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„No nest box is an island – neighbor personalities influence reproductive success in tits. An interspecific comparison."

verfasst von / submitted by
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Abstract

To test if small scale breeding densities, intra- and interspecific, and the behavior of immediate con- and heterospecific neighbors affect the reproduction of focal individuals, we measured the exploratory behavior and reproductive success in a wild population of great and blue tits over one breeding season. Overall, we observed 220 breeding pairs, testing 325 adult birds for their exploratory behavior, and determined the number and average exploration score for each breeding pair's immediate neighbors. As fitness measurements we used clutch size, nestling condition and the number of fledglings per nest. The findings show that while female great tits with more explorative great tit neighbors only tended to lay less eggs, they laid significantly less eggs with more explorative blue tits as neighbors. On the other hand, female blue tits tended to lay more eggs with more explorative blue tits as neighbors, while more explorative great tit neighbors had no effect on their clutch size. During the nestling stage, great tit nestlings with more explorative conspecific neighbors tended to weigh less, while they weighed significantly more with more explorative blue tits as neighbors. The nestling condition of blue tits was not affected by the exploratory behavior of either neighbor species. Furthermore, the probability for a nest of either species to produce at least one fledgling was not affected by the exploratory behavior of neighboring blue or great tits. This was also true for the number of fledglings that a focal nest produced, with one exception: great tits produced significantly more fledglings with more explorative blue tits as neighbors. Independent of species, the number of neighbors had no effect on the clutch size, nestling condition and the number of fledglings of a focal blue or great tit nest. This was also true for the probability of a focal nest to produce at least one fledgling, with one exception: great tits with more blue tit neighbors had a significantly higher probability to produce at least fledgling. These findings demonstrate that the behavior of neighboring con- and heterospecifics can affect the reproductive success of individuals, whereas the absolute number representing small scale breeding density seems to be less important. The negative effects of small-scale densities might be outbalanced by higher territory quality causing this density in the first place. Furthermore, the exact behavior of neighbors might be unpredictable and could therefore influence food availability and social interactions beyond the absolute number of neighbors. Thus, neighbor behavior could be more influential on reproductive success.

Introduction

Competition and its effect on animal behavior: an overview

Competition is a fundamental process in nature, with individuals competing for resources and mating opportunities. In order to survive and reproduce, each individual has to enter such competition, which can thus strongly affect various morphological and life-history traits via natural and sexual selection (Alatalo et al. 1985; Gosler et al. 1994; Garant et al. 2007; Dhondt 2012).

In general, competition can be defined as the negative effects that one organism or species exerts upon another (Keddy 1989). It can be grouped into intraspecific- (among individuals within the same species) and interspecific- (among individuals between different species) competition (Keddy 1989). Interspecific competition may increase if the niches that two different species occupy show a higher degree of overlap. At the same time, spatio-temporal and/or behavioral differences can in- or decrease competition (Mittelbach et al. 2019). For instance, ecological similar bird species reduce interspecific competition by foraging at different heights of the vegetation or by breeding at different times of the year (Gibb 1954; Codey 1974). The two underlying mechanisms present in intra- and interspecific competition are exploitative and interference-competition. The former arises from indirect negative interactions where each competitor affects others solely by depleting a shared limiting resource (Case et al. 1974; Vance 1984). The latter is due to direct negative interactions like overt aggression between competitors (e.g., territorial defense) (Schoener 1983). In this case, each competitor restricts access to another competitor's limiting resource (Vance 1984). The limiting resources over which individuals compete can fluctuate extensively, as can the timing and strength of competition, throughout the course of a year (Oksanen 1987; Fretwell 1972). For instance, if environmental conditions are favorable and resources plentiful, individuals may relax competition (Fretwell 1972; Dhondt 2012). At the species level, competition may result in the exclusion of one species if it experiences a stronger competitive effect from another species than within its own species (Gause 1932; Chesson 2000). From an individual's point of view, the factors affecting the outcome of competitive interactions can be divided into two groups: intrinsic factors encompass an individual's morphology, physiology, genotype and behavior; extrinsic factors can differ among populations and include environmental conditions, the number of competing con- and heterospecifics and their respective behavior, and also the intensity of intra- and interspecific competition (Bolnick et al. 2010; Dhondt 2012; Stenseth et al. 2015; Mittelbach et al. 2019).

In both cases, interference and exploitation competition, individuals need to adjust their own behavior in order to cope with changing environmental conditions (e.g., decrease in food availability), or during social interactions (e.g., physical fights for resources). The mechanism behind behavioral adaptions is called behavioral plasticity (Snell-Rood 2013; Stamps 2015). Behavioral plasticity is a heritable trait and describes a reversible mechanism that allows a certain genotype (i.e., an individual) to create different behavioral phenotypes (so-called within individual variation), depending on environmental conditions (Piersma et al. 2003; Aubin-Horth et al. 2009). For instance, competitors may deplete food sources forcing the focal individual to adjust its foraging behavior, or to reassess the quality of its habitat, potentially leading to differences in reproductive investment.

While behavioral plasticity in response to environmental conditions has been the traditional focus of behavioral ecology, similar changes in response to conspecifics' phenotypes are less well understood: social responsiveness occurs due to individuals altering their behavior as a function of their previous interactions with social partners of the same species (Dingemanse et al. 2015). Therefore, a focal individual may change a specific behavior either in response to the same trait, or to a different trait expressed by its conspecifics (Moore et al. 1997; Santostefano et al. 2016). For instance, individuals adjust their own level of aggression in response to a competitor's level of aggression in escalating fights, or in response to a competitor's body size (Moore et al. 1997; Santostefano et al. 2016). It is not yet clear whether social responsiveness is heritable or evolvable (Chenoweth et al. 2010; Bailey et al. 2012).

A special case of social responsiveness occurs when the involved traits of the focal and conspecific individual are heritable. In such cases, genes expressed in one individual alter the expression of a (behavioral) trait expressed in a social partner (Moore et al. 1997; Wolf et al. 1998; Wolf 2000; McGlothlin et al. 2010). This is referred to as indirect genetic effects (IGEs). IGEs are expected to exist in traits that are expressed specifically as part of social interactions, for instance, in aggression and dominance (Moore et al. 1997). Also, since the social environment itself is heritable and likely to evolve due to IGEs, major evolutionary consequences may ensue (McGlothlin et al. 2010). For instance, IGEs can slow down or speed up the evolution of traits and change the direction of evolution from what would be predicted in the absence of IGEs (Moore et al. 1997; Wolf et al. 1999; Wolf 2003; McGlothlin et al. 2010). IGEs can also impact the expression of behaviors within interspecific or multitrophic interactions (Genung et al. 2013a, 2013b).

A prime example for a behavioral trait playing an essential role in competition is exploratory behavior. It is defined as the rate at which an individual moves through a novel environment (Verbeek et al. 1994, Dingemanse et al. 2002). By exploration, individuals learn where resources can be found and where they can hide from predators. The acquired knowledge about their habitat may thus impact the outcome of competitive interactions (Krebs 1982;

Drent 1983; Stamps 1987). Individuals can differ consistently in exploratory behavior, which can be characterized along an axis ranging from slow to fast explorers: while slow explorers move through a novel environment slowly and carefully, the opposite is true for fast explorers (Verbeek et al. 1994; Groothuis et al. 2005). Moreover, numerous studies have linked exploratory behavior to different information gathering strategies in foraging contexts, generating two contrasting hypotheses: under the 'information gathering hypothesis' (IGH) fast explorers are expected to be more active and to specifically search for new resources in previously unexplored areas more than slow explorers, who are expected to return to formerly sampled patches (Arvidsson et al. 2016; Rojas-Ferrer et al. 2020). In contrast, under the 'behavioral flexibility hypothesis' (BFH) fast explorers are expected to seek out and sample previously visited patches due to behavioral constrains stemming from the formation of routine-like behaviors, while slow explorers are expected to be more flexible and look for new resources in novel areas (Verbeek et al. 1994; Koolhaas et al. 1999; Coppens et al. 2010). These individual differences in information gathering in foraging contexts may impact reproductive success. For instance, if the IGH holds true, fast explorers may be more efficient in providing for their young when prey is scarce, since they don't waste time and energy to return to previously explored patches that likely contain no more prey items. Ultimately, this may improve nestling condition and shift competition in the individual's favor. Furthermore, exploratory behavior in many different taxa is positively correlated with aggression, meaning that fast explorers are more aggressive than slow explorers (Oortmerssen et al. 1985; Benus et al. 1987, 1990; Hessing et al. 1994; Verbeek et al. 1996). For instance, fast individuals initiate more fights than slow explorers, and birds that start fights also win more fights (Verbeek et al. 1996). Consequently, focal birds with more explorative neighbors also have to cope with their neighbors' higher level of aggression and the subsequent negative effects. This pattern might be even more pronounced among species, especially if the two species differ in morphology, e.g. size, or fighting ability. These differences may reduce the costs of aggression for the dominant species, dramatically shifting competition in its favor. In the end, focal parents that are frequently involved in time and energy-consuming fights with more aggressive con- or heterospecific neighbors may produce a smaller clutch or have nestlings in poorer condition than breeding pairs without more aggressive neighbors.

