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Research article

Associations between human non-motorised recreational activity on nest box occupation, exploratory behaviour and breeding success in a passerine bird

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Anthropomorphic activities have a large impact on ecosystems in many ways, one of which is how animals behave. Non-motorised nature recreation is a popular human activity of which the impacts on nature are largely unknown. These activities, which include hiking, biking, pet walking and horseback riding, tend to increase during the commencement of the breeding activity for most passerine forest birds in temperate zones. We here investigated whether variation in recreational activity associates with patterns of nest box occupation and reproductive success in a long-term study of personality-typed great tits Parus major. We measured human disturbance in the area by recording the frequency of non-motorised recreational activities by observations. We were particularly interested in the relationship between disturbance levels and nest box occupancy as well as the relationship between disturbance levels of occupied nest boxes and exploratory scores of the great tits that occupied them. We also investigated whether reproductive characteristics such as fledging success, clutch size, chick weight and tarsus length varied with disturbance levels at occupied nest boxes. We did not find a direct association between nest box occupation and disturbance. Habitat quality rather than disturbance explained the nest occupation. Furthermore, more exploratory individuals occupied boxes in less disturbed areas, independent of habitat quality. Fitness decreased with increasing disturbance independent of habitat quality. Chicks were heavier and had longer tarsi, and clutch sizes were bigger in less disturbed areas. In conclusion, we found breeding site choice of great tits to be independent of human activity, although there are clear fitness effects of human disturbance.

Keywords: animal personality, disturbance, hole nesting birds, nature recreation, nest box occupation



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Introduction

The numbers of people that engage in recreational activities are increasing globally. Especially non-motorised recreational activities such as hiking, biking and wildlife observation are gaining in popularity. Although such activities mostly cause negligible physical changes in the habitat, collectively, they can have indirect negative effects on wildlife. For example, recreational activities are linked to an increased stress level in some wild animals (Thiel et al. 2011, Tarjuelo et al. 2015), which could lead to negative effects on reproduction (Giese 1996). It can also cause animals to move away from otherwise suitable areas (Sutherland and Crockford 1993, Burger et al. 1995, Gander and Ingold 1997), which can have direct effects on survival (Wauters et al. 1997, Harris et al. 2014). Since humans may be perceived as predators by wild animals (Frid and Dill 2002, Zeller et al. 2024), these effects may be similar to when animals perceive an increase in predation risk in their environment.

Birds are especially sensitive to recreational activities in natural habitats (Steven et al. 2011). For example, Bötsch et al. (2018) showed that in those forest areas where human density was highest, bird population density was 13% lower compared to the areas with similar habitat type and lower human density. In another study, parts of the forest were experimentally disturbed while other areas with similar habitat types were left undisturbed (Bötsch et al. 2017). The experimentally disturbed areas showed fewer bird territories and bird species compared to the undisturbed area. The breeding window for many bird species during spring in the Northern Hemisphere is short and it coincides with the time when the rate of recreational activities increases due to improved weather conditions. The effect of increased human disturbance can also have serious consequences for breeding success in birds. For example, nest building activity, clutch size, hatching rates and fledging success can decrease due to recreational activities in natural areas (Liddle 1997, Buckley 2004, Müllner et al. 2004, Liley and Sutherland 2007) and such changes may have long-term effects in these areas (González et al. 2006). For example, blue tit Cyanistes caeruleus breeding success in parklands, where human disturbance is high, was lower than in the forest, where human disturbance was low (Glądalski et al. 2016). The same study also found that, with an increase in the number of rainy days in the breeding season, the number of human visits to the park decreased, causing an increase of the breeding success. Although it is not clear whether other urban characteristics in addition to human presence have affected the breeding success. In another study in blue tits, human recreational activities in nature influenced the number of antibodies in nestlings, possibly affecting nestling survival considerably due to a weakened immune system (Bötsch et al. 2020). In great tits, recreational activity caused an overall decrease in reproductive success (Hutfluss and Dingemanse 2019). There are also studies suggesting that, although the human activities in recreational trails have short-term behavioural effects, this does not influence breeding success (Smith-Castro and

Rodewald 2010). However, studies reporting positive effects or lack of an effect of non-motorised recreational activity on birds are in the minority (reviewed by Steven et al. 2011).

