



Winter food selection and exploratory behavior vary with natal territory characteristics in wild great tits

Eva Serrano-Davies¹ · Nina Bircher² · Bernice Sepers^{1,2} · Kees van Oers^{1,2}

Received: 10 October 2022 / Revised: 9 May 2023 / Accepted: 12 May 2023 / Published online: 7 June 2023
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Abstract

Differences in habitat characteristics experienced during rearing associate with variation in a range of behavioral phenotypes such as exploratory behavior, foraging behavior and food selection. The habitat-dependent selection hypothesis predicts that animals develop behavioral characteristics fitted to their rearing environment. Yet, little is known about how habitat characteristics during rearing shape how animals face winter conditions and adjust their winter foraging behavior. The aim of this study was to explore how fine-scale rearing habitat characteristics associate with exploratory behavior, food selection, and foraging performance during winter. For this, we measured habitat characteristics during the breeding season in territories of wild great tits (*Parus major*) and tested first-year juvenile birds that fledged from these territories for exploratory and foraging behavior at feeders during winter. We found evidence that faster explorers were raised in territories with lower quality habitat characteristics. In addition, fast exploring fledglings visited the feeders significantly more (total visits). Moreover, the rearing environment, via caterpillar availability and tree species composition, determined diet selection during winter in first-year birds. These results show support for the habitat-dependent selection hypothesis, since exploratory behavior as well as food selection during winter associate with habitat features of the rearing territories during development. This pattern can be caused either by the kinds of natural foods prevalent during rearing at these sites or because of intrinsic individual differences. Further experiments are needed to disentangle these two.

Significance statement

Individuals vary in how they behaviorally adapt foraging and food selection strategies to the environmental conditions. A number of studies have shown that animals develop behavioral characteristics fitted to their rearing environment. However, how habitat characteristics during rearing shape the foraging strategy that animals use to face winter conditions is still unknown. We studied these links in yearling great tits using automated feeders that recorded their visits during winter. Fledglings with a higher exploratory score were born in territories with lower quality habitat characteristics and visited the feeders more. Furthermore, we found an association between caterpillar availability and tree species composition in the rearing territory of juveniles and their subsequent food selection in winter. Our study indicates that certain environmental conditions might favor the development of particular behaviors in birds and that early nutrition could shape food choice later in life.

Keywords Habitat variability · Exploratory behavior · Feeders · Non-breeding season · *Parus major*

Communicated by N. A. Dochtermann

✉ Kees van Oers
k.vanoers@nioo.knaw.nl

Eva Serrano-Davies
E.Serrano@nioo.knaw.nl

¹ Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), 6708 PB Wageningen, The Netherlands

² Behavioral Ecology Group, Wageningen University and Research (WUR), 6700 AH Wageningen, The Netherlands

Introduction

One major challenge wild animals have to face during winter is to meet the high-energy demands imposed by the season. Hence, optimizing winter foraging performance, while minimizing both thermoregulation costs and predation risk (Villén-Pérez et al. 2013), requires a flexible behavioral strategy which allows individuals to discover new feeding sites or food types (Sol et al. 2005). Thus, individuals vary in how they behaviorally adapt foraging and food selection strategies

to the environmental conditions (Veřký et al. 2011; Reif et al. 2016). Based on the habitat-dependent selection hypothesis (Réale et al. 2007), animals develop behavioral characteristics fitted to their rearing environment (Van Oers et al. 2015; Quinn et al. 2016), e.g., mediated through received food types and nutritional content or food quantity. Studies have explored how the presence of behavioral phenotypes varies depending on habitat type (urban/non-urban, Miranda et al. 2013; coniferous/deciduous, Serrano-Davies et al. 2017a), habitat quality (Wilkin et al. 2009) or habitat characteristics in which they were reared or that they live in (Holtmann et al. 2017). It is, however, less clear how differences in habitat composition may contribute to explain variation in behavioral phenotypes such as exploratory behavior, foraging behavior, and food selection strategies, outside of the breeding period.

Foraging strategies, food choice, and behavioral phenotypes are tightly related in the wild. For instance, exploratory behavior has been shown to be a repeatable and heritable trait (Dingemanse et al. 2002; Quinn et al. 2009; Class et al. 2019) that predicts (1) how individuals manage predation risk (van Oers et al. 2004; Quinn and Cresswell 2005; Quinn et al. 2012), (2) competitive foraging ability (Riebli et al. 2011; David et al. 2012) and (3) foraging flexibility (Verbeek et al. 1994; Coomes et al. 2022). Exploratory behavior is often used as an operational measure for an individual's personality. Also individual foraging selection has been previously linked to variation in personality traits in captivity (Serrano-Davies et al. 2017b) as well as individual reactions to food availability (Arvidsson and Matthysen 2016). The classical theory on optimal diets and central place foraging (MacArthur and Pianka 1966; Pulliam 1974; Charnov 1976) predicts that an animal should maximize the rate of energy delivery to successfully exploit resources, and as individuals may have personality-specific energy demands, the costs and benefits associated with different strategies have been shown to vary (Toscano et al. 2016). In fact, several studies have found evidence of a positive correlation between individual metabolic rate and proactivity, lending support to this argument (see Biro and Stamps (2010) for a review). It is thought that the relationship between behavioral traits may contribute to the development of alternative foraging strategies within populations by driving differences in individual food resource use (reviewed in Toscano et al. 2016). For example, individuals that adopt energy-demanding foraging strategies may need to rely on high-quality, energy-rich food items as a trade-off. Therefore, determining how individuals differ in regards to food intake, including food choice, is crucial for our understanding of the relationship between exploratory behavior, foraging, and the environment.