The model organisms

As mentioned, competition is not restricted to the within-species level; different species can compete for the same or overlapping resources. A textbook example of species co-existence – that is, the persistence of two species in the same habitat – resulting in potential interference and exploitation competition for breeding and roosting sites, and for food, are

great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*) (Codey 1974; Dhondt 2012; Møller et al. 2018). Both species are secondary cavity-nesting breeders and accept nest boxes as breeding sites (Svensson et al. 2009). As a result, their populations can reach high densities which allows researchers to conduct extensive experimental and descriptive work while accumulating large sample sizes (e.g., Pettifor 1988; Tinbergen et al. 1990). In both species the females alone build the nest and incubate the clutch, but both parents contribute to provide the nestlings with caterpillars, whilst they themselves eat also other insects during the summer months (Gibb 1950; Betts 1955; Lack 1966; Perrins 1970, 1979, 1991; Cramp et al. 1993; Gosler 1993). Since nestlings utterly depend on parental efforts for survival (Kluyver 1951; Ricklefs 1983; Tinbergen et al. 1990; Gebhardt-Heinrich et al. 1991) the foraging performance of the parents is an important determinant of reproductive success and a central link between environment and fitness (Naef-Daenzer et al. 1999). In the case of co-existing great and blue tits, blue tits can preemptively outcompete great tits for food by consuming the smaller instar of the same caterpillar species that is also eaten by great tits (Nour et al. 1998; Török 1993; Török et al. 1999). Great tits, on the other hand, as the larger and more dominant species of the two, can gain preferential access to other (food) resources (Dhondt 2012). These overlapping ecological requirements should result in strong interspecific competition, in addition to the existing intraspecific one. Ultimately, this may lead to altered fitness for the two species via direct and indirect interactions, although the effects may differ, depending on the species. For instance, great tits, as the physically dominant species, may be less affected by blue tits than by other great tits, whereas blue tits might suffer more from the presence of their bigger relatives. But clearly, such effects also depend on the habitat quality and overall breeding densities, as poor habitat qualities and high breeding densities would increase competition and thus any detrimental effect – that is, for instance, decreasing clutch sizes with increasing breeding density, both intra- and interspecific (Dhondt et al. 1980; Garant et al. 2007; Dhondt 2010, 2012; Møller et al. 2018).

Aims

While effects of population density or limiting resources on reproductive output have been the focus of numerous studies (Dhondt et al. 1980; Dhondt 2012; Møller et al. 2018), less research has been dedicated to investigate how the behavior of immediate neighbors may affect the reproduction of focal individuals. Since the collected data for exploratory behavior only includes one measurement per adult bird (exploration score), the results of this thesis cannot give evidence about effects on IGEs, social responsiveness or animal personality per se. Instead, the findings can be used as an indicator for future work. Therefore, the aims of this thesis are to establish whether small scale breeding densities,

intra- and interspecific, and the behavior of neighbors, affect the reproductive success of co-existing great and blue tits in the wild.
Overall, I predict that (1) for both species the number of neighbors has a negative effect on the reproductive output of a focal nest, as have (2) more explorative neighbors.

Materials and methods

Study area and study population

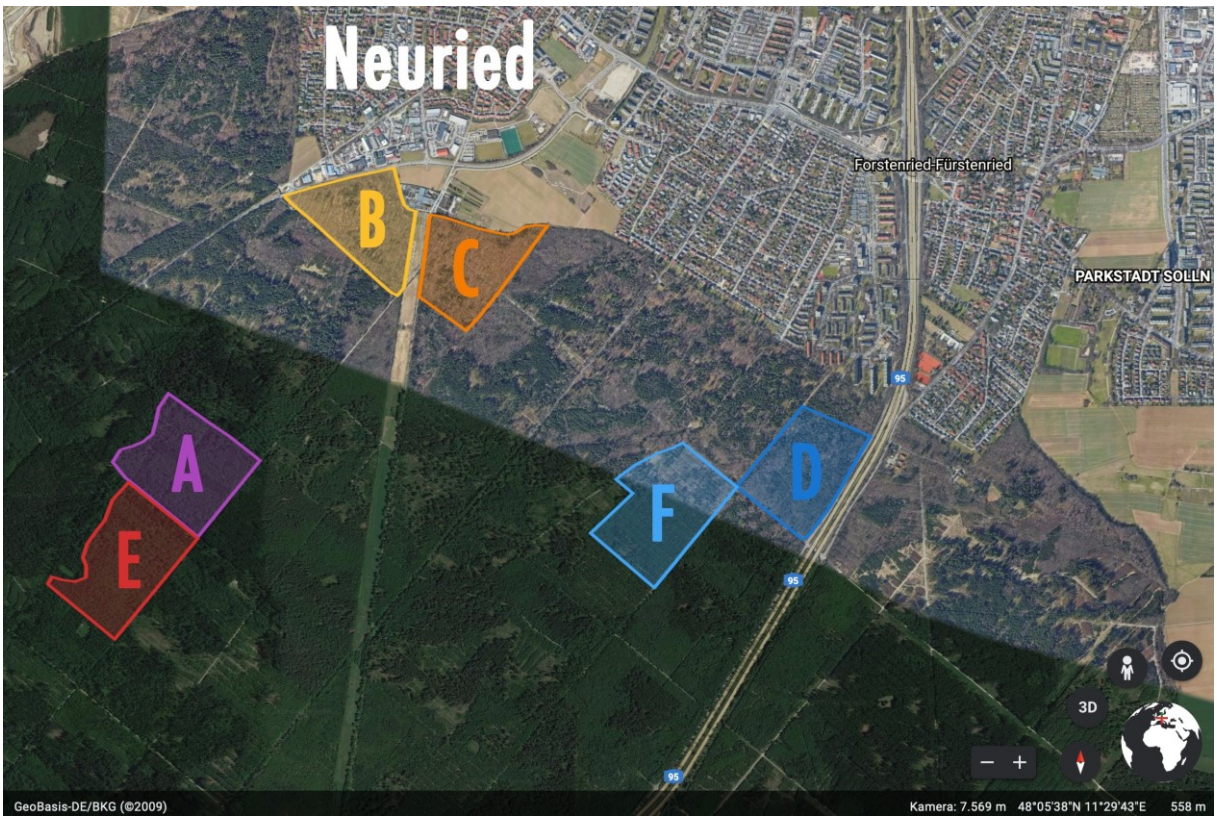

Figure 1: Satellite image displaying the study area with all six plots (A-F) and the surrounding towns. Screenshot was taken from Google Earth. The outlines of the individual plots were drawn in later.

The fieldwork for this thesis was carried out as part of a larger study on a wild population of great and blue tits in the Forstenrieder Park just south of Neuried/Munich in Bavaria, Germany (Figure 1). The study began measuring both bird species in the breeding season of 2020. The study area held 210 nest boxes for great tits, 210 nest boxes with a smaller entrance hole for blue tits (to prevent the larger great tits from entering), and 45 nest boxes with a blocked entrance hole, resulting in a total of 465 nest boxes. The nest boxes were set up in six plots, containing each 70 (plots E, C, D) or 70+15 (plots A, B, F) nest boxes. The six plots were grouped in three pairs (B+C, E+A, F+D) with the two plots of a pair lying side by side (B+C, E+A) or in close proximity to one another (F+D). In all plots 70 nest boxes were laid out in a grid with approximately 50m between neighboring boxes. In plot C, E and F the entrance holes of 15 nest boxes lying closely together were blocked to create low density areas. In plots A, B and F 15 additional nest boxes were placed in the immediate vicinity (4-5 m) of 15 unblocked boxes creating high density areas. The area size of the individual plots

varied from 16 to 21 ha. All plots were part of a large mixed or/and deciduous forest. All nest boxes were fixed on trees approximately between 2 and 2.2 m above ground.

