Exploratory behaviour and territory quality in Great Tits (Parus major)
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Exploratory behaviour and territory quality in Great Tits (*Parus major*)

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Abstract

Choosing a proper territory for reproduction is an important choice for many bird species. To understand how territory distribution comes about it is necessary to study what the effect of their behaviour is on this distribution. We measured exploratory behaviour in great tits (*Parus major*) using the classical observation room approach before breeding and a cage test during the breeding season. The birds explored the cage to find a way out and usually made calls when doing so. Territory quality was estimated using historical breeding data and current frass fall. Behaviour shown in the laboratory was not correlated with behaviour shown in the field. We found that male behaviour shown in the field had an effect on initial nest box choice, with more mobile males having nest boxes with a higher occupancy rate and a higher chance of having a successful nest, and males that called more had nest boxes with later laying dates. Female behaviour measured in the field had on itself no effect on territory choice, but pairs with on average more active parents tended to have territories and pre-breeding nest boxes with earlier laying dates and higher occupancy rates. Our results might indicate some important effects of behaviour on territory distribution, but the behavioural tests should be repeated and compared over several years before more convincing conclusions can be made.

Introduction

Many animals defend territories to secure various resources, such as food, nesting sites or mates. Defending a territory takes energy, so for the territory to be profitable the benefits should be greater than the costs (Brown 1964, in Krebs 1993). This can be illustrated by a study of the golden-winged sunbird (*Nectarinia reichenowi*), where Gill and Wolf (1974, in Krebs 1993) calculated the energy needed for feeding, resting and defending a territory. They showed that by defending a territory the amount of nectar in the bird's flowers increased enough to cover the costs of having a territory. For many hole nesting passerines that do not excavate their own cavities, nesting sites are a limiting resource. For great tits (*Parus major*) nesting cavities are a major clue for nest-site selection (Hildén 1964, in Mänd et al., 2005), and providing nest-boxes increases the population density (Maícas et al., 2012; Mänd et al., 2005).

But a territory does not only provide a safe nesting place, but also food, and the quality of a territory can have a substantial influence on both parents and young. Food abundance limits parental foraging and provisioning behaviour in great tits and blue tits (*Cyanistes caeruleus*). A lower food abundance increases foraging distance and decreases provisioning rate in blue tits (Tremblay et al., 2004) and changes the prey composition in great tits from caterpillars to other

prey items (Naef-Daenzer et al., 2000). Even though the blue tits were able to bring the same amount of biomass in both good and poor habitats, the young in poor habitats were significantly smaller, which might be due to a higher parasite pressure (Tremblay et al., 2004). Tree density in a territory was positively correlated with hatching rate in blue tits, and although there was no difference in quality of the fledglings the parents lost energy investing in failed eggs (Maícas et al., 2012). Blue tits living in evergreen, caterpillar-poor woodland have a lower provisioning rate and provide a lower proportion of caterpillars than those breeding in deciduous, caterpillar-rich habitats (Blondel et al., 1991). One of the main prey items for great tits are caterpillars of the winter moth (*Operophtera brumata*) and the green tortrix (*Tortrix viridana*) living on oak trees (Gosler 1993 in Wilkin et al., 2009). A higher abundance of oaks in a territory is related with earlier breeding and a higher fledgling mass (Wilkin et al., 2009). One reason for earlier breeding in high quality habitats can be a preference for these habitats (Maícas et al., 2012) and preferred habitats are filled first. Another reason might be the abundance of snails, a calcium source for egg shells, which is higher in deciduous forests than coniferous forests, allowing females to start laying earlier because they reach their threshold body condition earlier (Mänd et al., 2005). Territory quality is found to have a stronger effect on hatching date and offspring condition than parental quality (Przybylo et al., 2001).

Great tits and other passerines prefer deciduous forests over coniferous which naturally have a more potential nesting cavities and a higher food abundance (Mänd et al., 2005 and references therein). And also within deciduous habitats do great and blue tits actively choose and prefer certain territories, while pied flycatchers (*Ficedula hypoleuca*) do not. This might be because the resident tits have time to explore and select territories before breeding, while pied flycatchers start breeding shortly after arriving from their wintering grounds (Goodenough et al., 2009). Blue tits prefer old, tall and closed canopies which contains a greater supply of invertebrates, while great tits prefer a more varied height profile offering a better access to larger branches and the ground (Hinsley et al., 2002). Favourable territories are quickly taken over when the previous occupants are removed, as was shown in great tits (Krebs 1971 in Krebs 1993). Such system can be caused by a hierarchy where dominant, more aggressive individuals first choose the most preferred territories over less preferred ones (Maícas et al., 2012; Scales et al., 2013).

Aggressiveness and defensiveness are correlated to exploration score in great tits, such that fast explorers are more aggressive (Verbeek et al., 1996) and more defensive (Amy et al., 2010; Hollander et al., 2007) than slow explorers. Great tits with different exploration scores showed different strategies when presented with intruders; faster explorers stay longer near an intruder or predator and call and sing more, while slower explorers are more active but move away and sing for a shorter period of time but more different songs (Amy et al., 2010; Hollander et al., 2007). These differences can cause that animals with different personalities end up in different habitats; less explorative and aggressive animals could end up in qualitatively worse habitats and more explorative and aggressive animals in better habitats.

