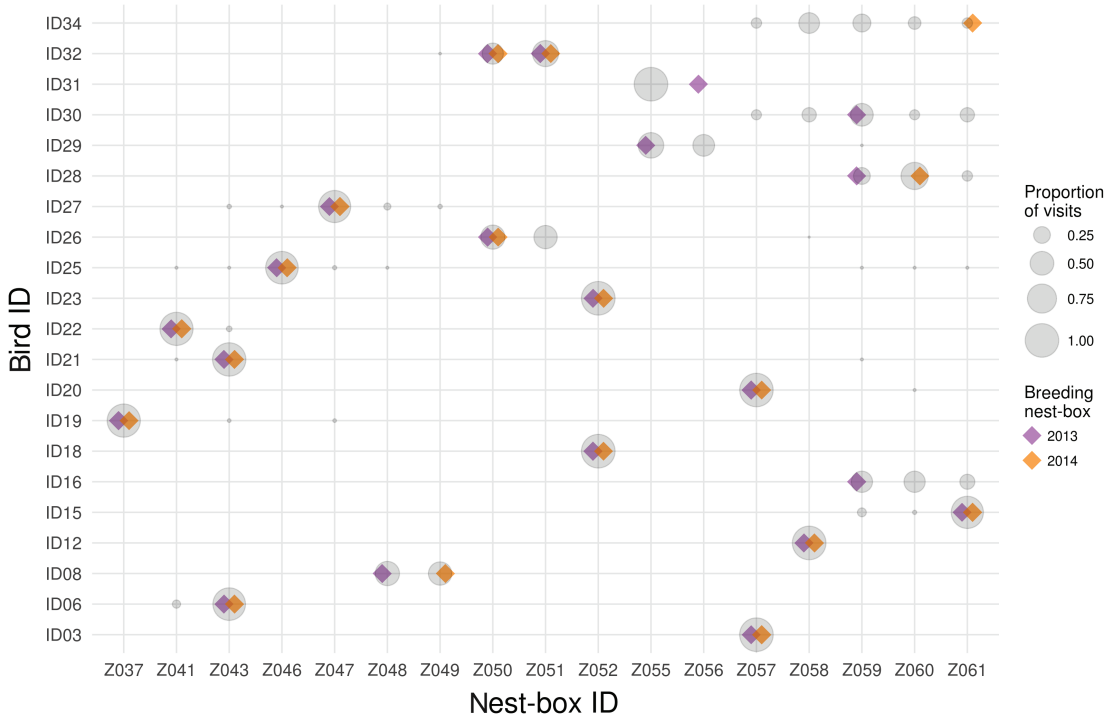

Figure 1. Adults' proportions of visits to the 18 RFID-equipped nest-boxes in the Lundy Island house sparrow population during the winter of 2013. Only birds that did not lose their transponder and that bred in at least one of the 18 nest-boxes in either 2013 or 2014 are represented (n = 21 individuals). Coloured rhombi correspond to the individual's breeding nest-box(es) in 2013 (purple) and/or 2014 (orange). Circle size represents the proportion of visits. Notice that an individual (ID32) bred in two different nest-boxes per year.

birds measured after their first breeding season. Sex was also fitted as a categorical fixed effect since males often hold a territory in house sparrows (Weaver 1939, Summers-Smith 1963), hence differences between the sexes can be expected.

To test the hypothesis (2) that first-time breeders (i.e. juveniles) show more frequent winter territory prospecting than older, more experienced birds (i.e. adults), we constructed a zt-GLMM ('age group' model) with sex, age group and their interaction as fixed effects, and year and bird identity as random effects. To test whether conclusions remained similar, this zt-GLMM was also run including age as a continuous instead of a categorical predictor (range: 0–4, 0 = juveniles, 'age continuous' model). Age squared was included as a predictor in this model to test for a non-linear relationship between the response variable and age. Due to the limited sample size, individuals older than four years were assigned as age four (n = 3 individuals, 5 data points). Furthermore, an additional zt-GLMM ('age continuous adult' model) was constructed to test whether adults prospected less with increasing age. Only birds older than zero were included in this analysis. The model contained sex, continuous age, their interaction and continuous age squared as fixed effects, and year and bird identity as random effects.