One way how the recreational activities can affect fitness is via changes in the behaviour of birds. These behavioural changes can be short term, such as being flushed off the nest or the territory, or long term such as changing habitat preferences for territory settlement. Both types of behavioural changes may have lasting fitness consequences. For example, flying off the nest due to repeated disturbances caused by human activities may leave chicks or eggs more vulnerable to predation and may influence the amount of food chicks receive from their parents (Lima 2009). Changes in habitat preferences due to disturbance may cause birds to select habitats that are less suitable for them. Habitat selection is an adaptive trait, and every individual tries to obtain the optimal habitat available to maximise their fitness (Chalfoun and Martin 2007). This is also the case when nest box breeding birds settle in a nest box during breeding seasons (Valkama and Korpimäki 1999). The nest box preference can have direct effect on offspring fitness (Goodenough et al. 2008). For example, even though increased human activity does not have to increase the predation rate, birds will avoid these areas even if only the perceived predation risk increases. If birds do stay in that area during the breeding season, they may decrease chick provisioning activity due to this perceived predation risk (Fernández and Azkona 1993). How birds perceive predation risk may vary across individuals. Animal personality, often defined as consistent between-individual differences in behaviours (Biro and Stamps 2008, van Oers and Naguib 2014), explain how individuals could vary their behavioural response in relation to increased predation risk. Exploratory behaviour is an operational measure of one animal personality trait and it measures the individual tendency to explore and gather information from new environments. Exploratory behaviour is also known to predict how individuals may respond to potential predation threats (Baugh et al. 2013, Nácarová et al. 2018).

In this study, we therefore investigated how individuals vary in their response to unmotorised recreational activity in a natural forest. Our main aim was to determine whether patterns of nest box occupation and measures of reproductive success, such as clutch size, chick weight, tarsus length and fledgling success covary with human recreational activities in great tits Parus major using 20 years of occupational and fitness data. Most studies investigate the effect of human disturbance in bigger areas where the human density is estimated through the number of people within the whole area (Steven et al. 2011). In our study we aim to show the impact on a finer scale. Great tits are territorial, hole-nesting passerines that tend to prefer nest boxes over natural cavities. Once settled, birds remain at their nesting territory unless one of the partners dies or in the case of divorce (Harvey et al. 1979). Females make a nest and incubate the eggs, males provision females during the incubation period and both sexes provision the chicks from hatching to fledging, which takes around 17 to 22 days (Kluijver 2002). In addition, we have investigated the personality of the great tits occupying the nest boxes.

We used exploratory behaviour as an operational measure of animal personality (Dingemanse et al. 2002, Dingemanse 2004). Former studies in our study population have shown that this trait is repeatable (Dingemanse et al. 2002), heritable (Drent et al. 2003) and genetically correlated to various behaviours such as risk taking (van Oers et al. 2004).

We expected that areas with higher human disturbance would be less attractive for great tits to settle due to an increase in perceived predation risk. To investigate this, we assessed the human recreational pressure throughout our study area and used fitness data of our long-term breeding data set between 2012 and 2021. In addition, we expected that fast-exploring individuals were less affected by disturbance compared to slow explorers. The more exploratory individuals are higher risk takers and therefore may be less affected by human disturbance (Drent et al. 2003).

Material and methods

Study area, nest occupation and reproductive measures

The study was conducted in Westerheide forest (Groot Warnsborn, 52°01′00′′N, 05°50′30′′E), near Arnhem, the Netherlands. The forest is predominantly deciduous with some coniferous patches and covers 250 ha. The area is popular for non-motorised recreational activities such as hiking, walking pets, horseback riding and biking. There are several clear interconnected paths through the forest, including some predetermined hiking trails. These paths are uniform and there are no special interest areas in the forest where most visitors accumulate. There are 230 nest boxes in the study area and the bird population that is making use of them has been monitored since 1996. We used nest box breeding occupancy data, clutch size, chick biometric measures (weight and tarsus length) and the number of fledged chicks, that were collected during breeding seasons (April–June) from 2012 to 2021. To record these measures, bi-weekly checks were conducted on nest boxes in order to determine the state of the nest building from the end of March onwards. When nest building occurred, nest boxes were checked every other day in order to determine the exact laying date, clutch size and start of incubation. The exact hatch date was determined by checking the broods daily around the expected hatch date. Parents were caught inside the nest box using spring traps on day 7 after hatching. We equipped individuals with uniquely numbered aluminium leg rings if they did not already have one and measured their body mass and tarsus length. On day 14 after hatching, we ringed the chicks with uniquely numbered metal rings and measured tarsus length (0.1 mm) and body mass (0.1 gr). To determine the number of fledged chicks, we checked nest boxes 22 days after hatching.