Habitat characteristics can influence many of the components, mostly related to abundance of food supply and variability in shaping foraging behavior and dietary specialization that determine an individual's foraging strategy. In birds, it

has been widely demonstrated that habitat type affects foraging travel distance. For example, blue tits (*Cyanistes caeruleus*) double their mean foraging travel distance in coniferous forest compared to deciduous forest (Tremblay et al. 2005), and forest degree of fragmentation strongly impacts parental food provisioning rates of northern saw-whet owls (*Aegolius acadicus*; Hinam and Clair 2008). Moreover, some studies have emphasized habitat attributes such as increasing habitat complexity, which has been shown to affect foraging patch selection in the common chaffinch (*Fringilla coelebs*, Butler et al. 2005), or the number of native plant species, which increased food availability for the Carolina chickadee (*Poecile carolinensis*, Narango et al. 2017). How other quality characteristics of the habitats (i.e., breeding territory tree composition and food sources) may shape winter foraging strategies remains largely unknown.

Likewise, food selection is likely influenced by the habitats individuals are raised in. Either because of the type of food prevalent in those habitats or because of intrinsic differences in metabolism linked to, for example, stress associated with living in or developing in those habitats (Suorsa et al. 2003). The association between dietary selection and habitat of origin has been described in several animal species ranging from earthworms (Amador et al. 2013) to bison (*Bison bison*; Hernández and Laundré 2005). This includes various bird species such as the capercaillie (*Tetrao urogallus*; González et al. 2012), house and tree sparrows, and the blue and great tit (*Passer domesticus*, *P. montanus*, *C. caeruleus*, *Parus major*; Veřký et al. 2011; Isaksson et al. 2017; Serrano-Davies et al. 2017b). Despite this, most of the available literature on wild birds has been focusing on parental provisioning (e.g., Stauss et al. 2005; Tremblay et al. 2005; Wilkin et al. 2009; Serrano-Davies and Sanz 2017), with one recent paper analyzing microhabitat use during provisioning in great tits (Telve et al. 2020). Therefore, what is currently lacking are studies that investigate the effect of habitat quality characteristics experienced during development on individual variation in foraging strategies and food selection during winter. This opens up the possibility that individuals might vary in their winter foraging strategies and food selection depending on variation in the habitat they were reared in.

In this study, we therefore focus on how territory characteristics associate with exploratory behavior, food selection, and foraging performance in winter, using wild great tits as a model species. Exploratory behavior in great tits is a heritable and repeatable trait in our population (Dingemanse et al. 2002) and in other populations (Dingemanse et al. 2012). Also, studies on great tits have shown that the first measure of exploratory behavior in a novel environment is a good proxy for the personality of an individual (Niemelä and Dingemanse 2018), since the average value of multiple measurements strongly correlates with the first measure (Mouchet et al. 2021; Nicolaus et al. 2016). We

used automated feeding stations equipped with passive integrated transponder (PIT) readers to track individual foraging strategies and food selection throughout the winter. Feeders contained two types of food, i.e., sunflower seeds and peanuts, which differ in nutritional content. First, we predicted that individuals would show behavioral characteristics fitted to their rearing environment, for example, differences in preferences for food types, nutritional content, or food quantity. To maintain stasis despite greater stressors, such as high competition or patchy resource distributions, we predicted that birds born in lower quality territories would show higher exploratory scores. Therefore, we expected that birds in lower quality habitats would forage and rely more on artificial feeding than those raised in higher quality patches (Serrano-Davies et al. 2017a) and would predominantly select the lower quality food (Serrano-Davies et al. 2017b).

Materials and methods

Study subjects and site

We tested winter foraging behavior in wild great tits, in our long-term nest box study site Westerheide (52° 01'

00N, 5° 50' 30E, Arnhem, The Netherlands) from December 2018 to March 2019. The Westerheide forest covers 120 ha of mixed wood, with patches of predominantly birch (*Betula pendula*), pedunculate oak (*Quercus robur*), red oak (*Q. rubra*), pine (*Pinus sylvestris*), larch (*Larix decidua*), and beech (*Fagus sylvatica*). There are 228 nest boxes in Westerheide (Fig. 1). During the 2018 breeding season (April–June), all chicks and adults were provided with a PIT-tag identifier and aluminum ring. A PIT-tag is a radio frequency identification (RFID) tag encapsulated in a polypropylene leg ring (Eccel Technology Ltd., UK).