With this study we try to find out if great tit personalities correlate with territory quality. In our research area we have two distinct habitat types; coniferous and deciduous, which make this the ideal place for this research. We use historical data on traits of breeding success which we assume reflect habitat quality, but are not necessarily cues for great tits to choose certain territories. By testing the exploration score both before and during the breeding season and calculating historical breeding success as well as current frass fall we try to answer this question. In Northern Europe, great tits still prefer deciduous habitats or trees over coniferous

(Mägi et al., 2009; Mänd et al., 2005; Rytkönen & Krams, 2003), even though in our population broods in coniferous forests perform better (Mänd et al., 2005).

Since males are the ones showing territorial behaviour, like singing, we expect male behaviour to have a higher effect on territory choice than females. Because territories usually contain more than one nest box and females build the nest, we expect female behaviour to have a higher impact on nest box choice. We expect more explorative, and aggressive birds to have better territories, with higher historical breeding success.

Materials and methods

Study area

The study area was located close to Kilingi-Nõmme (58° 7' N, 25° 5' E) in SW Estonia and consisted of an approximate 50 km² mosaic of coniferous and deciduous forest. Deciduous patches are mostly secondary forests of 45 to 55 years old, growing on fertile soil and contain a rich understory. They appear either as isolated patches within agricultural lands or as 250 to 500 m wide riparian strips. The most common deciduous tree species are grey alder (*Alnus incana*) and silver birch (*Betula pendula*). Coniferous forests are dominated by Scots pine (*Pinus sylvestris*), which can form mixed stands with Norway spruce (*Picea abies*) or downy birch (*Betula pubescens*). These stands are typically managed forests growing on nutrient-poor sandy or peat soils about 65 to 85 years old. Great tits bred in wooden nest boxes with dimensions of 11 x 11 x 30 cm and an entrance diameter of 3.5 to 4.0 cm. Most of the nest boxes were placed along double lines, usually with a road in between, but some were placed in groups further into the forest. The nest boxes were mounted on trees at heights of 1.5 to 1.8 m, with a distance between neighbouring nest boxes of 50 to 60 m. Nest boxes were cleaned annually to remove old nest material and repaired or replaced when needed before the beginning of the breeding season. Forestry was a main cause of nest box-loss as large patches of coniferous forest were felled in the study area. This year we experienced extreme weather conditions with snow and temperatures below zero until halfway through April, after which the temperatures increased to about 25-30 °C in a timespan of two weeks.

Basic breeding parameters

At the beginning of the breeding season of 2013 all nest boxes were checked weekly for nests, until most great tits had completed their first clutch. After that only nest boxes with breeding great tits were tracked. We recorded laying date and clutch size. For other research purposes feeding stations were placed in the vicinity of nest boxes of tagged birds (see below) during the incubation period. Since feeding the birds altered territory quality, the current nestling data could not be used for this study.

Personality scores

Because of the severe winters in northern and north eastern Europe many resident passerines migrate to more human inhabited areas where they can find more food (pers. obs.). For this reason we caught birds just before the breeding season and during the breeding season to assess their behaviour.

At the beginning of April, three weeks before the firs egg was laid, we started catching roosting great tits from the nest boxes by checking nest boxes at night. When catching birds, we checked for eggs and left the birds in the nest box if eggs were present. The birds were then taken to the field station where they stayed in cages (dimensions of 27 x 51 x 55 cm) overnight. The cages were put in a room without heating or light (either artificial or natural). The birds were thus able to hear, but not see each other, unless we entered the room. We stopped catching birds ten days after the first egg was laid, since the risk of desertion of the nests was too high by then. In total 100 birds were caught, of which 82 females and 18 males.

The next morning we started observing the birds before sunrise in an observation room. This room was a replica of the observation room described by Dingemanse et al. (2002). The only difference was that we had to move the cages to the observation room as we had only one entrance for the birds. We used the same method of switching the light on and off as Dingemanse et al. (2002) to get the birds to move to the observation room from their cage. We gave the birds three minutes to do this voluntarily, and after that rattled the cage slightly to scare them into to observation room. Observation time started once the bird entered the observation room. The time between opening the entrance to the observation room and the entering of the bird was recorded.

During the first two minutes we noted all hops, flights of the bird and the location of the bird. We also noted when the bird visited all five trees. When the bird did not visit all trees within two minutes, the observation time was extended up to five minutes. If the birds did not visit all trees within five minutes, the observation was stopped. After the observations measurements of the bird's body size were taken and they were given a pit tag underneath their skin between their shoulder blades. The pit tags were used for a different research than described in this paper. After all measurements were taken, the birds were released at the plot they were caught. From previous experience we know that all females will abandon the nest box they were caught in, but most females will start building a new nest in a nearby nest box.

The birds that returned as breeding birds were later recaptured together with their mate when their chicks were eight days old. In total 48 out of 82 females were detected as breeding bird of which 33 were recaptured with 22 of their mates. None of the 18 males that were tested in the observation room were found as breeding bird. After the birds were caught they were placed individually in bird cages in the forest 30-40 m away from their nest box and filmed for approximately three minutes while we left the vicinity of the cage. This way we measured explorative behaviour of the bird trying to find a way to escape the cage. Later we counted the number of movements and calls. The first 30 seconds of film after releasing the bird into the cage were omitted to take into account the effect of handling the bird and the presence of people on its behaviour. Before releasing the birds back into the forest, their body weight, tarsus and wing length were measured, a blood sample was taken and if the bird was not tagged, a tag was placed.