Measuring human disturbance

To measure the disturbance caused by recreational activities, we counted the number of people we encountered on the 12 path junctions in the study area. We separated the paths according to intersections. Continuous lines between two intersections were considered one path. The rationale for this was that we did not know in which direction the visitor continued after the next intersection. The junctions were selected in a way where we could see the moving direction of the visitors. The measurements were taken between March and April 2021. The path structure of the area and the position of nest boxes has not changed between 2012 and 2021. The activities that were considered recreational activities were hiking, walking, cycling, pet walking and horseback riding. As we do not know whether each activity has different impact on birds, each individual activity was considered as one disturbance unit. In addition, each individual in a group activity (such as family of 3 walking together) were counted as one disturbance unit. In each junction, we recorded the number of visitors and from which paths visitors were coming from and where they were going to for 30 minutes. Each visitor was assigned to a specific path that they were observed. The measurements were taken between 09:00 h in the morning until 15:00 h in the afternoon. Each path has been observed four times during the weekdays (Monday-Friday) and 2 times during the weekends (Saturday, Sunday). On each junction, the measurements were taken the same number of times in two separate time periods that we pre-determined: morning (09:00–12:00 h) or afternoon (12:00–15:00 h). The rationale for this was to account for possible visitor number fluctuations during the morning and the afternoon and to have a balanced design. A kernel interpolation was performed using ArcGis Pro ver. 3.1.0 to estimate the disturbance levels of each nest box in the study area. Kernel values were calculated by taking into account the number of visitors on the paths and the distance of nest box to all paths around it. These values were used as the disturbance measure in our models. In ArcGis, the output cell size of the kernel density was 5351 \times 10⁻⁵ and we used the planar distance when calculating distance between a nest box and the paths around it. The resulting interpolated surface is visualized as a raster layer, where each pixel represents the estimated number of visitors across the study area (Fig. 1b). Highest levels can be observed at the edges of the study area and on the marked hiking trails in the area.

Exploratory behaviour

To measure exploratory behaviour, we performed a novel environment test in the indoor facilities of the Netherlands Institute of Ecology (NIOO-KNAW). This standard test was developed for assessing exploratory behaviour in small passerines (Verbeek et al. 1994, Dingemanse et al. 2002, Drent et al. 2003, van Oers and Naguib 2014). Outside of breeding season (August–February), wild great tits were captured using mist-nets or during nest box roost checks from the Westerheide area and brought into the animal facility at NIOO-KNAW, Wageningen, the Netherlands. To minimise transportation stress, we moved the birds from the forest to the animal facility in special wooden transportation boxes



Figure 1 (a) The map of the study area (Copyright by *Esri Community Maps Contributors, Kadaster, Esri, HERE, Garmin, Foursquare, GeoTechnologies, Inc, METI/NASA, USGS*) indicating the paths as white lines. Green colours with grey texture indicate forest patches. Green without texture resembles meadows. (b) Disturbance levels on the paths (colour gradients represent the disturbance levels; the darker the colour, the higher the disturbance levels). Red dots with grey circles in both figures represent locations of the nest boxes.

that could carry 10 birds at a time in individual compartments. At the animal facility, birds were kept in individual cages of $0.9 \times 0.5 \times 0.5$ m with access to water, mixed seeds, mealworms and dry food that contained egg, animal fat and grains. Birds were tested the morning after they were caught. To measure exploratory performance, the birds were introduced to a novel environment containing five artificial wooden trees. The holding cages opened to the testing room directly through a small sliding door. By manipulating the light before the test, the birds were allowed to enter the testing room without handling. We used the total number of flights and hops within the first 2 minutes corrected for June date as our measure of exploratory behaviour (Dingemanse et al. 2002).

Habitat quality

During the 2019 breeding season, we assessed the quality of the territory around each nest box (50 m radius). Based on the two most abundant tree species within the territory we assigned each nest box to be of 'high' or 'low' quality. A territory was considered to be of 'high' quality when the two most abundant tree species were deciduous (pedunculate oak, Quercus robur; beech, Fagus sylvatica; red oak, Q. rubra; birch, Betula pendula; larch, Larix decidua), while it was considered as 'low' quality when there was a species mixture, one deciduous of the above mentioned and one coniferous (pine, Pinus sylvestris; silver fir, Abies alba) (Serrano-Davies et al. 2023). Fledgling weight (habitat type: estimate = -11 341 ± 1706, $F_{1,71}$ =44.184, p < 0.001) and the number of fledglings (habitat type: estimate = -52.66 ± 12.49 , F_{1.73} = 17.781, p < 0.001) were significantly higher in the 'deciduous' territory type than in the 'mixed' when tested using the 10 years of breeding data in our population (2011-2020), indicating the quality difference between the two habitat types. All measures were taken by the same observer (ESD).