To test the hypothesis (3) that more active behavioural types will prospect more than less active behavioural types, we constructed two models. The first zt-GLM ('nestling' model) compared territory prospecting to nestling activity and contained sex, nestling activity score and year as fixed effects. Year was included as a fixed effect because it had only two levels for the two years in which nestling activity data was taken. Furthermore, this model only included juveniles for which nestling activity was measured in the previous summer and, thus, it did not include bird identity as a random factor because there were no repeated measures. The second zt-GLMM ('post-fledging' model) compared territory prospecting to post-fledging activity and contained age group, sex, their interaction, post-fledging activity score and its interaction with age group as fixed effects, and year and bird identity as random effects. Results remained qualitatively the same when this model was re-run including age as a continuous variable instead of a categorical one. Notice that, although age was included in the 'post-fledging' model, we decided to run a separate set of models to test for the effect of age (see above) due to the reduced number of individuals tested for post-fledging activity. Finally, conclusions remained qualitatively the same when all models containing age as a continuous variable were run with age ranging from 0 to 7. In all models, co-variables were mean centred, the number of iterations was set to 3 million, burn-in period to 0.3 million and thinning interval to 200 (900 for the 'age continuous adult' model). We used the inverse-wishart prior distribution for the random effects and the residual variance (V = 1 and nu = 0.002) in all models. The auto-correlation within the chains was < 0.1 in all cases. Furthermore, the fit of the models was confirmed by posterior predictive model checking following Korner-Nievergelt et al. (2015).

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.b6m41> (Sánchez-Tójar et al. 2016).

Results

We recorded 359 individual birds visiting nest-boxes during the four winters of the study. The subset of individuals that

we knew that survived and kept their transponder (i.e. the subset analysed here) was 188 different birds (106 males and 82 females) of which 78 and 140 were tested for nestling and post-fledging activity, respectively (Supplementary material Appendix 1, Fig. A5 and A6).

The total mean number of visits per adult per winter was 58.8 (range: 2–178) in 2011, 93.1 (range: 37–123) in 2012, 107.4 (range: 1–244) in 2013 and 82.8 (range: 2–134) in 2014 (details shown in Supplementary material Appendix, Table A1). On average, individuals visited 2.8 (range: 1–12) different nest-boxes during winter, entered 11.4 (range: 1–84) squares during the nestling activity tests and carried out 14.7 (range: 0–107) movements during the post-fledging activity tests. Males and females did not differ in the number of nest-boxes visited during winter (see below).

The individual number of visits in winter showed that adults focused their attention to their breeding nest-box(es). They visited those nest-box(es) that corresponded to the individual's previous and/or future breeding nest-box(es) in 92.3 % of the cases (n = 60 out of 65; Fig. 1 and Supplementary material Appendix 1, Fig. A2–A4).

Overall, juveniles visited almost twice as many nest-boxes during winter than adults (Table 1, Fig. 2). The results remained similar when age was fitted as a continuous variable (Table 2, Fig. 3). The squared effect of age was small (Table 2); the analysis excluding juveniles showed that the number of nest-boxes visited during winter did not decrease with age (Table 2). Hence, the main decrease in nest-boxes visited occurred between the first and the second winter.

The total number of nest-boxes that an individual visited during its first winter was not correlated with nestling activity (Table 3). Similarly, post-fledging activity was not associated with the number of nest-boxes that an individual visited during the first or subsequent winters (Table 4).

Discussion

House sparrows' territory prospecting during winter is not linked to activity but associated with life-history stage, and most likely territory fidelity, supporting our first and second hypotheses. However, we found no support for our third hypothesis, as neither nestling nor post-fledging activity predicted winter territory prospecting.

Table 1. Effect of life-history stage (juvenile vs adult) on the individual number of nest-boxes visited per winter in the Lundy Island house sparrow population.