Data collection

Nest box checks

Fieldwork started in the first week of April and lasted until mid-June. Thereby nest boxes were checked for potential nest-building and its progress twice a week (Figure 2).

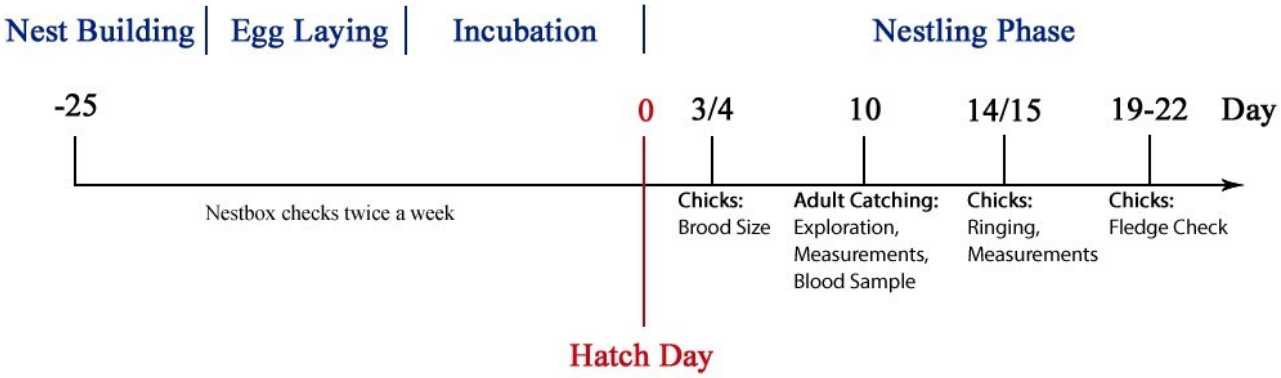

Figure 2: Overview of the breeding season: the timeline is given in relative days to the hatch day of the chicks (day 0). Brood size was determined on days 3/4. The adults were caught on nestling day 10. The chick measurements were taken on days 14/15. The fledge checks took place between day 19 and 22.

The date of the first egg in the nest was back-calculated with the assumption that one egg was laid per day and that the last new egg was laid on the day the nest box was checked. Once the female started incubating the eggs (the start of incubation was assumed to be on the day the nest box was checked) the clutch size was determined. During incubation the nests were not checked, since disturbances can cause the female to abandon the nest. Two days before the expected hatch date (i.e., 14 days after the start of incubation) the nest was checked daily for hatchlings. The hatching date was defined as day 0. On days 3/4 the brood size was determined. Ten days after hatching the adults were caught and their exploration score was determined via the cage test. The chick measurements were taken on days 14 or 15 and included the weight of each chick, its fat score (assessed by the amount of fat in the furcular), and its wing- and tarsus-length. The fledge checks took place between days 19 and 22. The schedule and methods of the data collection were derived from information given by van Balen (1973) and following the procedures of Nicolaus et al. (2009).

Cage test, video analysis and exploration score

On day 10 the parents were caught by means of a metal spring-trap blocking the exit hole of their nest box after the adult birds entered and triggered the trap. Subsequently, they were tested for exploratory behavior via a ‘Cage Test’ based on the ‘Novel Environment

Test' developed by Verbeek et al. (1994) for great tits. It was adapted and detailed by Dingemanse et al. (2002) and Stuber et al. (2013).

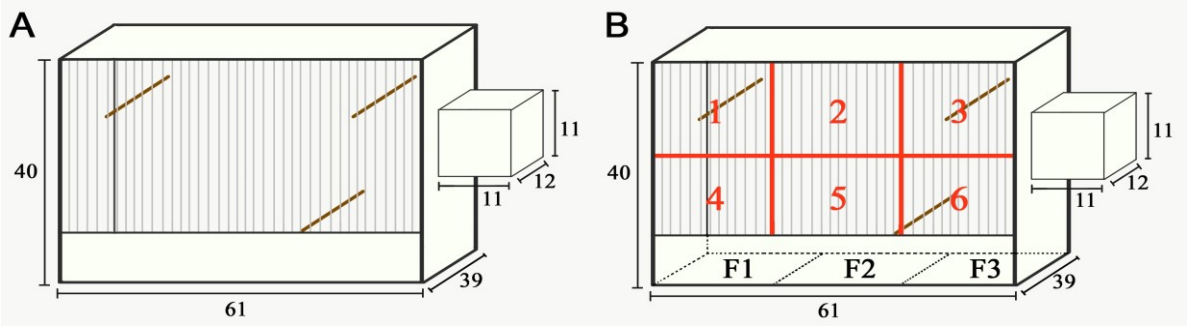

Figure 3: A: shows the dimensions of the cage (61 cm x 40 cm x 39 cm) used for the cage test. A small acclimation box (11 cm x 11 cm x 12 cm) attached to the right wall of the cage was connected to the experimental room via a sliding door. The cage was mainly made of white plastic, except for the front, which was made of metal bar grating. The three brown lines represent wooden perches. B: shows the sectioning of the cage for video analysis: the metal bar grating was divided into six (1-6), and the cage floor into three (F1-3), equally large sections. A and B were redrawn after Stuber et al. (2013).

A cage with a small box attached to its side was placed on the forest ground (Figure 3). The cage and box were connected via a sliding door. Within the cage were three wooden perches. At first, the birds were placed in the small box and shortly after introduced to the cage by opening the sliding door; thus, at the beginning of the test, each bird entered the cage without being handled by the observer. Subsequently, the behavior of the birds was recorded for two minutes with a video camera. The camera was mounted on a tripod at about 30 cm of height and at a distance of approximately 1.5 m from the front of the cage. The observer kept out of the bird's vision for the duration of the recording. Afterwards, the videos were analyzed at reduced speed using the software BORIS (Friard et al. 2020): therefore, the metal bar grating was divided into six, and the cage-floor into three, equally large virtual sections (Figure 3). Every time the bird moved from one section to the next (metal bars, floor), settled on one of the three perches or pecked at the floor, the metal bars or the perches, the movement was recorded. The total number of movements and pecks, within and between different sections, was used as a proxy for exploratory behavior and resulted in the exploration score.

Neighbor assignment

From the outset, nest boxes positioned at the edge of a plot had fewer potential neighbors than those placed in the center of a plot. All neighbors were determined in relation to their position in the grid and to the focal nest box, meaning that only boxes occupied by blue or great tits immediately surrounding a focal nest box were counted as neighbors. The number of neighbors per nest was counted separately for each species. Boxes occupied by coal tits or nuthatches were excluded from the count and treated as unoccupied. Empty nest boxes

were also not included in the count. After the count was complete, the mean exploration score of all neighbors was calculated separately for each neighbor species.

Statistical analysis

To test if small scale breeding densities, intra- and interspecific, and the behavior of neighbors affected the reproductive success of great or blue tits, univariate linear mixed-effects models were run, using the following measures of fitness as response variables: I) Clutch Size, II) Nestling Condition (weight of the chicks on day 14/15), III) the Number of Fledged Nestlings. Arguing that the zero-inflated distribution of the number of fledglings was caused by two distinct mechanisms, the data was split into two response variables: "Fledged" and "Number Fledged". For the first mechanism it was assumed that external factors (e.g., weather, predation) can lead to the death of all chicks in a nest ("Fledged"). For the second process it was assumed that as soon as a nest "produced" fledglings, other factors (e.g., quality of parental care) influence the number of fledglings ("Number Fledged").

For each response variable two models were run. The first included the number of con- and heterospecific neighbors as separate fixed effects, the second the exploration scores for all con- and heterospecifics as separate fixed effects. In addition, all models included "Plot" as random effect. Furthermore, all models that examined the effects of the number of con- and heterospecific neighbors also included "Species" and "Nr.GT/BTneighbor" as an interaction between the two as fixed effects. All models that examined the effect of the mean exploration score of con- and heterospecific neighbors also included "Species" and "MExpScoreGT/BT" as an interaction between the two as fixed effects. The two models for Clutch Size and the two models for Nestling Condition were modeled with Gaussian errors. The two models for Nestling Condition included the time of day when the nestlings were measured (D14 Time of Day) and a correction accounting for the fact that weight-measurements were taken either on day 14 or on day 15 (D14/15) after hatching as additional fixed effects. Both models for Nestling Condition were modeled with Gaussian errors. The models for Fledged were modeled with binomial/binary errors and, due to non-convergence, the mean exploration score of both neighbor species had to be standardized. The models for Number Fledged were also both modeled with Gaussian errors and the clutch size was added as a covariate. The separate analysis of number and exploration behavior of neighbors was done to avoid overfitting and to make better use of differing sample sizes, as birds with zero great tit or zero blue tit neighbors would otherwise have been excluded from the analysis.