Territory quality

To determine the quality of a territory we used the available historical data from 2001 to 2012. For some years (2003, 2006, 2010 and 2011) no data was available or the data was not usable because of the nature of the experiments conducted in those years. For the remaining years we used average clutch size, laying date and occupancy, and fate of the nest. The fate of the nest

was set to 1 if the at least one young fledged and to 0 if no young fledged. Because of the low occupancy rate (2013: 138 out of 1137 nest boxes was occupied by great tits, or 12%), it was not uncommon that a nest box had not been previously occupied and therefore no historical data was available. We assumed that the habitat quality did not differ between nest boxes that were direct neighbours. To increase the amount of historical data for a nest box we also used the historical data of the neighbouring nest boxes, which was then called a cluster. Some nest boxes did not have any direct neighbours because of forestry and some were in a group and surrounded on all sides, so the number of nest boxes used for a cluster ranged from one to five. For the statistical analyses both individual nest boxes and clusters were used for pre-breeding and breeding territories. If there was still no historical data for either cluster or nest box, the cluster and nest box were omitted from the statistical tests.

To control for year effects on laying date, like different weather conditions, we calculated the mean laying date for each year and then subtracted that from the actual laying date in each individual nest box. With this relative laying date we could calculate the timing of the nest boxes and territories. The occupancy was calculated over the years by checking if a nest box was occupied in a given year. An occupied nest box was given a 1 and an empty nest box a 0. These values were then averaged over the years. The chance of a nest box having a successful nest in a year was calculated by multiplying occupancy and fate. Clutch size and relative laying date were averaged over the years, but years in which a nest box was not occupied were omitted in these averages.

Apart from using the historical data we also collected frass from the nest boxes that were occupied by tagged birds. We did this between an age of the young of nine days until 11 days, since the young demand most food at this age (Perrins, 1965). To collect the frass we placed a round funnel with a diameter of 30 cm underneath each tree an occupied nest box was attached to and placed a coffee filter underneath it to collect the frass (Sisask et al., 2010). Samples that had been outside during rain were omitted from the analyses since the frass might have dissolved or the filters had broken. The samples (n=22) were put in a drying chamber for at least 48h at 40°c after which we separated the frass from the other debris in the filters. The frass was then weighed to the nearest 0.1 mg and calculated $mg*m^{-2}*d^{-1}$.

Statistical analyses

The correlation between the behaviour shown in the laboratory and the behaviour shown in the field, was calculated using Pearson's correlation. For this we used the number of movements per second and the number of calls per second over a 2 minute period. We also compared from the field data the number of movements per second and the number of calls per second over a 2 to 3 minute period within males and females, and between mates. In all analyses with territory quality parameters, only the field data was used, since we had recaptured none of the males observed in the laboratory. Because the females all bred in a different nest box than they were caught in before breeding, we used habitat quality data for a) the pre-breeding nest box, b) the pre-breeding cluster, c) the breeding nest box, and d) the breeding cluster. Most of the birds bred in a nest box close to their original nest box, so the clusters could overlap.

To test the correlation between exploration behaviour and habitat quality, we used General Linear Models (hereafter GLM), using the different behavioural traits (i.e. number of movements per second, the number of calls per second and calls/movements) of the males, females and the

averages of the pair as dependent variables and the habitat quality traits as independent variables. The chance of a nest box or cluster having a successful nest was implied in the models as an interaction between occupancy and fate. Occupancy and fate were also used as separate parameters. This resulted in 36 different GLMs with five covariates and one interaction. For the frass we built similar models, with behavioural traits as dependent variables and frass as independent variable (nine GLMs with one independent variable). Additionally we built models with frass as dependent variable and habitat quality traits of the breeding nest boxes and clusters as independent variables (two GLMs with five covariates and one interaction). To estimate how the chance of a nest box to produce a successful nest was affected by clutch size, laying date and habitat, we built a GLM with chance as dependent variable and the other parameters as independent variables. For this we used data of all the nest boxes available in the data base. Sample sizes differed depending on whether all historical and behavioural data was available. For some nest boxes one or more parameters were not known and not all pairs were complete as we sometimes could not capture either the male or the females. All statistical analyses were done in R (version 3.0.1) (S 1).

Results

We found no correlation between the number of movements per second in the observation room and in the field test (cor: r: 0.07, df: 30, p: 0.71, t: 0.37), or between the number of calls per second in the observation room and the field (cor: r: -0.23, df: 29, p: 0.21, t: -1.27) (Figure 1). In the cages, mobile males tended to have a higher number of calls per second (cor: r: 0.39, n: 22, p: 0.071, t: 1.91), but there was no such trend in female behaviour (cor: r: 0.21, n: 32, p: 0.25, t: 1.67) (Figure 2 a,b). Males and females did not differ in the number of movements per second or calls per second in the cages (t-test: t: -0.92, df: 47.4, p: 0.36, and t: -1.3, df: 51.6, p: 0.35 respectively). There was a trend that active males had active females (cor: r: 0.49, n:17, p: 0.047, t: 2.16), but the number of calls per second did not correlate between partners (cor: r: 0.18, n: 17, p: 0.48, t: 0.72) (Figure 2 c,d).