Fixed effects	Estimate	Lower and upper 95% CrI
(Intercept)	**1.10**	**(0.79, 1.41)**
Sex (male)[a]	–0.11	(–0.44, 0.20)
Age group (adult)[b]	**–0.67**	**(–1.02, –0.33)**
Sex (male)[a] × Age group (adult)[b]	0.20	(–0.25, 0.66)
Random effects		
Bird identity	0.06	(0, 0.22)
Year	0.05	(0, 0.15)
Residual variance	0.26	(0, 0.45)

Results from a zero-truncated Poisson GLMM. n = 188 individuals (263 cases). 95% credible intervals not spanning zero are highlighted in bold. CrI: credible interval.
[a]Relative to female.
[b]Relative to juveniles.

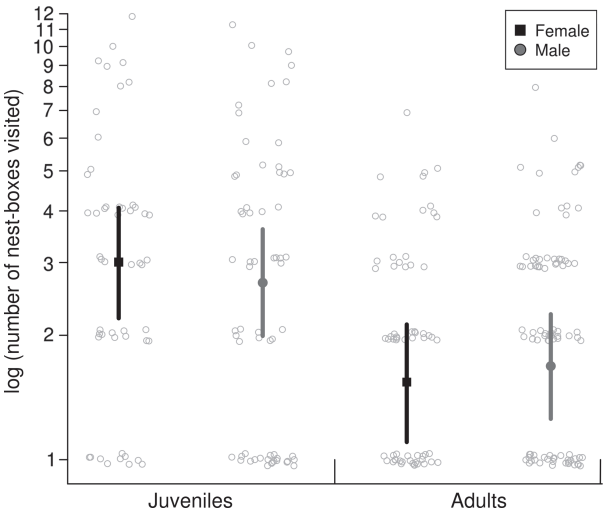

Figure 2. Independently of their sex, juveniles prospect more nest-boxes during winter than adults in the Lundy Island house sparrow population. Filled black squares (females) and grey circles (males) show estimates for the mean and the credible intervals of a zero-truncated Poisson GLMM. Open circles correspond to the raw data and are offset on both x- and y-axes to aid viewing. Y-axis is log-scaled but original values are shown to aid interpretation.

Most house sparrows breed in their first year and show high nest site fidelity in subsequent years (Summers-Smith 1963, Anderson 2006). Our data supports such between-year territory fidelity because most birds used the same (or an adjacent) nest-box(es) year after year, particularly males (Fig. 4). Moreover, previous observations suggest that house sparrows may roost in their nest-boxes year-round, and juveniles carry out territory prospecting-like behaviours in winter (Summers-Smith 1963, Veiga 1993). By automatically and continuously tracking winter nest-box use, we confirmed that house sparrows show winter territory fidelity, and adults almost exclusively focused their winter visits to their previous and/or following breeding nest-box(es). Thus, as in other birds species with high nest site fidelity (e.g. *Zenaida aurita*, Quinard and Cézilly 2012; *Haematopus moquini*, Loewenthal et al. 2015), house sparrows also show year-round territoriality.

High nest site fidelity might be an important factor explaining the dramatic decline of the house sparrow in recent decades (BirdLife-International 2015). Under the current scenario of rapid human changes in the environment (Hale et al. 2016), sparrows might be falling into an ecological trap by showing high fidelity to no-longer-suitable territories.

Many other non-migratory birds that breed in nest-boxes are commonly studied (e.g. *Parus major*; *Cyanistes caeruleus*). Complete knowledge of whether these and other model species also show year-round territoriality could be important, for example to investigate whether capturing birds roosting inside nest-boxes could lead to biased trapping. Recent studies have shown that this trapping method greatly reduces both the percentage of nest-boxes occupied in winter and winter nest-box re-use rate (Zdeněk et al. 2012). The effect might differ between different personality types (Stuber

Table 2. Effect of age on the individual number of nest-boxes visited per winter in the Lundy Island house sparrow population.