All statistical analyses were performed with R (R Foundation for Statistical Computing 2020) using RStudio Desktop (RStudio, Inc. 2020). For data analysis generalized linear mixed-

effects models were applied, for which the *glmer* function (lme4 package) was used, as well as linear mixed-effects models (GLMM), for which the *lmer* function (lme4 package) was used. Furthermore, the *sim* function (arm package) was used to simulate the posterior distribution of the model parameters and the extracted values were based on 2000 simulations (Gelman et al. 2007). The statistical significance of the fixed-effects and interactions were assessed based on the 95% credible intervals (CI) around the mean (β). An effect was judged as "significant" when the 95% CI did not overlap zero (Nakagawa et al. 2007). The model fit was checked by visual assessment of the residuals.

Results

During the breeding season 2020 325 cage tests were performed on the adult birds of 220 nests of which 133 (60%) were great tit nests and 87 (40%) blue tit nests. The cage tests generated n = 323 videos that were analyzed and used for statistical analysis. On average, a female blue tit laid ten eggs (mean = 9.63; standard error = ±0.21) and a female great tit laid about nine eggs (8.65 ±0.19). The mean probability for a great tit nest to produce at least one fledgling was 62.41%; for a blue tit nest it was 75.86%. Great tit nestlings (15.82 g ±0.17 g) were heavier than blue tit nestlings (11.07 g ±0.14 g) when weighed on day 14/15 post-hatch. Great tit nests produced around four fledglings (4.44 ±0.33), while blue tit nests produced about six fledglings (6.33 ±0.44). Blue tit nests had approximately two great tit (2.07 ±0.13) and one blue tit neighbor (1.13 ±0.13). Great tit nests had on average one great tit (1.34 ±0.11) and one blue tit (1.44 ±0.10) neighbor. The mean exploration score of all great tit neighbors per great tit nest was 67.52 ±1.62. The mean exploration score of all great tit neighbors per blue tit nest was 67 ±1.36. The mean exploration score of all blue tit neighbors per great tit nest was 50.04 ±1.28, and the mean exploration score of all blue tit neighbors per blue tit nest was 46.40 ±2.34 (Figure 4, 5).

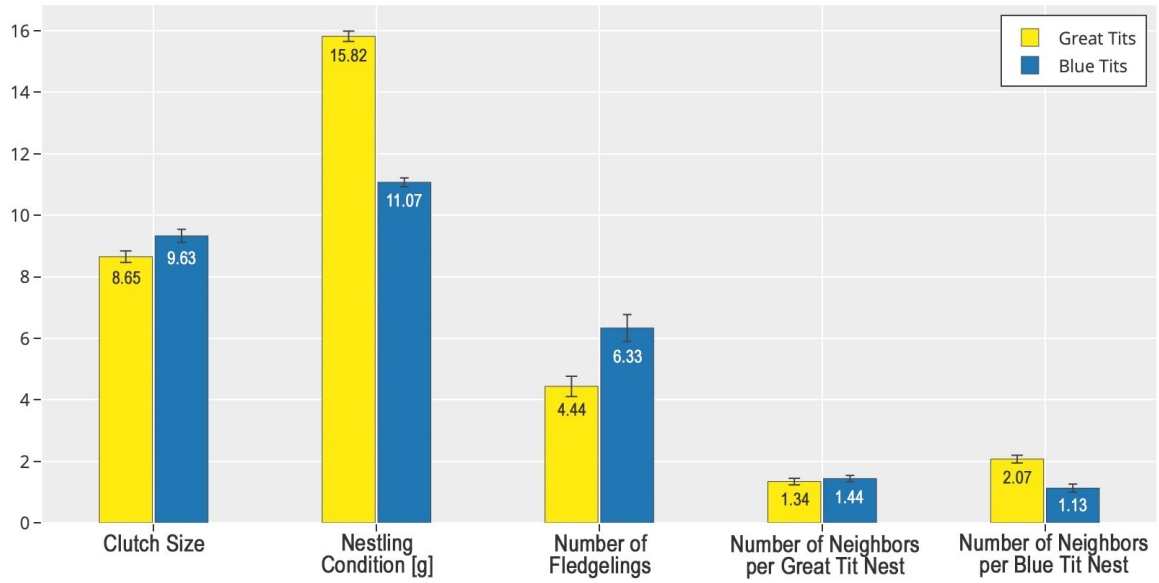

Figure 4*:* the bars display the mean clutch size per nest, the mean weight of a nestling [g], the mean number of nestlings that a nest produced, the mean number of immediate neighbors per great tit nest, and the mean number of immediate neighbors per blue tit nest. Blue bars indicate the results for blue tits, yellow bars for great tits. A vertical standard error bar and the mean value were added to the top of each bar.

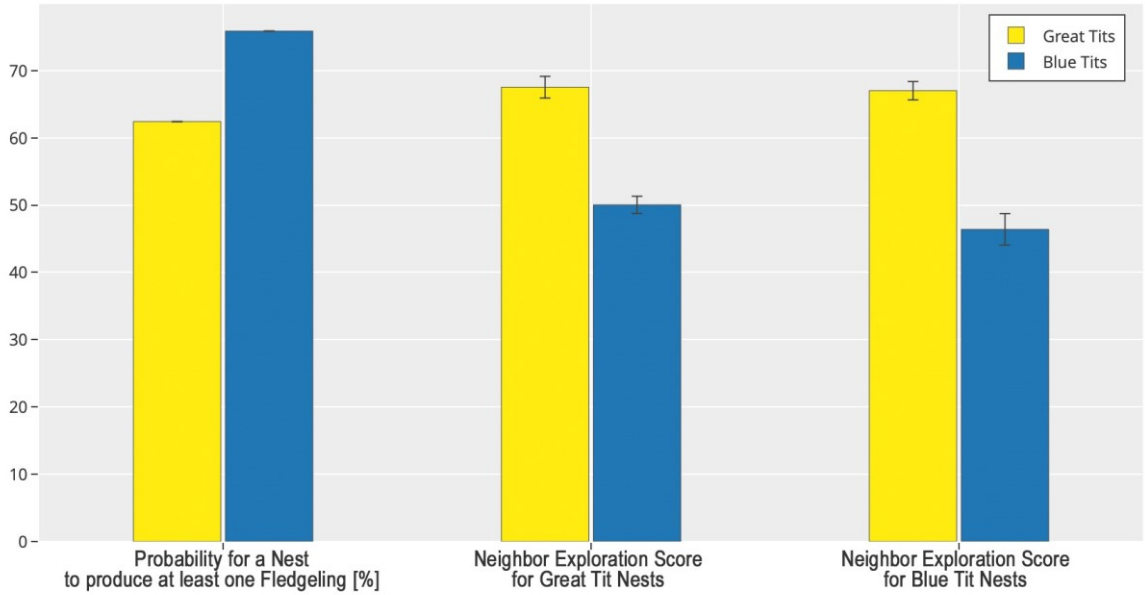

Figure 5: The set of bars on the left show the probability for a nest to produce at least one fledgling [%]. The two bars in the middle display the mean value of the neighbor exploration score per great tit nest. The set of bars on the right show the mean of the neighbor exploration score for a blue tit nest. Blue bars indicate the results for blue tits, yellow bars for great tits. A vertical standard error bar and the mean values were added to the top of each bar.