Automated feeding stations

We recorded the visits of great tits to seven feeding sites evenly distributed over the area (Fig. 1). At each feeding site, two feeders were present, each containing a different type of food: one with raw black sunflower seeds with shell, a high-quality but hard-to-obtain food item, and the other with dehusked raw peanuts, a low-quality but easy-to-obtain food item. We defined the quality of the two types of food based on their micronutrients content, as the nutritional value of the sunflower seeds may be higher due to the phytosterols content is much higher in those (534 mg/100 g) than in peanuts (220 mg/100 g; de

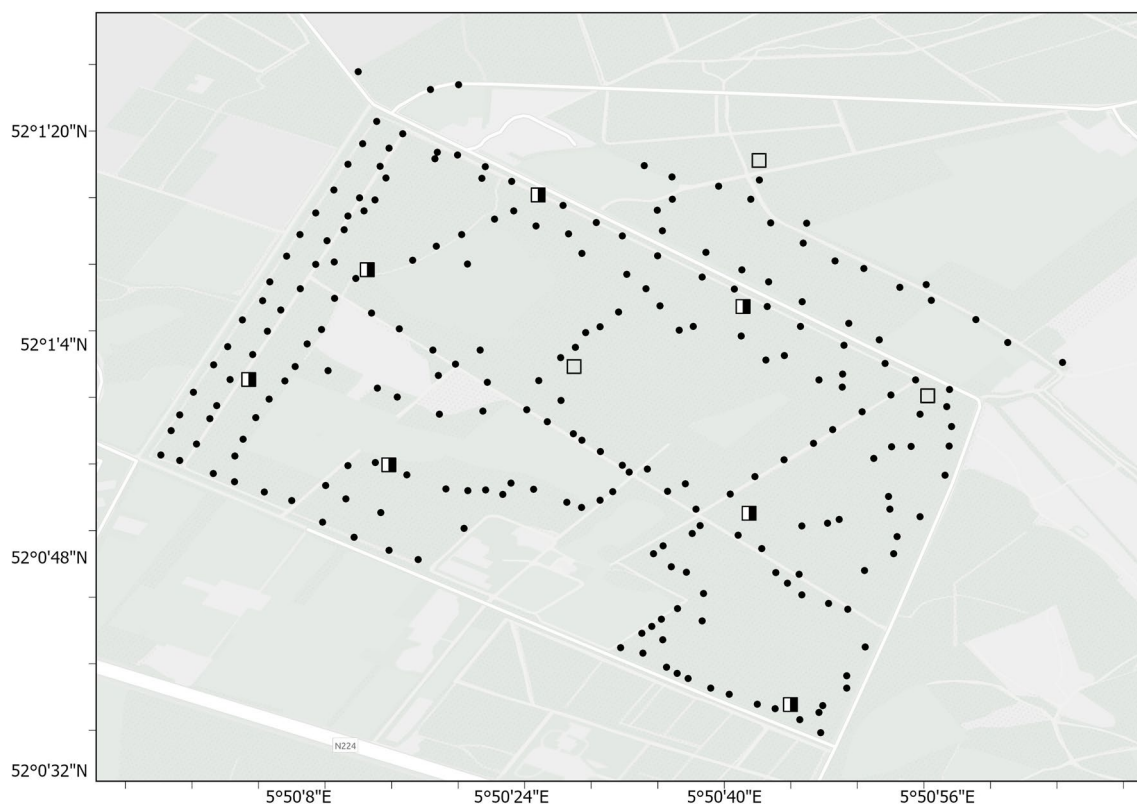


Fig. 1 Distribution of nest-boxes, feeders and *frass* nets through the Westerheide study area. Black circles: nest-boxes. Half open-half black squares: feeders and *frass* nets locations (7 sites). Open squares: only *frass* nets locations (3 sites)

Jong et al. 2008; Rudkowska 2010; Li et al. 2011). The feeders were replenished twice a week.

Each feeder was composed of (i) weatherproof (Perspex) external casing; (ii) a printed circuit board (PCB; RFID reader); and (iii) a unique passive integrated transponder (PIT) identifier (Fig. 2). The external casing was installed on a wooden stake planted in the ground (~0.5 m high). The identity of PIT-tagged individuals landing at the device was relayed to the PCB by an antenna located in the perch (Dorset Identification, NL). The perch was a horizontal plane of 10 cm × 5 cm × 1 cm and was small enough to hold only one bird at once. A 12 V-sealed lead-acid battery powered the whole system for each device, which was sufficient to power a device for at least three days in winter conditions. Along with each visit, date and time were recorded when a PIT-tagged bird landed on the device along with its individual/unique PIT-tag code. Visits recorded for the same individual within 3 s were considered one single visit.