	Juveniles and adults		Only adults	
Fixed effects	Estimate	Lower and upper 95% CrI	Estimate	Lower and upper 95% CrI
(Intercept)	**0.60**	**(0.31, 089)**	**0.57**	**(0.26, 0.91)**
Sex (male)[a]	–0.01	(–0.25, 0.24)	0.11	(–0.20, 0.43)
Age	**–0.33**	**(–0.52, –0.14)**	0.07	(–0.24, 0.36)
Age^2	0.09	(0, 0.17)	–0.09	(–0.26, 0.08)
Sex (male)[a] × Age	0.05	(–0.16, 0.29)	–0.03	(–0.38, 0.32)
Random effects				
Bird identity	0.06	(0, 0.22)	0.07	(0, 0.24)
Year	0.04	(0, 0.15)	0.03	(0, 0.11)
Residual variance	0.27	(0.06, 0.48)	0.07	(0, 0.24)

Results from two zero-truncated Poisson GLMMs. 'Juveniles and adults' shows the results for birds ranging from age 0 to 4 (n = 188 individuals, 263 cases), whereas 'Only adults' only shows birds ranging from 1 to 4 (n = 110 adults, 150 cases). 95% credible intervals not spanning zero are highlighted in bold. CrI: credible interval.
[a]Relative to female.

et al. 2013) and depend on the time of capture (Schlicht and Kempenaers 2015). Thus, an interesting next step is to investigate whether nightly nest-box trapping affects individual territory use and, more importantly, individual fitness in species showing year-round territoriality. Radio frequency identification devices are ideal for this purpose (Schlicht and Kempenaers 2015).

We have also shown that juveniles prospect for a territory already in their first winter. Males of many animal species obtain a territory and subsequently advertise it to attract females (e.g. anura: Ryan 2001; reptiles: Baird et al. 2007; fishes: Casaretto et al. 2015), including house sparrows (Weaver 1939, Summers-Smith 1963). Males failing to obtain a territory or acquiring a low quality one may remain unpaired. Timing might also be important as theory predicts that, when competition is high, high quality individuals gain a territory early or even remain resident year-round, while low quality individuals may have to take what is left over (Kokko 1999). In fact, empirical studies show that early territory acquisition and breeding are usually associated with greater reproductive success (Perrins 1970, Verhulst and Nilsson 2008, Matechou et al. 2015).

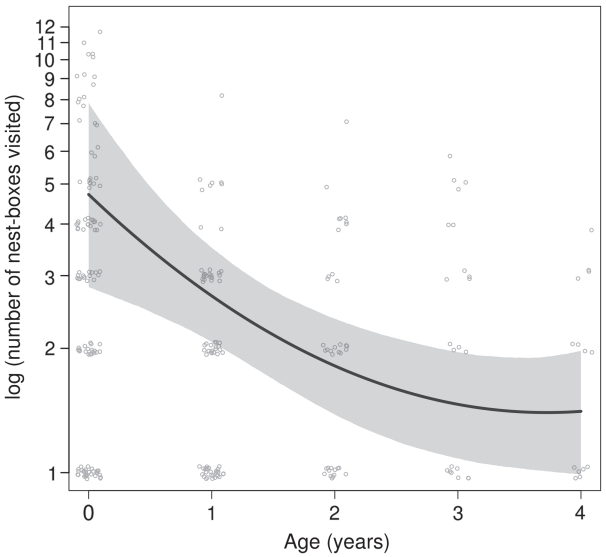

Figure 3. Younger individuals prospect more nest-boxes during winter than older individuals in the Lundy Island house sparrow population. The solid line represents the model fit, and the shading represents the 95% credible interval of a zero-truncated Poisson GLMM. Open circles correspond to the raw data and are offset on both x- and y-axes to aid viewing. Y-axis is log-scaled but original values are shown to aid interpretation.

Carry-over effects occur when an individual's previous history and experience are linked with its current performance (O'Connor et al. 2014). If individuals obtain a territory in their first year and hold it in subsequent years, the status acquired during that first year (in terms of territory and mate quality) could carry-over to their future lifetime fitness. Therefore it may be necessary to look at individual differences (e.g. in phenotype) during their first year of life to investigate the causes of current individual differences in fitness. Further research is needed to shed light on whether differences in territory prospecting and acquisition (e.g. extent, timing and quality) might affect current and future individual fitness.