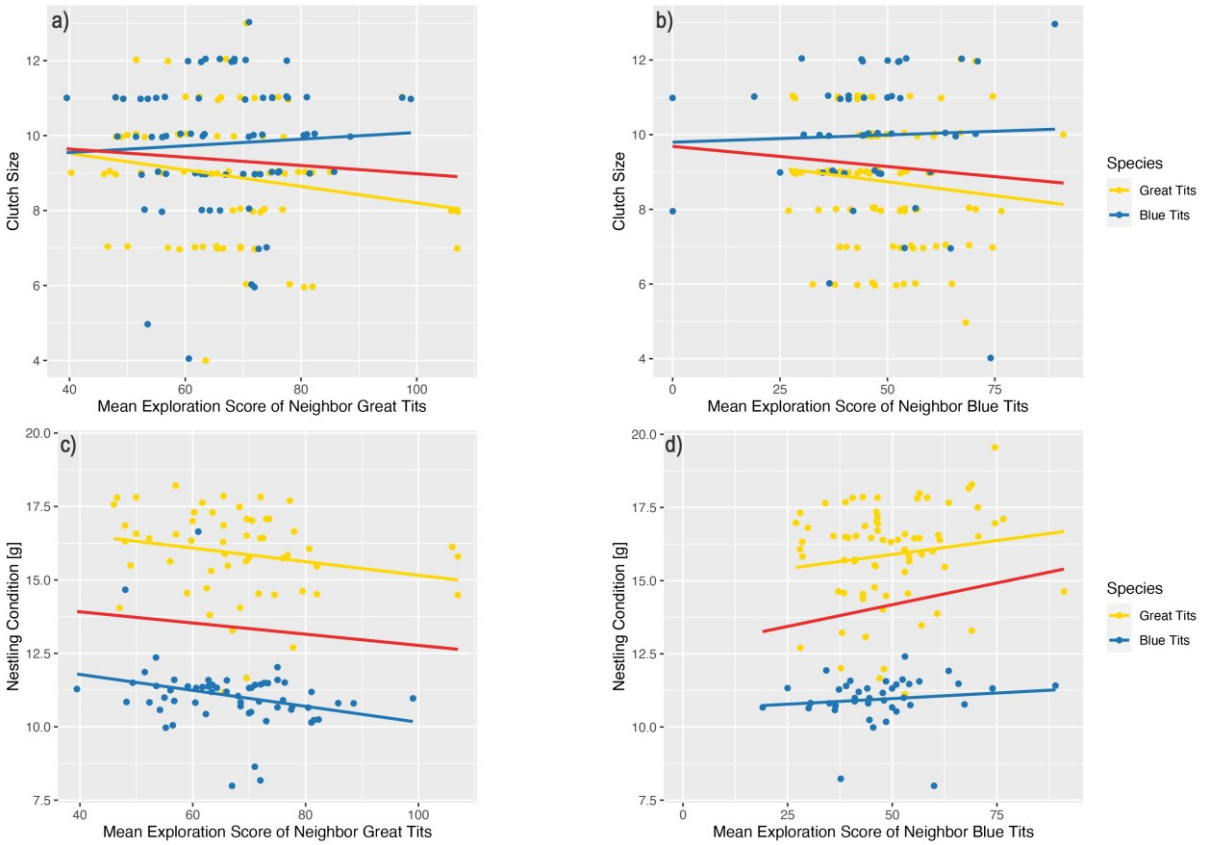

Figure 6: The four plots show the mean exploration score of neighbor great tits (a and c) or neighbor blue tits (b and d) in relation to clutch size (a and b) or nestling condition [g] (c and d) for a focal nest. The data points in all plots were colored according to species, and a regression line for each species (yellow for great tits, blue for blue tits), and for both species combined (red line), was added.

The results reveal that great tit (GT) clutch size was not affected by the number of immediate neighbors (GT: β=-0.26, 95% CI=-0.94, 0.42; BT: β=-0.31, 95% CI=-1.05, 0.42). The same held true for blue tit (BT) clutch size (GT: β=0.34, 95% CI=-0.47, 1.12; BT: β=0.14, 95% CI=0.67, 0.96) (Table 1a). While more explorative great tit neighbors tended to have a negative effect on great tit clutch size (β=-0.09, 95% CI=-0.19, 0.01), more explorative blue tit neighbors had a significantly negative effect on great tit clutch size (β=-0.14, 95% CI=-0.25, -0.04) (Figure 6a, 6b). This means that great tits, whose great tit neighbors were more explorative, tended to lay fewer eggs, while laying significantly fewer eggs with more explorative blue tits as neighbors. Furthermore, the exploratory behavior of neighbor great tits had no effect on blue tit clutch size (β=0.05, 95% CI=-0.08, 0.19), but the exploratory behavior of conspecific neighbors tended to have a positive effect on blue tit clutch size (β=0.09, 95% CI=-0.01, 0.19). This means that while the number of eggs a female blue tit laid was unaffected by more explorative great tit neighbors, they laid significantly more eggs with more explorative blue tits as their immediate neighbors (Table 1b).

Table 1: Estimated effect sizes and 95% CI around the mean of predictors for clutch size. Estimates were derived using univariate mixed-effect models for "Plot" fitted as random effect. Species (GT, BT), Nr.GTneighbors (number of immediate great tit neighbors), Nr.BTneighbors (number of immediate blue tit neighbors), MExpScoreGT (mean exploration score of all immediate great tit neighbors) and MExpScoreBT (mean exploration score of all immediate blue tit neighbors) were fitted as fixed effects [n = 323].

a)	Great tit clutch size	Blue tit clutch size
Fixed effects	β (95% CI)	β (95% CI)
Intercept[a]	8.57 (6.98, 10.22)	9.72 (7.62, 11.78)
Species	0.40 (-0.79, 1.60)	-0.38 (-1.57, 0.84)
Nr.GTneighbors	-0.26 (-0.94, 0.42)	0.34 (-0.47, 1.12)
Nr.BTneighbors	-0.31 (-1.05, 0.42)	0.14 (-0.67, 0.96)
Species → Nr.GTneighbors	0.20 (-0.26, 0.68)	-0.20 (-0.66, 0.28)
Species → Nr.BTneighbors	0.14 (-0.32, 0.63)	-0.15 (-0.63, 0.34)
Random effects	σ^2 (95% CI)	σ^2 (95% CI)
Plot	0 (0, 0)	0 (0, 0)
Residual	4.46 (3.68, 5.37)	4.48 (3.72, 5.42)

b)	Great tit clutch size	Blue tit clutch size
Fixed effects	β (95% CI)	β (95% CI)
Intercept[b]	20.17 (11.85, 29.73)	3.07 (-6.69, 13.02)
Species	-5.70 (-12.35, 0.27)	5.72 (-1.17, 11.74)
MExpScoreGT	-0.09 (-0.19, 0.01)	0.05 (-0.08, 0.19)
MExpScoreBT	-0.14 (-0.25, -0.04)	0.09 (-0.01, 0.19)
Species → MExpScoreGT	0.05 (-0.02, 0.12)	-0.05 (-0.12, 0.02)
Species → MExpScoreBT	0.08 (0.01, 0.15)	-0.08 (-0.14, -0.01)
Random effects	σ^2 (95% CI)	σ^2 (95% CI)
Plot	0 (0, 0)	0 (0, 0)
Residual	4.84 (3.69, 6.44)	4.87 (3.66, 6.45)

[a] Reference categories for fixed effects were set to clutch size for blue tits (Great Tit Clutch Size) or for great tits (Blue Tit Clutch Size), with zero great tit and zero blue tit neighbors.

[b] Reference categories for fixed effects were set to clutch size for blue tits (Great Tit Clutch Size) or for great tits (Blue Tit Clutch Size), with neighbor great tits and blue tits having an exploration score of 0.

The findings further show that regardless of neighbor species great tit nestling condition remained unaffected by the number of immediate neighbors (GT: β=0.44, 95% CI=-0.20, 1.08; BT: β=-0.07, 95% CI=-0.67, 0.50). The same was true for blue tit nestling condition (GT: β=-0.08, 95% CI=-0.75, 0.54; BT: β=-0.15, 95% CI=-0.76, 0.46) (Table 2a). While more explorative great tit neighbors only tended to have a negative effect on great tit clutch size (β=-0.04, 95% CI=-0.09, 0.01), more explorative blue tit neighbors had a significantly positive effect on great tit clutch size (β=0.06, 95% CI=0.00, 0.12). This means that great tits whose great tit neighbors were more explorative tended to have nestlings that weighed less, while they had significantly heavier nestlings with more explorative blue tits as neighbors. Interestingly, blue tit nestling condition was unaffected by the exploratory behavior of both neighbor species (GT: β=0.01, 95% CI=-0.06, 0.07; BT: β=-0.01, 95% CI=-0.07, 0.04) (Table 2b).

When looking at the number of neighbors and nestling condition, the results reveal that for both species it made no difference whether the data was collected on day 14 or on day 15 post-hatch (GT: β=-0.59, 95% CI=-1.84, 0.71; BT: β=-0.56, 95% CI=-1.85, 0.73). The same was found when looking at neighbor exploratory behavior and nestling condition (GT: β=-0.13, 95% CI=-1.02, 0.82; BT: β=-0.12, 95% CI=-1.09, 0.82). Surprisingly, when looking at the number of neighbors, the time when the chick measurements were taken had no effect on the nestling weight in both species (GT: β=0.04, 95% CI=-0.09, 0.17; BT: β=0.03, 95% CI=-0.09, 0.16). But it had a significantly positive effect (GT: β=0.13, 95% CI=0.00, 0.27), or showed a trend towards a positive effect (BT: β=0.13, 95% CI=-0.01, 0.27), when looking at neighbor exploration score, meaning that later in the day the nestlings of both species were heavier (Table 2).