Male behaviour had an effect on the distribution of the pre-breeding nest boxes, but not on pre-breeding clusters. We found no effect of female behaviour on either nest boxes or clusters. Males with more movements per second in the field cage test had pre-breeding nest boxes with a higher chance of having a successful nest (GLM: est: 2.66, df: 15, p: 0.020, t: 2.69) and with a higher occupancy rate (GLM: est: -1.99, df: 15, p: 0.040, t: -2.31) (Figure 3 a). However, males that called more often per second, or had a higher ratio of calls over movements, had pre-breeding nest boxes with later laying dates (GLM: est: 0.0245, df: 16, p: 0.027, t: 2.46, and est: 0.0282, df: 16, p: 0.027, t: 2.46) (Figure 3 b,c), indicating that these nest boxes were less preferred (Mänd et al., 2005). More mobile males had breeding clusters with a higher occupancy rate (GLM: est: 0.223, df: 21, p: 0.031, t: 2.32), but no other behavioural effect of either males or females was found on the breeding nest boxes or clusters.

The average behaviour of both mates tended to have effects on the choice of the initial nest box and cluster, and the breeding cluster. Pairs that were more mobile tended to have pre-breeding clusters that had earlier laying dates (GLM: est: -0.0199, df: 16, p: 0.081, t: -1.87), pre-breeding nest boxes with a higher occupancy rate (GLM: est: 0.389, df: 17, p: 0.080, t: 1.87), and breeding clusters with a higher occupancy rate (GLM: est: 0.175, df: 17, p: 0.098, t: 1.76). Pairs with a higher number of calls per second had pre-breeding clusters with a higher occupancy rate

(GLM: est: 0.183, df: 16, p: 0.090, t: 1.81). However, pairs with a higher number of calls relative to movements had pre-breeding nest boxes with later laying dates (GLM: est: 0.0183, df: 13, p: 0.094, t: 1.82). Pair behaviour had no significant correlation with the historical breeding success of the breeding nest box.

The chance of a nest box to produce a successful nest in any of the studied years was better in deciduous habitats compared to coniferous (GLM: est: 0.0582, df: 550, p: <0.001, t: 5.55). Nest boxes with relatively early laying dates were more successful than late nest boxes (GLM: est: -0.00360, df: 550, p: 0.032, t: -2.15). Breeding clusters with a higher occupancy rate tended to yield a higher amount of frass (GLM: est: 0.977, df: 21, p: 0.071, t: 1.91**Fout! Verwijzingsbron niet gevonden.**). None of the other habitat quality traits, including habitat type, had any significant correlation with frass, nor did any behavioural trait of either males, females or pairs.

Discussion

Our research was done in only one season, and we could only use the behavioural data of the cages in the field for which we measured the birds only once. Behavioural patterns found in one year can often change the next year, which makes it necessary to repeat such experiments both within and between years. Apart from too few repetitions, there were also several years missing from the historical database. To do a proper analyses of historical data a complete and consequent database is needed which has information of all nest boxes and birds over all the years that the population has been studied. With the experimental approach that was used to measure behavioural traits before the breeding season, birds were scared from the nest box they had chosen to breed in and forced into another nest box. Even though this does not seem to have a large effect on the breeding behaviour of the birds, it might bias a study about territory quality. In this research it meant that the number of GLMs used for territory quality and behaviour doubled from 18 to 36, making the statistics weak. With higher population densities or older databases it might even be reduced to only nine GLMs if clusters are no longer needed. Habitat quality could be severely altered within a few days' time because large patches of coniferous forest were cleared for timber. Since these changes were not recorded, it is not known when habitat quality changed. A nest box might have been in a high quality territory, but be in an extremely low quality territory this season because of the forestry. Therefore it would be better to study a population that is not housed in production forest or to keep track of all the changes in habitat quality. Even though all these limitations meant that our study cannot give any conclusive results, it does reveal some potentially interesting processes.

Behaviour tested in an observation room has been shown to be repeatable when the birds are tested under the same laboratory circumstances (Dingemanse et al., 2012, 2002; van Overveld & Matthysen, 2013). The same is true for the relatively new method we used in the field (Kluen et al., 2012), where activity in the cages is shown to be repeatable both within and between seasons (Kluen & Brommer, 2013). However, we found no correlation between the behaviour shown in the laboratory tests and the field tests. One reason for this lack of correlation could be that we had only females that had been tested in both laboratory and in the field, since none of the laboratory tested males returned as breeding bird. Males are in general more repeatable than females in their behaviour (Bell et al., 2009). Another reason could be that because of the set-up of the tests, we did not test the same behaviour both times. The laboratory room was a completely new environment for the birds, while the cages were put in familiar surroundings

where they could communicate with their mates and neighbours. In a few of the cage tests the focal bird was visited by other great tits. Activity in one situation might not be directly related to another situation as Amy et al. (2010) showed when exposing great tits to songs of a possible intruder; fast exploring males in the laboratory were less mobile in the field and sang less songs, though longer, while slow explorers moved more and sang more different songs. Since we did not repeat any of the behavioural tests and had only data for one sex, we do not know if this absence of direct correlation is repeatable and maybe caused by a more complex underlying behavioural structure, or if it is an artefact of the design of our study.