Contrary to our predictions, the two behavioural traits we measured did not predict winter territory prospecting. This agrees with a previous study showing that exploration (similarly measured to our post-fledging activity), did not correlate with summer nest-box prospecting in jackdaws *Corvus monedula* (Schuett et al. 2012). Thus, individual activity levels do not seem to correlate with territory prospecting neither in winter nor in summer. Our results could also be explained by several other mechanisms. First, our values of winter territory prospecting might be conservative as only a limited number of nest-boxes are equipped with a RFID antenna. Thus, any prospecting in nest-boxes

Table 3. Effect of nestling activity on the individual number of nest-boxes visited per winter in the Lundy Island house sparrow population.

Fixed effects	Estimate	Lower and upper 95% CrI
(Intercept)	**0.90**	**(0.54, 1.23)**
Sex (male)[a]	–0.14	(–0.56, 0.26)
Nestling activity	0	(–0.01, 0.01)
Year 2013[b]	0.22	(–0.20, 0.67)
Residual variance	0.37	(0.11, 0.69)

Results from a zero-truncated Poisson GLM. n = 78 individuals. 95% credible intervals not spanning zero are highlighted in bold. CrI: credible interval.
[a]Relative to female.
[b]Relative to 2012.

Table 4. Effect of post-fledging activity on the individual number of nest-boxes visited per winter in the Lundy Island house sparrow population.

Fixed effects	Estimate	Lower and upper 95% CrI
(Intercept)	**1.14**	**(0.77, 1.48)**
Sex (male)[a]	–0.22	(–0.62, 0.16)
Age group (adult)[b]	**–0.78**	**(–1.23, –0.33)**
Post-fledging activity	0.01	(–0.01, 0.02)
Sex (male)[a] × Age group (adult)[b]	0.24	(–0.35, 0.85)
Age group (adult)[b] × Post-fledging activity	–0.01	(–0.02, 0.01)
Random effects		
Bird identity	0.17	(0, 0.44)
Year	0.04	(0, 0.15)
Residual variance	0.18	(0, 0.44)

Results from a zero-truncated Poisson GLMM. n = 140 individuals (169 cases). 95% credible intervals not spanning zero are highlighted in bold. CrI: credible interval.
[a]Relative to female.
[b]Relative to juveniles.