Table 2: Estimated effect sizes and 95% CI around the mean of predictors for nestling condition (NC). Estimates were derived using univariate mixed-effect models for "Plot" fitted as random effect. Species (GT, BT), Nr.GTneighbors (number of immediate great tit neighbors), Nr.BTneighbors (number of immediate blue tit neighbors), MExpScoreGT (mean exploration score of all immediate great tit neighbors), MExpScoreBT (mean exploration score of all immediate blue tit neighbors), D14 Time of Day (time of day the data for body mass was taken) and D14/15 (data for body mass was taken on either day 14 or 15 post-hatch) were fitted as fixed effects [n = 323].

a)	Great tit NC	Blue tit NC
Fixed effects	β (95% CI)	β (95% CI)
Intercept[a]	19.80 (17.73, 21.80)	6.99 (3.70, 10.09)
Species	-4.25 (-5.79, -2.71)	4.29 (2.80, 5.85)
Nr.GTneighbors	0.44 (-0.20, 1.08)	-0.08 (-0.75, 0.54)
Nr.BTneighbors	-0.07 (-0.67, 0.50)	-0.15 (-0.76, 0.46)
Species → Nr.GTneighbors	-0.17 (-0.57, 0.22)	0.17 (-0.22, 0.57)
Species → Nr.BTneighbors	-0.03 (-0.40, 0.36)	0.03 (-0.36, 0.41)
D14/15	-0.59 (-1.84, 0.71)	-0.56 (-1.85, 0.73)
D14 Time of Day	0.04 (-0.09, 0.17)	0.03 (-0.09, 0.16)
Random effects	σ^2 (95% CI)	σ^2 (95% CI)
Plot	0 (0, 0)	0 (0, 0)
Residual	1.87 (1.46, 2.37)	1.87 (1.48, 2.35)

b)	Great tit NC	Blue tit NC
Fixed effects	β (95% CI)	β (95% CI)
Intercept[b]	20.16 (15.35, 25.01)	4.69 (-1.32, 10.94)
Species	-5.21 (-8.57, -1.88)	5.14 (1.75, 8.45)
MExpScoreGT	-0.04 (-0.09, 0.01)	0.01 (-0.06, 0.07)
MExpScoreBT	0.06 (0.00, 0.12)	-0.01 (-0.07, 0.04)
Species → MExpScoreGT	0.02 (-0.02, 0.05)	-0.02 (-0.05, 0.02)
Species → MExpScoreBT	-0.03 (-0.06, 0.01)	0.03 (-0.01, 0.06)
D14/15	-0.13 (-1.02, 0.82)	-0.12 (-1.09, 0.82)
D14 Time of Day	0.13 (0.00, 0.27)	0.13 (-0.01, 0.27)
Random effects	σ^2 (95% CI)	σ^2 (95% CI)
Plot	0 (0, 0)	0 (0, 0)
Residual	0.95 (0.65, 1.34)	0.94 (0.65, 1.31)

[a] Reference categories for fixed effects were set to nestling condition for blue tits (Great Tit NC) or for great tits (Blue Tit NC), with zero great tit and zero blue tit neighbors.

[b] Reference categories for fixed effects were set to nestling condition for blue tits (Great Tit NC) or for great tits (Blue Tit NC), with neighbor great and blue tits having an exploration score of 0.

The findings in table 3 show that while the number of immediate great tit neighbors had no effect (β=-0.61, 95% CI=-1.39, 0.15), the number of blue tit neighbors had a significantly positive effect (β=0.82, 95% CI=0.02, 1.64) on whether a focal great tit nest produced fledglings or not. Therefore, great tit nests with more immediate blue tit neighbors had a significantly higher chance of producing at least one fledgling. There was no such effect with more great tit neighbors. When looking at focal blue tit nests, the number of great tit (β=0.52, 95% CI=-0.37, 1.41) and blue tit neighbors (β=-0.43, 95% CI=-1.29, 0.43) had no effect on whether it produced at least one fledgling or not. Among the random effects, the

plot identity had a significantly positive effect on whether a focal great tit (β=0.01, 95% CI=0.00, 0.04) and blue tit nest (β=0.02, 95% CI=0.00, 0.04) produced at least one fledgling (Table 3a). Furthermore, neighbor exploration score had no effect on whether a focal great tit (GT: β=0.03, 95% CI=-1.60, 1.67; BT: β=-0.85, 95% CI=-2.43, 0.83) or blue tit nest (GT: β=0.78, 95% CI=-1.47, 3.15; BT: β=0.00, 95% CI=-1.54, 1.61) produced at least one fledgling or not. Among the random effects, the plot identity had again a significantly positive effect on whether a focal great tit (β=1.48, 95% CI=0.42, 3.11) or blue tit nest (β=1.50, 95% CI=0.38, 3.13) produced at least one fledgling or not (Table 3b).

Table 3: Estimated effect sizes and 95% CI around the mean of predictors for whether a nest produced fledglings or not (Fledged). Estimates were derived using univariate mixed-effect models for "Plot" fitted as random effect. Species (great tit, blue tit), Nr.GTneighbors (number of immediate great tit neighbors), Nr.BTneighbors (number of immediate blue tit neighbors), MExpScoreGT (mean exploration score of all immediate great tit neighbors) and MExpScoreBT (mean exploration score of all immediate blue tit neighbors) were fitted as fixed effects [n = 323].

a)	Great tit Fledged	Blue tit Fledged
Fixed effects	β (95% CI)	β (95% CI)
Intercept[a]	-0.31 (-1.98, 1.37)	1.44 (-0.77, 3.69)
Species	0.58 (-0.71, 1.82)	-0.59 (-1.86, 0.66)
Nr.GTneighbors	-0.61 (-1.39, 0.15)	0.52 (-0.37, 1.41)
Nr.BTneighbors	0.82 (0.02, 1.64)	-0.43 (-1.29, 0.43)
Species → Nr.GTneighbors	0.38 (-0.17, 0.92)	-0.37 (-0.87, 0.14)
Species → Nr.BTneighbors	-0.42 (-0.96, 0.11)	0.42 (-0.10, 0.92)
Random effects	σ^2 (95% CI)	σ^2 (95% CI)
Plot	0.01 (0.00, 0.04)	0.02 (0.00, 0.04)
Residual[c]	3.29	3.29

b)	Great tit Fledged	Blue tit Fledged
Fixed effects	β (95% CI)	β (95% CI)
Intercept[b]	-0.54 (-2.32, 1.26)	1.66 (-0.32, 3.73)
Species	0.74 (-0.31, 1.79)	-0.74 (-1.71, 0.28)
MExpScoreGT	0.03 (-1.60, 1.67)	0.78 (-1.47, 3.15)
MExpScoreBT	-0.85 (-2.43, 0.83)	0.00 (-1.54, 1.61)
Species → MExpScoreGT	0.24 (-1.05, 1.47)	-0.25 (-1.50, 0.98)
Species → MExpScoreBT	0.27 (-0.74, 1.23)	-0.30 (-1.34, 0.74)
Random effects	σ^2 (95% CI)	σ^2 (95% CI)
Plot	1.48 (0.42, 3.11)	1.50 (0.38, 3.13)
Residual[c]	3.29	3.29

[a] Reference categories for fixed effects were set to "Fledged" for blue tits (Great Tit Fledged) or for great tits (Blue Tit Fledged), with zero great tit and zero blue tit neighbors.

[b] Reference categories for fixed effects were set to "Fledged" for blue tits (Great Tit Fledged) or for great tits (Blue Tit Fledged), with neighbor great tits and blue tits having an exploration score of 0.

[c] Residual error distributions were binomial/binary.