Habitat characterization

In order to determine habitat composition in great tit territories, we recorded the two most dominant tree species



Fig. 2 One of the feeders distributed in Westerheide study area during winter 2018–2019. Above: feeder tube attached to a pole, connected to the printed circuit board, RFID reader, and 12 V battery. Below: great tit at the feeder access, perched on the reader antenna

in a 50 m radius around each breeding great tit pair nest box (April–June 2019). This radius accounts for the area that tits commonly used for feeding (Smith and Sweatman 1974; Grieco 2002). This area is usually referred to as the feeding range (Baldan and van Loon 2022). We categorized territories within one of two habitat types depending on tree species combinations: i.e., “deciduous”: two deciduous tree species (pedunculate oak, *Q. robur*; beech, *F. sylvatica*; red oak, *Q. rubra*; birch, *B. pendula*; larch, *L. decidua*); or “mixed”: two species mixture, one deciduous of the above mentioned and one coniferous (pine, *P. sylvestris*; silver fir, *Abies alba*). Fledgling weight (habitat type: estimate ± SE = -11341 ± 1706 , $F_{1,71} = 44.184$, $P < 0.001$) and number of fledglings (habitat type: estimate ± SE = -52.66 ± 12.49 , $F_{1,73} = 17.781$, $P < 0.001$) were significantly lower in the “mixed” territory type than in the “deciduous” when tested via two GLMs with number of fledglings and fledgling weight, respectively, using the last 10-year breeding data in our population, indicating the quality difference between the two habitat types.

We sampled the abundance of caterpillars by collecting caterpillar droppings with so-called *frass* nets (a cheesecloth of 0.25 m² in a metal frame, with a weight hung from the center of the net) (see Fig. 3a in Tinbergen 1960). From mid-April until early June 2019, we positioned *frass* nets beneath ten oak trees (*Q. robur*) distributed over the study area (Fig. 1). Two of these nets were placed under each tree (about 1–1.5 m from the stem), and every 3–4 days, we collected all caterpillar droppings, dried them at 60 °C for 24 h, sorted (i.e., all debris is removed), and weighed them, and from this, the caterpillar biomass was calculated (see Visser et al. (2006) for details). By using a Dirichlet tessellation technique in ArcGIS Pro, we formed Thiessen polygons (Rhynsburger 1973; Tanemura and Hasegawa 1980) around occupied nest boxes to estimate territories (see Wilkin et al. (2006) and around caterpillar biomass locations and overlapped both maps. We assigned the peak width value (number of days where the biomass is above 1 g m⁻² day⁻¹; for further details, see Visser et al. (2006) to each breeding pair territory. When a territory was included in more than one caterpillar biomass polygon, we calculated the average value of those.

Temporal consistency in caterpillar biomass production of individual trees may be important for birds because it can help predict territory quality (Péter et al. 2020). Since 2019 was the first year of *frass* collection in our study site, we calculated the repeatability of caterpillar biomass by site in the nearby forest (~5 km) of De Hoge Veluwe using a generalized linear mixed-effects approach as implemented by the “rpt” command of package “rptR” (Nakagawa and Schielzeth 2010). Across the 28 years of available data, the repeatability of caterpillar biomass of individual trees was relatively high and statistically

significant ($R=0.41$, $P<0.001$), indicating these measures stay relatively comparable in different years.

Novel environment test

Birds were trapped using mist nets at the feeding locations (two to three times a week from mid-June to September 2019, $N=64$), and nest boxes were inspected for roosting birds, four times during winter nights (December 2018–March 2019, $N=12$). All the fledgling birds captured had already been independent for over 2 weeks. We transported the selected birds to the Netherlands Institute of Ecology (NIOO-KNAW) in darkened transport boxes, weighed them, and housed them individually in cages of $0.9\times 0.4\times 0.5$ m high, with a solid bottom and top, side, and rear walls, a wire mesh front containing three perches, and a water bath. All birds were visually but not acoustically isolated from one another and kept under a natural light regime. The birds had ad libitum access to water, mealworms, a homemade mixture of ground beef heart, egg, calcium, and a multivitamin solution, sunflower seeds, and fat balls. As individual housing was limited, a maximum of 36 birds were housed at a time.