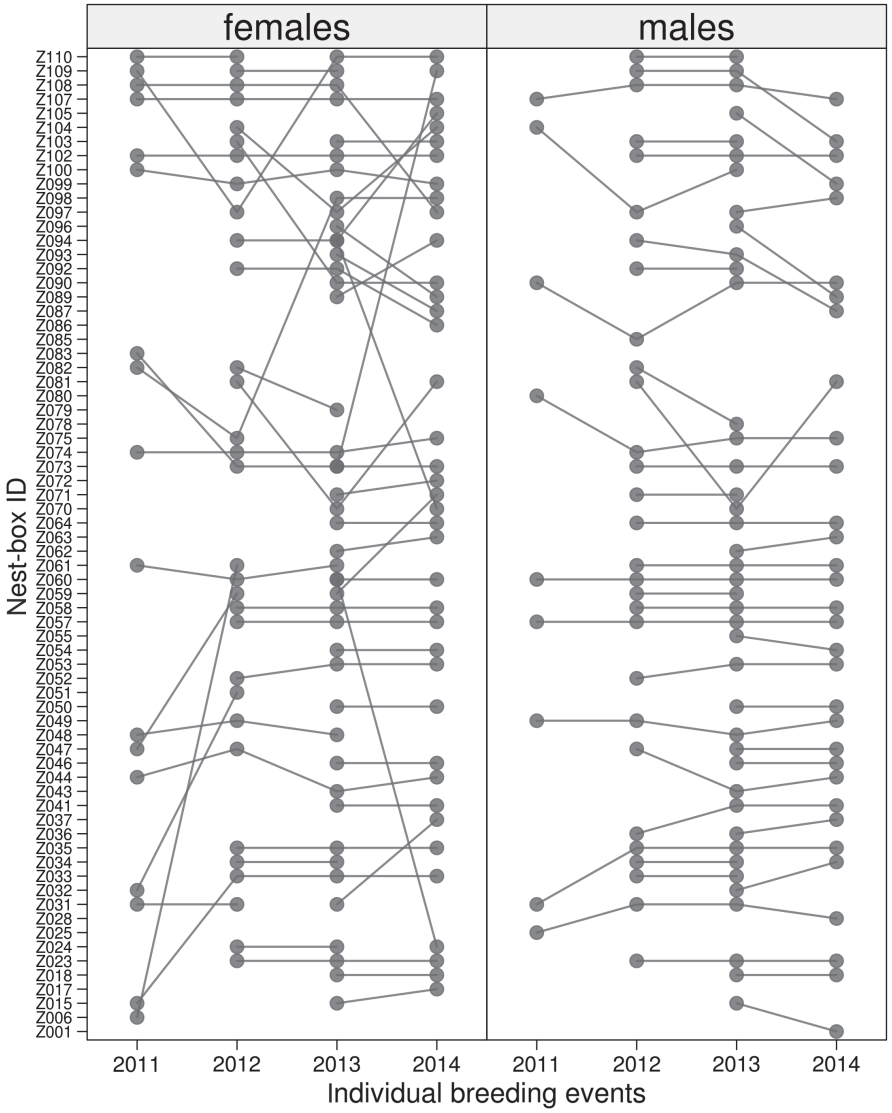

Figure 4. Individual breeding attempts in the Lundy Island house sparrow population from 2011 to 2014. Only the first breeding attempt of each individual in each year is represented. Individuals that bred in only one year during the study period are not included. Lines connect all breeding attempts of single individuals. The y-axis shows all the nest-boxes used (n = 86) sorted from the southeast to the northwest of the population. Overall, 239 individuals (122 females and 117 males, 238 broods) are shown. Notice how most birds seem to use the same (or adjacent) nest-box year after year and how males seem to be more nest-box faithful.

without antenna will be undetected. These undetected prospecting visits could be slightly biased, because the RFID antennae are attached to nest-boxes in the most popular breeding area on the island, where there is a great proportion of old males, who own and defend their nest-boxes. Second, our definition of territory prospecting (i.e. number of nest-boxes visited), although similar to what is commonly used in the literature (Doligez et al. 2004, Calabuig et al. 2010), might not fully capture such behaviour as arguably all individuals' movements add to information used for deciding where to breed (Reed et al. 1999). Both could make the detection of a correlation between territory prospecting and activity levels more difficult. Lastly, our results may also stress a need for reviewing whether commonly used captive behavioural assays predict behaviours that are hypothesized to be relevant to fitness in the wild. Surprisingly, the similarity of personality traits to analogous behaviours in the wild has seldom been tested. Two personality traits – exploration and neophobia – seem to be consistent between captivity and the wild in crickets (Fisher et al. 2015) and in blue tits (Herborn et al. 2010; but see Minderman et al. 2010 for negative results in starlings *Sturnus vulgaris*). Thus, activity seems to be inconsistent between both contexts (Herborn et al. 2010, 2014, Fisher et al. 2015). The contradicting results might be the consequence of the difficulties in distinguishing between exploration and activity (Herborn et al. 2014) and/or due to differences in time intervals between captive and wild testing (Bell et al. 2009). Further research should focus on testing captive versus wild personality measurements, paying special attention to the inconsistencies found for activity measurements. Moreover, more effort should be dedicated to clearly define personality traits as activity or exploration in personality research (reviewed by Carter et al. 2013).

In summary, using automatic and continuous monitoring of nest-box visits over four years, we have shown that house sparrows show year-round territoriality, confirming that this species not only show high nest site fidelity between seasons but also during the winter. Individuals search for a territory during their first winter, with juveniles visiting more nest-boxes than adults. Finally, the two behavioural traits studied here did not predict winter territory prospecting. Further research is needed to investigate whether, as predicted by theory (Kokko 1999), time of territory and mate acquisition differs among individuals and the possible influence on lifetime fitness.

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Supplementary material (Appendix JAV-01055 at <www.avianbiology.org/appendix/jav-01055>). Appendix 1.