Statistical analysis

Since great tits have priority to occupy nest boxes over other cavity-nesting birds in our study area population, we only considered the nest boxes that were occupied by great tits. We used generalised linear mixed models to determine whether the tendency for birds to occupy a nest box was affected by the disturbance level the nest box was exposed to. We included binary occupancy data (0 or 1) as the dependent variable and continuous disturbance level data as a fixed factor. Since we used data from 2011 to 2020, we included year as a fixed factor to account for variation in occupancy between years. To account for the habitat quality around each nest box, we included habitat quality (high quality/low quality) as fixed factor. We included nest box as a random factor to account for random variation associated with nest box.

To investigate how great tits' exploratory behaviour influences their nest box choice, based on the surrounding disturbance level, we performed a linear model. In this model, the disturbance value of the chosen nest box was the response variable, reflecting birds' specific nest box preference rather than the overall environmental disturbance levels, and the exploratory score was the independent variable. In order to control for a potential effect of habitat quality, we also included habitat quality (high or low) of the area surrounding each nest box.

We also constructed three models to test how disturbance levels covaried with measures of reproductive success. We choose clutch size, lay date and fledging success as measures of reproductive success. To determine whether clutch size and lay date varied along with disturbance levels if a box was occupied, we used two separate linear mixed models with either the number of eggs in a clutch or the date the first egg was laid as the response variable. The disturbance value, the brood year (2012–2021), exploratory score of parents and the habitat quality were included as the explanatory variables and, to account for random variation in clutch size between nest boxes, the nest box number, female ring number and male ring number were included as a random factor in both models. We used a linear mixed model to test whether fledging success varied along the levels of disturbance in the area. In this model, the number of chicks that fledged from the nest was the response variable and we included the disturbance level, the clutch size, habitat quality, exploratory score of parents and brood year as the explanatory variables. We included nest box number, female ring number and male ring number as random effects.

Finally, to test whether chick characteristics such as weight and tarsus length differed between broods that were raised in next boxes with different exposure to disturbance, we used two linear mixed models where chick weight or tarsus length were the response variables and we included the disturbance level, clutch size, habitat quality and brood year as independent variables and brood ID nested in nest box number as a random variable. Since we did not have the sexes of the offspring, we assumed equal sex ratios between the broods.

To control for the relationship between the habitat quality and the location of paths near the box, we performed an extra linear model test that had distance of the nest box to the closest path as a response variable and the habitat quality as the explanatory variable. The rationale behind this analysis was to check whether there is any tendency for paths to be built on higher- or lower-quality areas. We also performed another linear model to determine the relation between habitat quality and disturbance. We performed all our statistical analysis using R statistical software ver. 4.3.1 (R Core Team 2023) using the lme4 package (Bates et al. 2015) (www.r-project. org). We report full models in our study.

Results

We found no relation between the chance of nest box occupancy and the number of visitors on the closest path to this nest box after correcting for habitat quality (Table 1a). The model shows that not disturbance but habitat quality affects the occupancy. We found no significant association between habitat quality and disturbance levels (F = 3.0307, df = 183, p = 0.08) (Supporting information). However, we found that paths were significantly closer to nest boxes that were located in higher-quality areas (F=4.92, df=183, p=0.03; Fig. 2) (Supporting information). Year was significant in all models, indicating that the response variables (occupation probability, fledging success and clutch size) varied between years (Table 1). We found that fewer explorative individuals occupied nest boxes that were exposed to higher disturbance levels (F=4.4, df=1041, p=0.04; Fig. 3), while controlling for habitat quality (F= 3.7, df = 1041, p = 0.06).

Table 1. Relation between a) occupancy and disturbance, controlled for brood year and habitat quality of the nest box territory and the brood year, b) clutch size and disturbance, controlled for habitat quality of the nest box territory and the brood year, c) the first day of egg laying to disturbance, controlled for habitat quality and the brood year, d) number of fledged chicks and disturbance, controlled for clutch size, habitat quality and the brood year, e) exploratory score of great tits occupying the nest boxes and disturbance, controlled for habitat quality, f) chick weight and disturbance, controlled for clutch size, habitat quality and the brood year, g) tarsus length of chicks and disturbance, controlled for clutch size, habitat quality and the brood year.