The results presented in table 4 show that the number of immediate neighbors had no effect on how many fledglings a focal great tit nest produced (GT: β=0.39, 95% CI=-0.08, 0.89; BT: β=0.15, 95% CI=-0.56, 0.90) or on how many fledglings a focal blue tit nest

produced (GT: β=0.68, 95% CI=-0.13, 1.47; BT: β=0.09, 95% CI=-0.86, 0.70). But in both cases, the plot identity had significantly positive effect on how many fledglings a focal nest produced (GT nests: β=0.02, 95% CI=0.00, 0.06; BT nests: β=0.02, 95% CI=0.00, 0.06) (Table 4a). Moreover, while the exploration score of neighbor great tits had no effect (β=-0.06, 95% CI=-0.16, 0.03) on the number of fledged offspring of a focal great tit nest, the exploration score of neighbor blue tits had a significantly positive effect (β=0.13, 95% CI=0.02, 0.24) on how many fledglings a focal great tit nest produced. This means that great tits with more explorative blue tit neighbors produced significantly more fledged offspring, but the number of fledglings remained unaffected when they had more explorative great tit neighbors. The exploration score of neighbor great tits (β=0.07, 95% CI=-0.07, 0.17) and neighbor blue tits (β=-0.08, 95% CI=-0.18, 0.03) had no effect on how many fledglings a focal blue tit nest produced. Among the random effects, the plot identity had again a significantly positive effect on how many fledglings a focal great tit (β=0.38, 95% CI=0.06, 1.01) or blue tit nest (β=0.37, 95% CI=0.06, 0.95) produced (Table 4b).

Table 4: Estimated effect sizes and 95% CI around the mean of predictors for the number of fledged offspring (Nr. Fledged). Estimates were derived using univariate mixed-effect models for "Plot" fitted as random effect. Species (great tit, blue tit), Nr.GTneighbors (number of immediate great tit neighbors), Nr.BTneighbors (number of immediate blue tit neighbors), MExpScoreGT (mean exploration score of all immediate great tit neighbors) and MExpScoreBT (mean exploration score of all immediate blue tit neighbors) were fitted as fixed effects. Clutch Size was added as a covariate [n = 149].

a)	Great tit Nr. Fledged	Blue tit Nr. Fledged
Fixed effects	β (95% CI)	β (95% CI)
Intercept[a]	0.80 (-1.32, 2.95)	0.83 (-1.75, 3.38)
Species	-0.01 (-1.20, 1.12)	-0.09 (-1.17, 1.20)
Nr.GTneighbors	0.39 (-0.08, 0.89)	0.68 (-0.13, 1.47)
Nr.BTneighbors	0.15 (-0.56, 0.90)	0.09 (-0.86, 0.70)
Species → Nr.GTneighbors	0.39 (-0.08, 0.89)	-0.40 (-0.89, 0.11)
Species → Nr.BTneighbors	-0.08 (-0.56, 0.41)	0.14 (-0.40, 0.54)
Covariate		
Clutch Size	0.71 (0.55, 0.87)	0.78 (0.52, 1.03)
Random effects	σ^2 (95% CI)	σ^2 (95% CI)
Plot	0.02 (0.00, 0.06)	0.02 (0.00, 0.06)
Residual	2.92 (2.33, 3.65)	2.91 (2.12, 4.18)

b)	Great tit Nr. Fledged	Blue tit Nr. Fledged
Fixed effects	β (95% CI)	β (95% CI)
Intercept[b]	-2.28 (-11.71, 6.76)	0.90 (-4.89, 11.59)
Species	1.56 (-4.73, 7.10)	-0.97 (-6.90, 5.25)
MExpScoreGT	-0.06 (-0.16, 0.03)	0.07 (-0.07, 0.17)
MExpScoreBT	0.13 (0.02, 0.24)	-0.08 (-0.18, 0.03)
Species → MExpScoreGT	0.04 (-0.03, 0.10)	-0.04 (-0.11, 0.03)
Species → MExpScoreBT	-0.07 (-0.14, 0.00)	0.07 (0.00, 0.13)
Covariate		
Clutch Size	0.78 (0.52, 1.04)	0.78 (0.52, 1.03)
Random effects	σ^2 (95% CI)	σ^2 (95% CI)
Plot	0.38 (0.06, 1.01)	0.37 (0.06, 0.95)
Residual	2.94 (2.15, 4.19)	2.99 (2.12, 4.18)

[a] Reference categories for fixed effects were set to the number of fledged offspring of blue tits (Great Tit Nr. Fledged) or of great tits (Blue Tit Nr. Fledged), with zero great tit and zero blue tit neighbors.

[b] Reference categories for fixed effects were set to the number of fledged offspring of blue tits (Great Tit Nr. Fledged) or of great tits (Blue Tit Nr. Fledged), with neighbor great tits and blue tits having an exploration score of 0.

Discussion

This thesis investigated the inter- and intraspecific effects of fine-scale breeding density and exploratory behavior of neighbors on reproductive success. The findings reveal that while female great tits with more explorative great tit neighbors only tended to lay less eggs, they laid significantly fewer eggs with more explorative blue tits as neighbors. On the other hand, female blue tits tended to lay more eggs with more explorative blue tits as neighbors, while more explorative great tit neighbors had no effect on their clutch size. During the nestling stage, great tit nestlings with more explorative conspecific neighbors tended to weigh less, while they weighed significantly more with more explorative blue tits as neighbors. The nestling condition of blue tits was not affected by the exploratory behavior of either neighbor species. Furthermore, the probability for a nest of either species to produce at least one fledgling was not affected by the exploratory behavior of neighboring blue or great tits. This was also true for the number of fledglings that a focal nest produced, with one exception: great tits produced significantly more fledglings with more explorative blue tits as neighbors. Independent of species, the number of neighbors had no effect on the clutch size, nestling condition and the number of fledglings of a focal blue or great tit nest. This was also true for the probability of a focal nest to produce at least one fledgling, with one exception: great tits with more blue tit neighbors had a significantly higher probability to produce at least one fledgling. Overall, the results indicate that while the number of neighbors had no effect on almost all of the response variables, the exploratory behavior of intra- and interspecific neighbors influenced the reproductive success of focal individuals in most cases.

Influence of neighbor exploratory behavior

Great tits whose great tit neighbors were more explorative tended to lay fewer eggs and produce lighter nestlings. These findings are in line with the predictions, and there may be several factors mediating the link between neighbor exploratory behavior and clutch size in great tits. The first factor concerns territory quality, as in intraspecific interactions the correlation between reproduction and personality traits can be caused by variation in territory quality (Both et al. 2000). Therefore, the link between neighbor behavior and clutch size may in part be mediated via territory quality; and since fast-exploring male great tits outcompete slow males of the same species at clumped food sources in winter, these fast-exploring males can subsequently be expected to acquire territories with high-quality foraging habitats for the breeding season (Dingemanse 2003; Dingemanse et al. 2004; Both et al. 2005). The second factor is that birds from neighboring territories can experience

considerably different habitat qualities, as the distribution of caterpillars is clumped and depends strongly on the presence or absence of an oak tree in the territory (Keller et al. 1994; Naef-Daenzer et al. 1999). Consequently, being surrounded by more explorative great tit neighbors may indicate that the focal great tit individuals are occupying a low-quality habitat with few food sources, resulting in diminished egg-production and nestlings with reduced body condition. The last factor is the link between exploratory behavior and aggression (Hessing et al. 1994; Verbeek et al. 1996; Mutzel et al. 2013). Aggression plays an important role in mediating competitive interactions over mates and food resources, or in the acquisition and defense of a territory (Verbeek et al. 1994; Koskela et al. 1997; Duckworth et al. 2007). In great tits studies have shown that aggression and exploratory behavior are positively correlated (e.g. Verbeek et al. 1996), meaning that more explorative individuals are also more aggressive. Consequently, a female with more explorative neighbors would also have to cope with their neighbors' higher level of aggression, which could impede her foraging performance, especially during the egg-laying stage when caterpillars are not yet super-abundant, limiting her egg-production.

Contrary to expectations, blue tits with more explorative blue tit neighbors tended to lay more eggs. An explanation for this may revolve around the already discussed link between exploratory behavior and aggression. The more recent literature suggests that there is extensive variation in the strength and existence of correlations among two behavioral traits (Garamszegi et al. 2012, 2013). For instance, in studies on the great tit the exploration of a novel environment was linked to male reactions to a territorial intrusion stimulus (Verbeek et al. 1996; Amy et al. 2010), while in a different study aggression toward a free or caged intruder was not significantly related to movement in a novel environment (Carere et al. 2005). Another study on blue tits found that handling aggression was not correlated with exploratory behavior (Kluen et al. 2014). In the case of co-occurring great and blue tits one reason for the results of this thesis may be that, though the environmental conditions for both species were the same, they may have been experienced differently, as the two species occupy different ecological niches. This may have generated different selection pressures on exploratory behavior and aggression, resulting in different mean behavioral phenotypes among species. Consequently, in this study population blue tits may be on average less aggressive and have a lower exploration score than great tits (Figure 5). Therefore, a focal female blue tit wouldn't have had to cope with as high a level of conspecific aggression as a female great tit, leaving her more time to forage for food and more energy for egg-production.