We conducted the behavioral tests on the morning after capture, between 0900 and 1400 h. Exploratory behavior was measured using the novel environment test as described in (Drent et al. 2003). Great tits were tested individually in a closed room ($4.0\times 2.4\times 2.3$ m) with five artificial trees. Each housing cage was connected to the novel assay room via a 20×20 cm sliding door in the rear wall, so that birds could be moved between rooms without handling. We observed the behavior of the birds in the observation room for the first 2 min after entry. If the bird had not visited all five trees within this period, the observation time was extended until it had reached all trees, or up to a maximum of 10 min, after which observation stopped. To minimize observer bias, blinded methods were used when all behavioral data were recorded and/or analyzed. Exploratory scores were calculated as the sum of all the movements recorded during the first 2 min and corrected for the day the test was conducted (for further details on this test procedures and exploratory scores, see Dingemanse et al. (2002)). After the tests, we measured, weighed, and provided a PIT-tag identifier and aluminum ring to each bird when not present, after which we released the birds near their capture site.

Statistical analysis

We tested our hypotheses by running four models, both generalized linear models (GLZ) and general linear models (GLM). We first examined the relationship between rearing territory characteristics and exploratory behavior. After that we asked how the combination of both may associate

with winter food selection and foraging behavior in first year great tits (yearlings). Our first model used a Gaussian error distribution with exploratory score as response variable and the habitat type based on tree species composition (mixed or deciduous) and caterpillar biomass as continuous fixed effect predictors. We included peak width as the parameter to describe how long the caterpillar biomass peak was for each great tit breeding territory (Visser et al. 2006). Secondly, to examine the proportion of visits to the peanut feeders (using the *cbind* function, including the number of visits to the peanut feeders and the number of visits to the sunflower seed feeders, see Crawley (2012)), we fitted a model using a quasi-binomial distribution with the proportion of visits to the peanut feeders as response variable and habitat type, caterpillar biomass (peak width), and exploratory score as continuous fixed effect predictors. Thirdly, to investigate foraging behavior, we used the total number of visits to the feeders and the number of locations visited (maximum of seven) as response variables in two models fitted to a Gaussian distribution and habitat type, caterpillar biomass (peak width), and exploratory score as continuous fixed effect predictors.

We confirmed normality of model residuals by visual inspection of QQ plots and created graphs using the *ggplot2* package (Wickham 2011). All variables were standardized to two standard deviation units, so they are comparable across traits and models. Results are presented as estimates \pm standard error, F statistic, and P values. We used R version 3.5.3 (R Core Team 2019) for all analyses.

Results

We tested the relationship between rearing territory characteristics and exploratory behavior of the yearlings recorded using our winter feeders. We found that birds that were born and raised in territories with a narrower width of the caterpillar peak showed higher exploratory behavior scores, while habitat type did not show any significant relationship with exploratory score ($N=76$; GLM, peak width: estimate \pm SE = -0.367 ± 0.109 , $F=11.393$, $P<0.001$, Fig. 3; habitat type: estimate \pm SE = 0.001 ± 0.056 , $F=0.001$, $P=0.982$).

Next, we evaluated whether the food type birds ate during winter was associated with exploratory behavior and habitat type. We found that the proportion of visits to the peanut feeders was higher for those birds born and raised in territories with narrower caterpillar peak width ($N=76$; GLZ quasi binomial, peak width: estimate \pm SE = -0.870 ± 0.180 , $F=24.466$, $P<0.001$; Fig. 4a) and with a mixed (coniferous/deciduous) tree composition (habitat type: estimate \pm SE = 0.247 ± 0.091 , $F=7.377$, $P=0.008$; Fig. 4b). Exploratory behavior was not a significant predictor

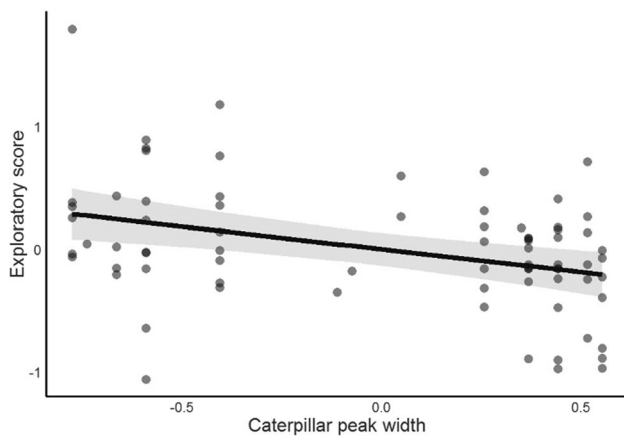


Fig. 3 The relationship between caterpillar peak width, as number of days in which caterpillar biomass was above $1 \text{ g m}^{-2} \text{ day}^{-1}$, collected during the 2019 breeding season and exploratory score of fledged great tits. Both variables were z-scored. The line is the fitted regression line, and the shaded area is the 95% CI

of whether yearlings visited more peanut feeders compared to sunflower seed feeders (exploratory score: estimate \pm SE = -0.253 ± 0.224 , $F = 1.274$, $P = 0.263$).