	Factors	Chi Square	df	p value
a) Occupation	Disturbance	2.12	1	0.15
	Brood year	72.36	9	< 0.001
	Habitat quality	16.49	1	< 0.001
b) Clutch size	Disturbance	6.0959	1	0.014
	Exploratory score	0.063	1	0.8
	Brood year	465.4	9	< 0.001
	Habitat quality	0.0039	1	0.95
c) Lay date	Disturbance	0.38	1	0.53
	Exploratory score	0.11	1	0.74
	Brood year	4167.55	9	< 0.001
	Habitat quality	0.1122	1	0.74
d) Fledging success	Disturbance	0.0092	1	0.92
	Exploratory score	0.0008	1	0.98
	Brood year	408.08	9	< 0.001
	Clutch size	87.4952	1	< 0.001
	Habitat quality	4.0242	1	0.045
e) Exploratory behaviour	Disturbance	11873	1	0.036
	Habitat quality	10078	1	0.053
f) Chick weight	Disturbance	7.3679	1	< 0.01
	Clutch size	63.6230	1	< 0.001
	Brood year	366.5679	9	< 0.001
	Habitat quality	13.5902	1	< 0.001
g) Tarsus length	Disturbance	4.0432	1	0.044
	Clutch size	19.6096	1	< 0.001
	Brood year	150.7936	9	< 0.001
	Habitat quality	13.4597	1	< 0.001



Figure 2. (a) Relation between habitat quality around the nest boxes and the nest boxes' distance to the closest path, (b) relation between disturbance and habitat quality. Habitat quality is a binomial measure, area around each nest box is assigned to be either 'high' or 'low' quality. Disturbance measures calculated using number of visitors and distance of each nest box to the closest point of the path. Error bars are 95% confidence intervals.

We found no relationship between disturbance levels and the first egg laying date ($\chi_1^2 = 0.38$, p = 0.53) or fledging success ($\chi_1^2 = 0.0092$, p = 0.92) (Table 1d). There was a negative association between the level of disturbance and clutch size ($\chi_1^2 = 6.1$, p = 0.014) (Fig. 4). The chicks born in areas with different disturbance levels differed in weight ($\chi_1^2 = 7.37$, p = 0.007) and tarsus length ($\chi_1^2 = 4.043$, p = 0.04), with higher disturbance levels resulting in lower chick weight and smaller tarsus length (Fig. 5a, b).

Clutch sizes and first egg-laying date did not differ between nest boxes that were situated in areas with high or low habitat quality (clutch size; $\chi_1^2 = 0.0039$, p = 0.95, lay date; $\chi_1^2 = 0.11$, p = 0.74). As expected, the chance that a chick fledged was positively related to habitat quality ($\chi_1^2 = 3.9$, p = 0.048). Higher habitat quality also resulted in heavier chicks with longer tarsi (weight; $\chi_1^2 = 13.59$, p < 0.001, tarsus length; $\chi_1^2 = 13.46$, p < 0.001). Variation in exploratory behaviour did not explain any of the reproductive parameters (Table 1).

Discussion

Here, we investigated whether the pattern of nest box occupancy is associated with the intensity of recreational activities and whether the disturbance from recreational activities is related to reproductive success. We did not find a relation between nest box occupancy and disturbance. Fast explorers occupied nest boxes that had lower disturbance levels. Birds that breed in nest boxes exposed to higher disturbance levels produce smaller clutches and lighter chicks with shorter tarsi, while they do not breed earlier, nor have a higher number of fledglings. These results indicate that although the choice for nest boxes is not affected by disturbance, disturbance levels do have an effect on reproductive success (Fig. 4). Our results show that great tits do not avoid nest boxes with high disturbance levels but occupy nest boxes in higherquality areas. Since our study is correlational, we cannot separate the effect of disturbance and habitat quality on nest box occupancy. In the light of these results, we can speculate on two possible reasons for this nest box occupancy distribution. First, birds choose areas where the environment provides optimal breeding conditions which have specific features and



Figure 3. The level of disturbance of an occupied nest box related to the exploratory score of great tits occupying the nest box.