We found that male behaviour and territory quality correlated, while we did not found such a correlation for female behaviour. One explanation could be that males choose territories, while females choose mates. Loukola et al. (2012) hypothesised that females might choose their mates based on male behaviour instead of on the quality of their territory. They suggested that male tits choose the breeding nest box, because in their study only the age of the male had an effect on nest box choice. Our results are partly supported by this suggestion in part, as we found no direct effect of female behaviour but did of male behaviour. However, we also found that the combined behaviour of the pairs tends to have an effect. Both et al. (2005) found that pairs with two extreme personalities (slow-slow, fast-fast) had a higher breeding success than intermediate or mixed personalities. With our dataset we cannot determine breeding success for 2013, but the behavioural data implies that more mobile pairs tended to have pre-breeding clusters with earlier laying dates, breeding clusters with a higher occupancy rate, and pre-breeding nest boxes with a higher occupancy rate. Since most of the females bred in nest boxes close to the pre-breeding nest box (except for one female that left to a nest box several km away), the pre-breeding and breeding territories are probably the same or at least overlapping. The amount of frass was higher in clusters with higher occupancy rates, indicating that the territories that the great tits prefer are also better territories in terms of food abundance. The most explorative pairs were therefore in better territories, which should render better offspring (Przybylo et al., 2001). Our experimental set-up did not allow us to determine where the differences in behaviour came from, especially since we used behavioural data found in the field. This means we do not know if behaviour affects territory choice or if territory quality affects behaviour. More explorative individuals could therefore have better territories because they are competitively stronger, or individuals in better territories are more explorative or aggressive because they are in a better territory.

However, slow exploring parents could compensate for the worse territory (Maícas et al., 2012; Tremblay et al., 2004) by investing in different aspects of the rearing of their offspring such as a longer nestling stage or longer care after fledging (Wilkin et al., 2009a). Compensation also seems to happen in our research area, where deciduous habitats had a higher occupancy rate than coniferous forests, earlier laying dates and higher clutch size, but in coniferous habitats more and heavier young fledged (Mänd et al., 2005). However, the chance of a nest box producing a successful nest in the studied years (excl. 2013) is higher in deciduous forest than in coniferous forest. Since a successful nest was defined as a nest fledging at least one young, this discrepancy might be caused by less successful nests, but fledging more young per successful nest.