The total number of visits by yearlings to the feeders during our winter sampling was positively associated with their exploratory score ($N = 76$; GLM, exploratory score: estimate \pm SE = 2.970 ± 1.471 , $F = 4.075$, $P = 0.047$; Fig. 5). Birds originating from different habitat types did not differ in the number of visits to the feeders (habitat type: estimate \pm SE = 0.844 ± 0.707 , $F = 1.425$, $P = 0.237$). Also, the caterpillar peak width experienced during early development did not explain variation in feeder use (peak width: estimate \pm SE = 1.704 ± 1.477 , $F = 1.332$,

$P = 0.252$). The number of locations visited was unrelated to variation in exploratory score, habitat type, or caterpillar peak width ($N = 76$; GLM, exploratory score: estimate \pm SE = -0.070 ± 0.170 , $F = 0.196$, $P = 0.659$; habitat type: estimate \pm SE = 0.026 ± 0.082 , $F = 0.116$, $P = 0.734$; peak width: estimate \pm SE = 0.023 ± 0.169 , $F = 0.022$, $P = 0.883$).

Discussion

Here, we aimed to test how rearing habitat characteristics and exploratory behavior could explain food selection and foraging performance during winter in wild yearling great tits. We found that faster explorers were raised in territories with lower quality habitat characteristics (narrower caterpillar biomass peak), while slower great tits were raised in high-quality territories. Moreover, birds born in territories with a mixed tree composition and narrower caterpillar biomass peak visited the peanut feeders more compared to feeders with sunflower seeds. We also found support for the total visits to the feeders to be positively related to exploratory score; however, we did not find evidence that exploratory behavior or habitat characteristics during rearing led to differences in the number of locations visited.

Exploratory behavior and habitat quality determinants

In accordance with our expectations, caterpillar biomass, one of the studied habitat quality characteristics of the rearing territory, showed a relationship with exploratory behavior

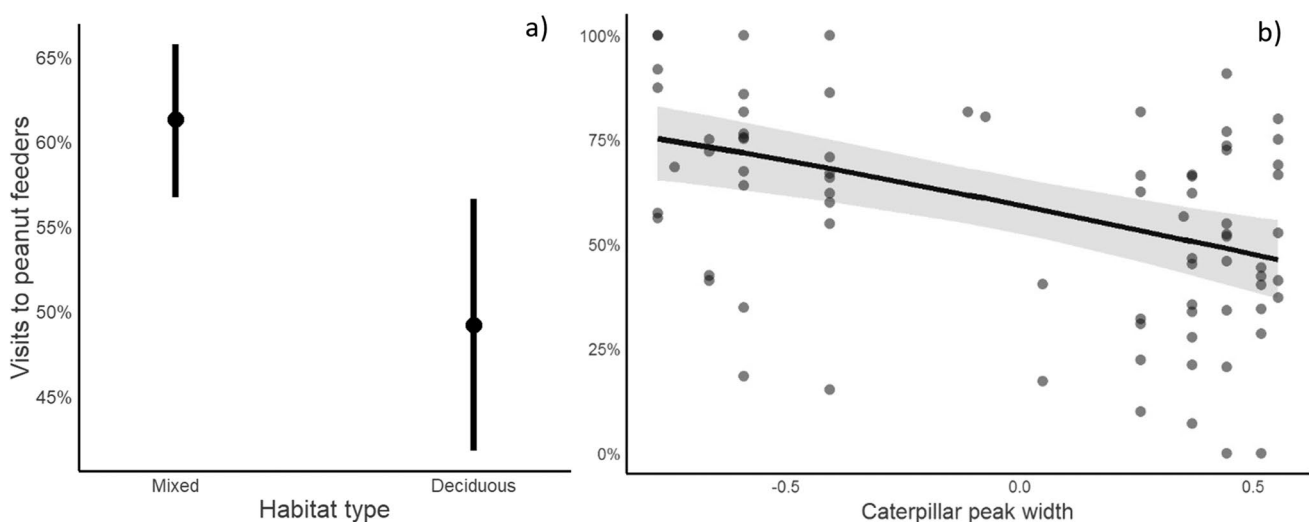


Fig. 4 Proportion of visits to the peanut feeders by great tit yearlings in winter 2018–2019 associated with **a** habitat type (“mixed”, “deciduous”) and **b** relationship with caterpillar peak width of their rearing territory ($n = 76$). Means \pm SE in **a** and 95% CI shaded area in **b** are shown