Great tits, with more explorative blue tit neighbors laid a significantly smaller clutch, but produced significantly heavier nestlings and significantly more fledglings. These results are only partly in line with the predictions. To explain this, two factors may be important: one concerns the individual differences of slow and fast explorers in information gathering while

foraging, the other the changing abundance of caterpillars – the main food of nestlings – over the course of the breeding season: during the egg-laying phase, food is assumed to be a major determinant of the number of eggs that a female can produce (Perrins 1970; Nilsson 1991; Dhondt 2010, 2012). As caterpillars are not yet super-abundant slow exploring females may waste time and energy by returning to already sampled, but now empty patches. As a result, these females may have less food available for egg-production, resulting in smaller clutches. During the nestling stage, when both parents contribute to feeding the nestlings, nestling condition largely reflects food conditions (Dhondt et al. 1990; Dhondt 2010). In this particular year the results indicate that the peak abundance of caterpillars matched well with the nestling feeding peak, as slow exploring individuals now save time and energy by returning to already sampled areas, since they still contain prey items. Ultimately, slow explorers may now provision their nestlings with more food, resulting in significantly heavier nestlings and more fledglings. The findings in both contexts (egg-laying stage, nestling stage) lend further support to the IGH.

Influence of the number of neighbors

Contrary to predictions, the results show that the number of neighbors had no effect on clutch size, nestling condition and the number of fledglings that a nest produced. The expectation was that since great and blue tits differ in body size, they also differ in competitive ability: while the physical dominance of great tits is usually advantageous, it can limit their foraging opportunities since the smaller blue tits can additionally forage on twigs and buds to expand their range of food sources (Gibb 1954; Dhondt 1977, 2010). Consequently, blue tits were expected to have a considerable amount of food sources that is inaccessible to great tits, whereas only a very minor proportion of the food available to great tits is not taken by blue tits as well (Betts 1955). As a result, blue tits should have faced much fewer interspecific competitors, therefore weakening intraspecific competition in comparison with great tits. Therefore, during the egg-laying phase, when food is assumed to be a major determinant of the number of eggs that a female can produce (Perrins 1970; Nilsson 1991; Dhondt 2010, 2012), female blue tits should have had an easier access to food sources and thus should have laid larger clutches than their great tit counterparts when surrounded by more explorative conspecifics. The lacking effects might be explained by individuals following the ideal free distribution (IFD): this theory states that individuals spread themselves out among the different resource patches within their habitat in a way that allows them to minimize resource competition and maximize their fitness (Fretwell et al. 1969; Fretwell 1972). That means that more individuals will settle in high quality habitats with abundant food sources than in low quality habitats with less abundant food sources, making the available amount of food per individual equal between the two habitat types.

Consequently, small-scale breeding densities will differ among territories, but intra- and interspecific competition will be similar across them. Since, for this study, both species were offered an abundance of nest boxes, it can be assumed that they were not a limiting resource and that both species' breeding density did not exceed the available amount of food in the respective habitats. In addition, assuming that high breeding densities characterize high quality habitats, it could be argued that food availability and low predation risks balance out the negative effects of breeding density (e.g., transfer of diseases, increased competition, aggressive encounters) (Newton 2003).

Temporal fluctuations in competition

Importantly, this thesis is based on only one breeding season and a single behavioral measurement per adult individual, making it impossible to account for year-to-year variation in environmental factors and to distinguish within- from among-individual effects. Previous studies have shown that breeding density and food availability, and thus competition, strongly vary among years (Dhondt 2010; Møller et al. 2018). The overall good nestling condition, high probability to produce at least one fledgling and the number of fledglings (Figure 4) strongly indicate that the year this study took place was a comparably successful year with sufficient food available. This might explain the lacking effects of breeding density and the moderate support for many effects of neighbor exploratory behavior on reproductive parameters. In years with higher breeding densities or lower food availability, or both, the studied patterns might thus be stronger or more detectable (Dhondt 2010; Møller et al. 2018).

Again, since exploratory behavior is repeatable (Dingemanse et al. 2002), a single behavioral measurement can only be seen as an approximation. Therefore, drawing conclusions on effects on personality or social responsiveness is not possible. But with the same data gathered over several consecutive years this would be feasible. For instance, it would allow the separation of within- and among-individual effects in personality traits. It would also be possible to detect IGEs since both exploration and clutch size are heritable traits.

Conclusion

The findings of this thesis demonstrate that neighbor exploratory behavior can influence reproductive parameters and thus the overall fitness of individuals, further highlighting competition and the social environment as important drivers of selection. It also indicates that these effects are not limited to competition with conspecifics, but expand to the interspecific level as well. Interestingly, the effects of exploratory behavior are not necessarily negative, depending on the specific trait and species, and inter- and intraspecific effects can even be opposite. Ultimately, future research should use multi-year datasets to account for temporal variation in breeding density, food availability and selection pressures. This would also allow the separation of within- and among-individual effects. Importantly, adding the measure of individual aggression levels would give further insights into the mechanisms by which competition might influence reproductive success.

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Zusammenfassung

Um herauszufinden ob die Anzahl an direkten Nachbarn (Blau- und Kohlmeisen), oder deren Verhalten die Fortpflanzung von brütenden Blau- und Kohlmeisen beeinflusst, wurde im Rahmen dieser Masterarbeit das Explorationsverhalten und der Reproduktionserfolg einer wilden Population von Blau- und Kohlmeisen im Zeitraum einer Brutsaison untersucht. Von den 220 beobachteten Brutpaaren wurden 325 adulte Vögel gefangen und ihr Exploration Score mit Hilfe eines Käfig-Tests ermittelt. Zudem wurde für jedes Brutpaar die Anzahl direkter Nachbarn ermittelt, sowie deren durchschnittlicher Exploration Score. Als Fitnessmaß dienten die Gelegegröße, das Gewicht der Nestlinge und die Anzahl an Fledglingen pro Nest. Die Ergebnisse zeigen, dass brütende Kohlmeisen die Kohlmeisen-Nachbarn mit einem höheren Exploration Score hatten, dazu neigten weniger Eier zu legen. Wenn die Nachbarn Blaumeisen mit einem höheren Exploration Score waren, legten sie hingegen signifikant weniger Eier. Blaumeisen hingegen tendierten in Gegenwart benachbarter Artgenossen mit einem höheren Exploration Score dazu mehr Eier zu legen. Benachbarte Kohlmeisen mit einem höheren Exploration Score hatten keine Wirkung auf die Gelegegröße von Blaumeisen. Kohlmeisen-Nestlinge die Kohlmeisen-Nachbarn mit einem höheren Exploration Score hatten, neigten dazu weniger zu wiegen; aber sie wogen signifikant mehr, wenn Blaumeisen mit höherem Exploration Score ihre Nachbarn waren. Das Gewicht von Blaumeisen-Nestlingen wurde nicht vom Explorationsverhalten der Nachbarn beeinflusst. Des Weiteren war die Wahrscheinlichkeit eines Brutpaars wenigstens einen Fledgling zu produzieren nicht vom Explorationsverhalten der Nachbarn beeinflusst. Das galt ebenso für die Anzahl an Fledglingen, die ein Brutpaar produzierte – mit einer Ausnahme: Kohlmeisen-Nester mit Blaumeisen-Nachbarn die einen höheren Exploration Score hatten, produzierten signifikant mehr Fledglinge. Die Anzahl an Nachbarn hatte keinen Effekt auf die Gelegegröße, das Gewicht der Nestlinge und die Anzahl an Fledglingen. Dasselbe traf auf die Wahrscheinlichkeit eines Nests zu, wenigstens einen Fledgling zu produzieren – mit einer Ausnahme: Kohlmeisen-Nester mit mehr Blaumeisen-Nachbarn hatten eine signifikant höhere Wahrscheinlichkeit wenigstens einen Fledgling zu produzieren. Die Ergebnisse zeigen, dass das Verhalten der Nachbarn den Reproduktionserfolg eines Brutpaars tatsächlich beeinflussen kann, die Anzahl der direkten Nachbarn aber nur in geringem Maß. Ebenfalls interessant ist, dass die Effekte des Explorationsverhaltens nicht immer negativ sind, sondern von der Nachbarart und dem untersuchten Fitnessmaß abhängen.