Our study indicates that there is a correlation between great tit personalities and territory quality, although it does not show what the underlying mechanisms are and which way this correlation works. However, our findings are an interesting starting point for further studies.
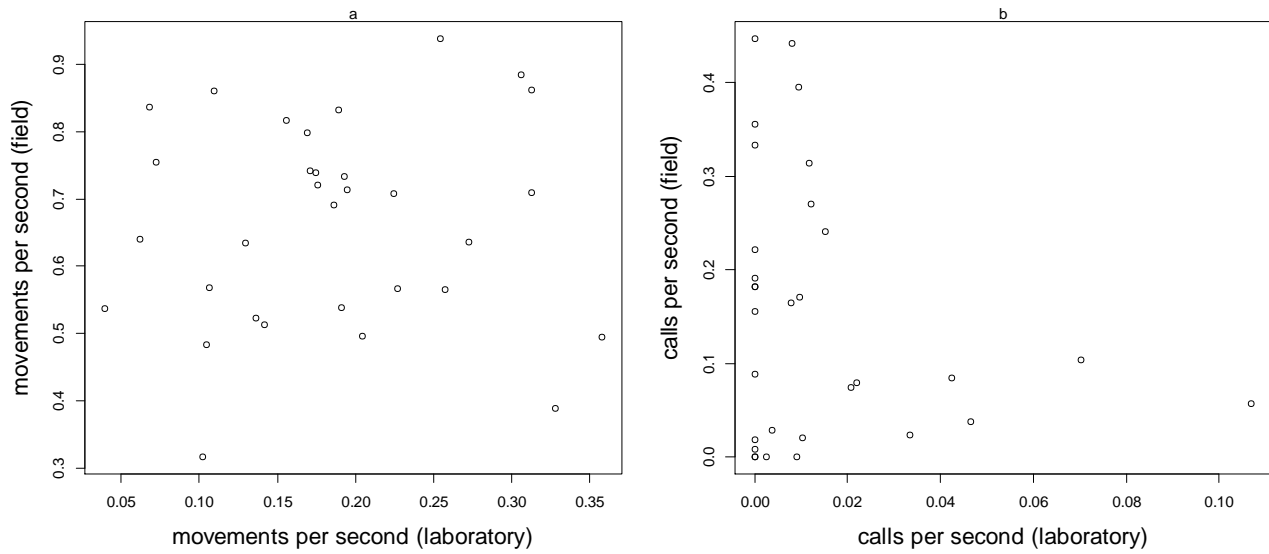
Figure 1 Correlation of two behavioural tests on individual female great tits in Kilingi-Nõmme, Estonia, before breeding in the laboratory (x-axis) and during nestling feeding (y-axis). The number of movements per second (a) and the number of calls per second (b) measured over a two minute interval did not significantly correlate between the laboratory and the field (r = 0.0678, df = 30, t = 0.37, p = 0.713, t = 0.37, and r = -0.229, df = 29, p = 0.215, t = -1.27 respectively).
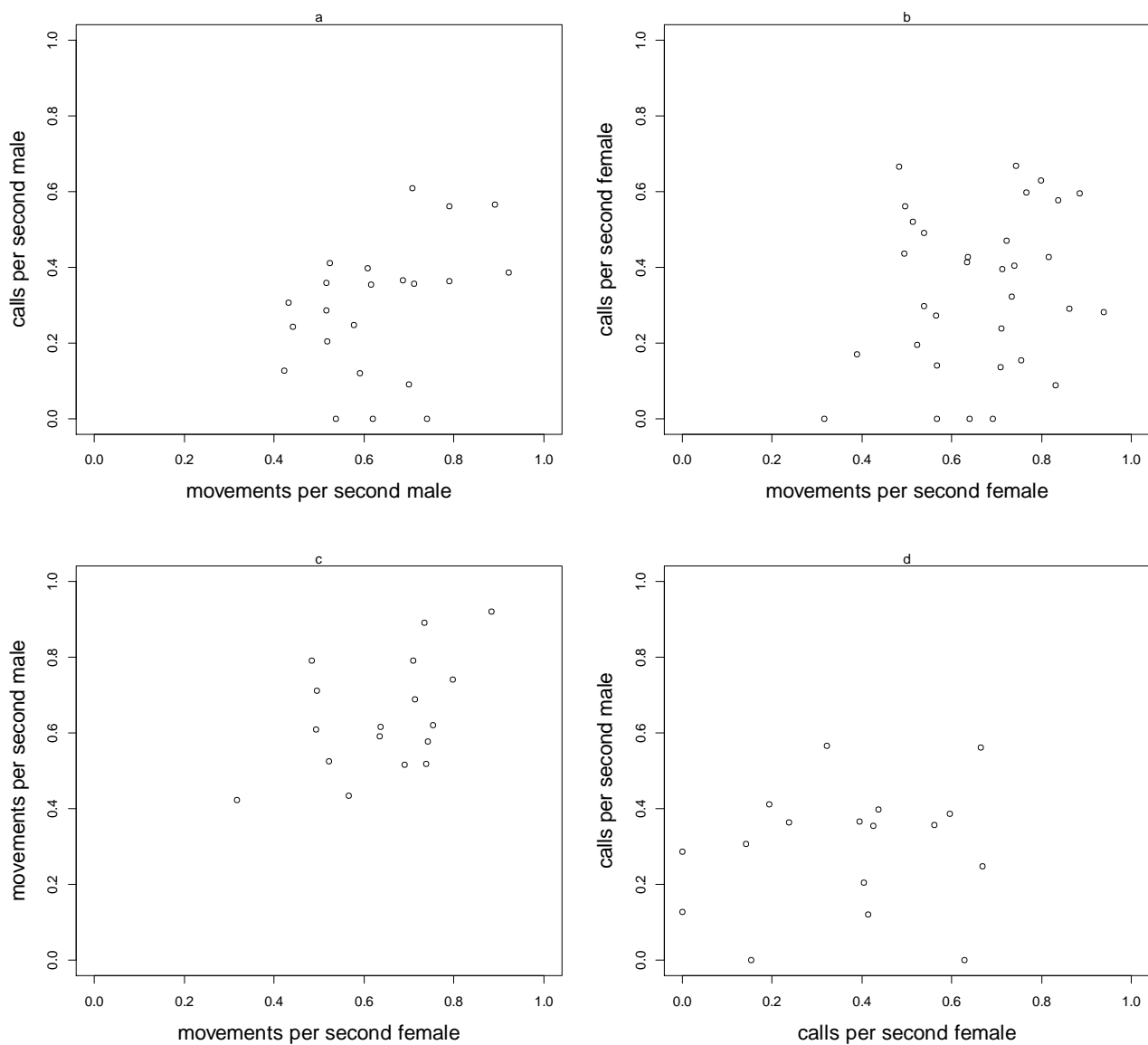
Figure 2 Correlations of a two to three minute long behavioural test in individual great tits in the field during nestling feeding, in Kilingi-Nõmme, Estonia. The number of movements and calls per second showed a trend in males (r = 0.392, n = 22, p = 0.071, t = 1.91)(a), but not in females (r = 0.208, n = 32, p = 0.253, t = 1.17) (b). Males and females did not differ in the number of movements and calls per second (t = -0.923, df = 47.4, p = 0.361, and t = -1.291, df = 51.6, p = 0.346 respectively). The number of movements per second was significantly correlated between males and females (r = 0.488, n = 17, p = 0.0471, t = 2.16) (c), but the number of calls per second was not (r = 0.183, n = 17, p = 0.483, t= 0.72) (d). Of the calls of both males and females a square root was used to make the data normally distributed.
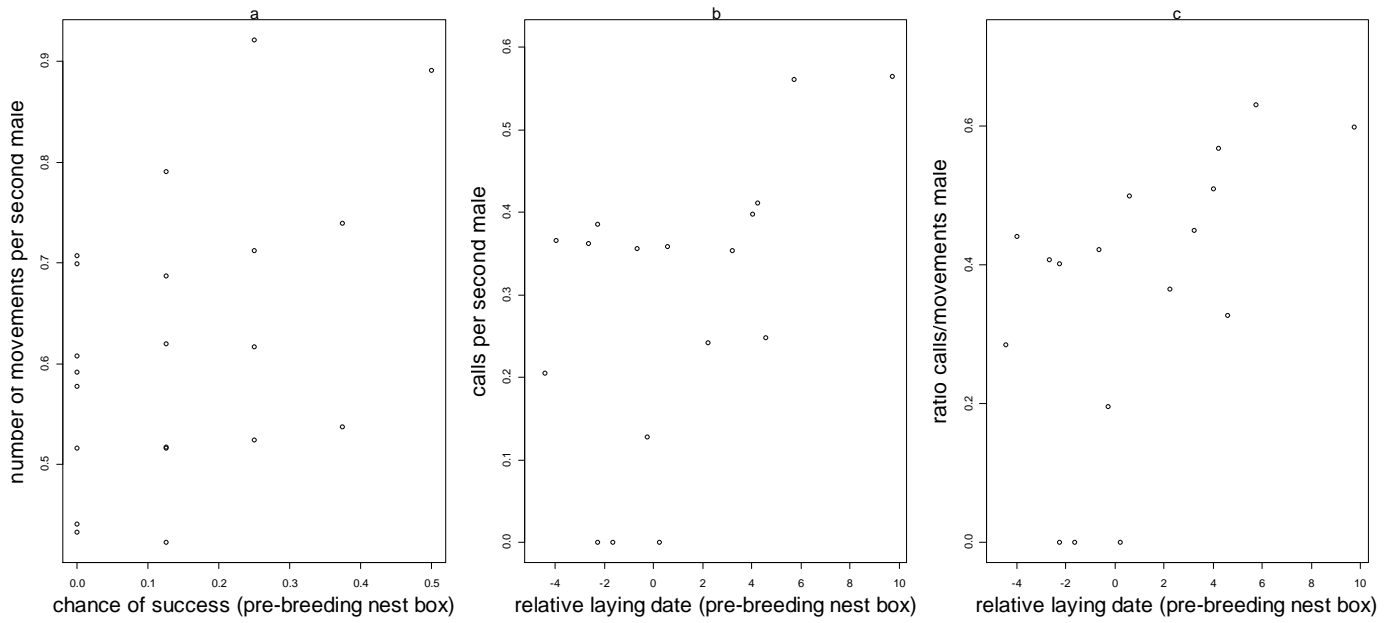
Figure 3 Correlation between a two to three minute long behavioural test in individual male great tits in the field in Kilingi-Nõmme, Estonia during nestling feeding (x-axis) and historical breeding data between 2001 and 2012 (y-axis). The chance of having a successful nest in previous years increased for pre-breeding nest boxes with the number of movements per second (est = 2.66, df = 15, p = 0.0197, t = 2.69) (a). The relative laying date increased with the number of calls (b) and the number of calls compared to number of movements (est = 0.024, df = 16, p = 0.0265, t = 2.46, and est = 0.0268, df = 16, p = 0.0268, t =2.46).