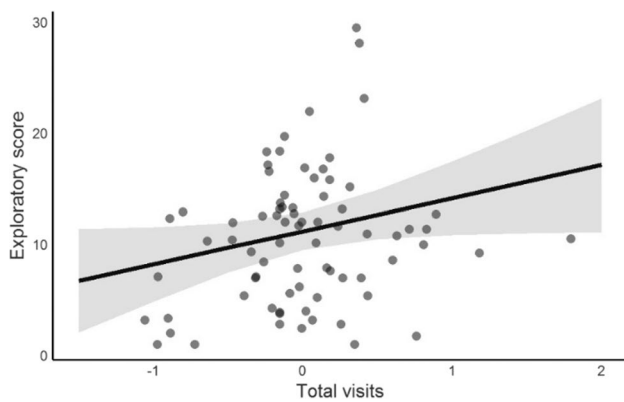


Fig. 5 The relationship between total number of visits to the feeders in winter and the exploratory behavior scores of great tit yearlings. Each dot represents one individual. A regression line shows the significant relationship, and the shaded area is the 95% CI

in yearling great tits. Indeed, the spatiotemporal distribution and quality of food in the environment determine the quality of early nutrition, which in case of the great tit is relying on caterpillars in oaks as the main food source for their nestlings (Perrins 1991; Naef-Daenzer et al. 2000). Caterpillars are only available during a relatively brief period; thus, caterpillar phenology determines the optimal time window for great tit reproduction, as nestling development outside this period has severe fitness consequences (van Noordwijk et al. 1995; Verboven et al. 2001; Visser et al. 2006; Samplonius et al. 2016). By directly analyzing the effect of the main food source availability at a small-scale (territory), our findings indicate that the extensively described links between caterpillar biomass and food provisioning in insectivorous birds (Naef-Daenzer and Keller 1999; Tremblay et al. 2005; Wilkin et al. 2009; Narango et al. 2017) can shape differences in behavioral phenotypes within a single continuous piece of woodland. All of this reinforces our suggestion that early nutrition, which is shaped by both spatial (trees species composition) and temporal (synchronicity) availability of food during the nestling stage, could be an important factor that determines great tit fledgling exploratory behavior. This could also explain why the “habitat type” component included in our analysis did not show a significant relationship with exploratory score in yearlings, as its influence in offspring behavioral development would be direct via caterpillar food supply instead of due to tree composition.

We specifically demonstrated here that birds born in territories of narrower caterpillar peak width, showed higher exploratory scores. This expands on earlier studies that showed that the handling stress response, a predictor for exploratory behavior in great tits (Fucikova et al. 2009), is strongly related to parental food provisioning (van Oers et al. 2015). This finding is important as it confirms experimental findings that higher exploratory behavior is associated with

situations of poorer food conditions (Carere et al. 2005) in captivity. However, we can now also relate this to territorial habitat features in an ecological context. Whether this is caused by the fact that fast exploring birds are occupying more the low-quality territories or whether it is specifically a plastic effect needs to be further studied using cross-foster experiments.

Foraging behavior and local adaptation

Birds living in low quality habitats have been described to show preference for low-quality food and to have a higher food intake than those in higher quality patches (Serrano-Davies et al. 2017a, b). Hence, we expected yearlings raised in low-quality territories to mostly select peanuts instead of sunflower seeds and to visit the feeders more frequently compared to yearlings raised in high-quality territories. In accordance with this, our results show that yearlings that were raised in mixed tree species territories and with lower amounts of caterpillars visited the low-quality easy to obtain peanut feeders more frequently than the sunflower seeds. As birds need to store fat reserves in order to offset the higher energetic requirements of winter (Gosler 2002), individuals raised in lower quality territories might need to compensate for the reduction of caterpillar biomass during development. As a consequence, they rely more on the higher energy content (peanuts = 7.18 kcal/g, sunflower seeds = 6.12 kcal/g; Gibb 1957) and easier to obtain type of food (peanuts are dehusked), meaning they enter the winter season in a poorer condition than those from high-quality territories. On the other hand, the nutritional value of the sunflower seeds may be higher due to the phytosterols content is much higher in those (534 mg/100 g) than in peanuts (220 mg/100 g). Phytosterols have been shown to protect against inflammation, improve the antioxidant capacity, and facilitate growth performance (de Jong et al. 2008; Rudkowska 2010; Li et al. 2011). This would explain why high-quality birds relied more on this type of food, as their need of fat is not so critical and they may also have been more willing to pay the added vigilance cost associated with handling sunflower seeds which, unlike the peanuts, were still husked. Additionally, as Dekeukeleire et al. (2019) showed in great tit populations in Northern Belgium, tree species composition may affect reproductive success (fledgling weight and number of fledglings) in our population (see “Methods” section). The “mixed” type territories in our study area are mainly composed of pine and birch, while the “deciduous” territories mostly consist of pedunculate oak and birch. Pedunculate oak has a very high number of associated arthropod species (Kennedy and Southwood 1984; Brändle and Brandl 2001), and oak-rich forest stands are often characterized by a diverse shrub layer (De Groote et al. 2018), which can also harbor many prey species for tits. These characteristics could

explain the difference in quality of the great tit breeding territories in our area, which would influence body condition of yearlings and therefore shape food-type selection later on.

In investigating the behavioral and habitat composition factors contributing to explain diverse feeder use strategies, previous examples suggest the existence of personality-specific food preferences (Quinn et al. 2012; Serrano-Davies et al. 2017b) and discovery of food patches (Herborn et al. 2010). Here, we provided evidence for a positive relationship between total number of visits to the feeders by great tit yearlings and their exploratory score. Despite the fact that more experiments are needed to verify this link, our results support the idea that individual differences in exploratory behavior arise early in life (Verbeek et al. 1994; Drent et al. 2003) and might be the cause of differential feeder use. Fast-exploring great tits are usually more aggressive, form foraging routines that are more rigid, and are more likely to use social learning than slow explorers (Verbeek et al. 1994, 1996; Reader and Laland 2000). All these behavioral characteristics support the idea of faster explorers having a higher dominant rank (Dingemanse and de Goede 2004) when exploiting predictable food sources, such as feeders in our study site, which have been provided in winter during the last 20 years. Along the same lines, it might also be the case that slow explorers, for instance, are able to find natural food sources more efficiently, as they usually rely more on detailed information available in their environment than faster explorers (Mathot et al. 2012), and therefore may have used the supplementary food less. On the other hand, another possible explanation for this is that the association between foraging and exploratory behavior becomes apparent under certain environmental conditions, for example, under the low winter temperatures, when food is scarce, or under high predation risk (Coomes et al. 2022). Hence, many links between personality traits and functional behavior have been found to be context dependent (Dingemanse and de Goede 2004; Quinn et al. 2009; Schuett and Dall 2009).

Parid species winter in dominance-structured flocks, in which yearlings are socially subdominant to adults (Lahti et al. 1996; Piper 1997), reducing their possibilities for choices when searching for food and imposing higher survival risk (Krams et al. 2013). Furthermore, juveniles disperse more frequently and/or farther than adults in order to get vacant territories, which are probably of bad quality, and move to better ones when they are older and are able to defend them (Andreu and Barba 2006). This would explain the absence of a clear pattern in our data when related to the quality of the patch where yearlings were born and raised. In addition, despite the fact that the number of locations birds visit may reflect winter movement strategies intended to optimize food search, we could not detect behavioral nor habitat-dependent differences in relation to number of locations visited by the yearlings. We

expected that the lower availability of food resources in low-quality territories during development would induce birds to undertake larger movements during winter (van Overveld et al. 2011), as well as that faster explorers would be visiting a higher number of locations (Dingemanse et al. 2003). It is therefore possible that other determinants of winter foraging behavior such as lower body condition and subordinate rank of yearling birds as opposed to adults (Krams et al. 2013) played a key role. We think that, for instance, they might have been forced to forage to a greater extent (higher number visits; Serrano-Davies et al. 2017b) but not necessarily to visit more locations, avoiding in this way the costs of moving around that may be risky in terms of predation and costly in terms of energy expenditure (Careau et al. 2008; Abbey-Lee et al. 2016).

Conclusions

In conclusion, our study indicates that territory characteristics associate with exploratory behavior for birds raised in such territories. Faster explorers were raised in territories with lower quality habitat characteristics. Our results suggest that low-quality first-year individuals tried to compensate their shortage of caterpillar biomass during development. Therefore, they relied on the high-energy content and easy to obtain food type. These findings may provide new directions to study how fine-scale habitat features and exploratory behavior interact in explaining foraging strategies in the wild. A multilevel approach examining how individual differences, habitat quality, and environmental conditions influence foraging decisions in natural populations would allow us to draw conclusions about the direction of causality of such relationships.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00265-023-03335-5>.

Acknowledgements We thank Piet de Goede, Manon Kaandorp, Peter de Vries, Martijn van der Sluijs, and all the students for their help in the field and data collection. We thank Ruben de Wit, Mary-Lou Aldering, and Anne Dijkzeul for taking care of the birds in the lab, Louis Vernooij for managing the great tit database, and two anonymous reviewers for comments that improved an earlier version of the manuscript. We are grateful to “Gelders Landchap en Kasteelen” for permission to work on their properties.

Author contribution ES-D and KvO conceived and designed the study; ES-D, NB, and BS performed fieldwork; NB wrote the R code to extract the feeders' data; ES-D performed data analyses and wrote the manuscript with input from all co-authors. KvO revised throughout the study.

Funding ES-D, BS, and NB were supported by open competition grants OCENW.KLEIN.253 and ALWOP.314 to KvO and an open competition grant (825.15.012) to Marc Naguib, respectively, which are funded by the Netherlands Organization for Scientific Research (NWO).

Data availability The raw data are available as supplementary material.

Declarations

Ethics approval All applicable international, national, and institutional guidelines for the care and use of animals were followed. All experiments were approved by an ethical committee (DEC-KNAW license no. NIOO 14.12 to KVO), and daily health checks were carried out to ensure the birds' welfare. Birds returned to the stock population after the behavioral experiments.

Competing interests The authors declare no competing interests.

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