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Supplementary data

S 1 Overview of all statistical tests used in this study. In total six correlations, two t-tests and 42 GLMs were done. Chance is defined as an interaction between fate and occupancy when it is used as a covariate. When used as a dependent variable it is defined as occupancy*fate. All p-values lower than 0.1 are mentioned in the Results section, all the other tests did not render any significant results. GLM ovariates that have a p-value lower than 0.1 are marked with an asterix (*). The test results for all correlations and the t-tests are shown and marked with an asterix (*) if the p-value is lower than 0.1. If one test rendered more than one significant result, the test results are placed in the same order as the covariates are listed. For the GLMs only the test-results for the significant covariates are shown, the rest is marked as not significant (N.S.).

Test	x	y	Comments	Test results
Pearson's correlation	Movements laboratory	Movements field	Only female behaviour	r: 0.07, df: 30, p: 0.71, t: 0.37
	Calls laboratory	Calls field	Only female behaviour	r: -0.23, df: 29, p: 0.21, t: -1.27
	Movements male	Calls male	Field	r: 0.39, n: 22, p: 0.071, t: 1.91
	Movements female	Calls female	Field	r: 0.21, n: 32, p: 0.25, t: 1.67
	Movements male	Movements female	Field	r: 0.49, n:17, p: 0.047, t: 2.16
	Calls male	Calls female	Field	r: 0.18, n: 17, p: 0.48, t: 0.72
Student's T-test	Movements male	Movements female	Field	t: -0.92, df: 47.4, p: 0.36
	Calls male	Calls female	Field	t: -1.3, df: 51.6, p: 0.35
GLM	**Dependent variable**	**Covariates**		
	Movements male	Clutch size, relative laying date, occupancy*, fate, chance*, habitat	Pre-breeding nest box	est: -1.99, df: 15, p: 0.040, t: -2.31, est: 2.66, df: 15, p: 0.020, t: 2.69
	Movements male	Clutch size, relative laying date, occupancy, fate, chance, habitat	Pre-breeding cluster	N.S.
	Movements male	Clutch size, relative laying date, occupancy, fate, chance, habitat	Breeding nest box	N.S.
	Movements male	Clutch size, relative laying date, occupancy*, fate, chance, habitat	Breeding cluster	est: 0.223, df: 21, p: 0.031, t: 2.32
	Calls male	Clutch size, relative laying date*, occupancy, fate, chance, habitat	Pre-breeding nest box	0.0245, df: 16, p: 0.027, t: 2.46
	Calls male	Clutch size, relative laying date, occupancy, fate, chance, habitat	Pre-breeding cluster	N.S.
	Calls male	Clutch size, relative	Breeding	N.S.

	laying date, occupancy, fate, chance, habitat	nest box	
Calls male	Clutch size, relative laying date, occupancy, fate, chance, habitat	Breeding cluster	N.S.
Ratio calls/movements male	Clutch size, relative laying date*, occupancy, fate, chance, habitat	Pre-breeding nest box	est: 0.0282, df: 16, p: 0.027, t: 2.46
Ratio calls/movements male	Clutch size, relative laying date, occupancy, fate, chance, habitat	Pre-breeding cluster	N.S.
Ratio calls/movements male	Clutch size, relative laying date, occupancy, fate, chance, habitat	Breeding nest box	N.S.
Ratio calls/movements male	Clutch size, relative laying date, occupancy, fate, chance, habitat	Breeding cluster	N.S.
Movements female	Clutch size, relative laying date, occupancy, fate, chance, habitat	Pre-breeding nest box	N.S.
Movements female	Clutch size, relative laying date, occupancy, fate, chance, habitat	Pre-breeding cluster	N.S.
Movements female	Clutch size, relative laying date, occupancy, fate, chance, habitat	Breeding nest box	N.S.
Movements female	Clutch size, relative laying date, occupancy, fate, chance, habitat	Breeding cluster	N.S.
Calls female	Clutch size, relative laying date, occupancy, fate, chance, habitat	Pre-breeding nest box	N.S.
Calls female	Clutch size, relative laying date, occupancy, fate, chance, habitat	Pre-breeding cluster	N.S.
Calls female	Clutch size, relative laying date, occupancy, fate, chance, habitat	Breeding nest box	N.S.
Calls female	Clutch size, relative laying date,	Breeding cluster	N.S.

	occupancy, fate, chance, habitat		
Ratio calls/movements female	Clutch size, relative laying date, occupancy, fate, chance, habitat	Pre-breeding nest box	N.S.
Ratio calls/movements female	Clutch size, relative laying date, occupancy, fate, chance, habitat	Pre-breeding cluster	N.S.
Ratio calls/movements female	Clutch size, relative laying date, occupancy, fate, chance, habitat	Breeding nest box	N.S.
Ratio calls/movements female	Clutch size, relative laying date, occupancy, fate, chance, habitat	Breeding cluster	N.S.
Movements pair	Clutch size, relative laying date, occupancy*, fate, chance, habitat	Pre-breeding nest box	est: 0.389, df: 17, p: 0.080, t: 1.87
Movements pair	Clutch size, relative laying date*, occupancy, fate, chance, habitat	Pre-breeding cluster	est: -0.0199, df: 16, p: 0.081, t: -1.87
Movements pair	Clutch size, relative laying date, occupancy, fate, chance, habitat	Breeding nest box	N.S.
Movements pair	Clutch size, relative laying date, occupancy*, fate, chance, habitat	Breeding cluster	est: 0.175, df: 17, p: 0.098, t: 1.76
Calls pair	Clutch size, relative laying date, occupancy, fate, chance, habitat	Pre-breeding nest box	N.S.
Calls pair	Clutch size, relative laying date, occupancy*, fate, chance, habitat	Pre-breeding cluster	est: 0.183, df: 16, p: 0.090, t: 1.81
Calls pair	Clutch size, relative laying date, occupancy*, fate, chance, habitat	Breeding nest box	N.S.
Calls pair	Clutch size, relative laying date, occupancy, fate, chance, habitat	Breeding cluster	N.S.
Ratio calls/movements pair	Clutch size, relative laying date*, occupancy, fate,	Pre-breeding nest box	est: 0.0183, df: 13, p: 0.094, t: 1.82

		chance, habitat		
Ratio calls/movements pair	Clutch size, relative laying date, occupancy, fate, chance, habitat	Pre-breeding cluster	N.S.	
Ratio calls/movements pair	Clutch size, relative laying date, occupancy, fate, chance, habitat	Breeding nest box	N.S.	
Ratio calls/movements pair	Clutch size, relative laying date, occupancy, fate, chance, habitat	Breeding cluster	N.S.	
Chance	Clutch size, relative laying date*, habitat*	All nest boxes	est: -0.00360, df: 550, p: 0.032, t: -2.15, est: 0.0582, df: 550, p: <0.001, t: 5.55	
Frass	Clutch size, relative laying date, occupancy, fate, chance, habitat	Breeding nest box	N.S.	
Frass	Clutch size, relative laying date, occupancy*, fate, chance, habitat	Breeding cluster	est: 0.977, df: 21, p: 0.071, t: 1.91	
Frass	Movements, calls male		N.S.	
Frass	Movements, calls female		N.S.	
Frass	Movements, calls pair		N.S.	