Figure 4. The comparison between breeding measures; (a) number of chicks fledged from the nest, (b) number of eggs in a clutch, and (c) the number of days past after first of April before the first egg laid, and disturbance levels in the area. Lines and 95% confidence intervals are derived from the linear mixed models.

resources that are considered high quality for specific species. For example, great green macaws *Ara ambiguus* prefer to build their nest in environments where they can find specific nest cavities, which can improve reproductive outcomes (Lewis et al. 2024). Similarly, Tahiti petrels *Pseudobulweria rostrata* increase their reproductive success by building their nests in forests with slopes and deep soil (Pagenaud et al. 2022). Studies in the Paridae family, for example in varied tits *Sittiparus varius*, show that birds prefer to nest near broadleaf patches that had higher food availability (Kondo et al. 2017). Also, Japanese tits *Parus minor* prefer to build their nest in low shrub density as these areas provide better foraging possibilities (Li et al. 2023).

Second, although we did not find that nest boxes in highquality areas experienced higher levels of disturbance, we found that they are situated closer to the paths, which might increase the perception of disturbance in higher-quality areas. Human choice for path construction may not be random but the higher-quality areas may be preferred as they can be more attractive locations for hiking or are closer to forest edges. Another possible reason is that the presence of hiking paths changes the species composition of the area, making the habitat more suitable for great tits. Since the composition of tree species determined the quality of the area, such humaninduced change in the species composition may directly influence the suitability of the area. Experimentally changing disturbance levels will be able to separate the effects of habitat quality from disturbance. Since we did not find any relationship between disturbance and habitat quality, we are confident that habitat quality cannot explain all our results regarding disturbance.

Reproductive measures, such as egg laying date and fledging success, were not associated with variation in recreational activity levels. However, the clutch size in more disturbed areas was smaller, indicating that disturbance caused great tits to lay fewer eggs and as the environment may seem unpredictable due to disturbance. Similarly, the clutch sizes of little terns *Sterna albifrons* in Portugal were negatively affected by human disturbance and this effect could be reversed using protective measures against human disturbance (Medeiros et al. 2007). The weights and the tarsus length of great tit chicks were lower in the more humandisturbed areas, showing an effect on chick quality. This can be explained by a decrease of foraging activity as a response to perceived predation risk (Verdolin 2006, Abbey-Lee et al. 2016). Foraging efficiency and foraging rate are crucial parts of chick provisioning (Wennerskirch et al. 1996, Senécal et al. 2021) and chick quality is known to affect recruitment probability (Tinbergen and Boerlijst 1990) and thus fitness. The perceived predation risk during chick feeding likely caused a difference in chick mass for great tits by decreasing feeding frequency (Dunn et al. 2010). Parents optimise their clutch size during egg laying and the effects on chick quality likely appear later in the season. This, in most cases, prevents them from having a high number of low-quality chicks through a trade-off between the clutch size and chick size (Smith et al. 1989). In our population some parents experienced a higher recreational pressure, which they may have perceived as predation risk, already during egg laying and they therefore decreased their clutch size. However, this reduction in brood size was not sufficient to result in raising bigger chicks, since they likely faced the consequences during chick feeding. The fact that the body mass and tarsus lengths of the chicks were positively correlated with the habitat quality, and clutch size was negatively correlated with disturbance, makes this a likely explanation. Interestingly, the increased clutch size was negatively correlated with tarsus length and body mass in general. A similar negative significant association between chick mass-tarsus size and clutch size was previously demonstrated in other populations (Smith et al. 1989). Future work should manipulate chick numbers in relation to habitat quality and disturbance levels to experimentally test this hypothesis. In addition, recording how often chicks are fed by parents in areas that are differing in level of disturbance can inform us whether increased perceived predation risk due to human disturbance influences the foraging efficiency of parents.

We would like to emphasize again that our study uses a correlative dataset, and therefore results must be interpreted



Figure 5. Associations between disturbance and (a) chick weight (g) and (b) chick tarsus length (mm). Black dots represent raw brood means. Lines and standard error are derived from the linear mixed model.

with caution. In addition, in our study, we assumed that the human activity in the specific paths stayed relatively stable over the years. Although the path structure stayed the same, changes in the human disturbance levels over the years was something we were not able to control for. Nevertheless, our study shows that the highest disturbance was coming from predetermined hiking routes that stayed stable throughout our study period (Fig. 1b). Also, we assumed that a bird chooses its nest box from all available boxes in the area. However, since great tits are territorial birds, the set of nest boxes they can choose from is restricted to a subset of nest boxes that are present within their territory.

In conclusion, we showed that birds were more likely to occupy nest boxes in higher-quality areas and that nest boxes that experienced higher human disturbance were chosen more by great tits with lower exploratory scores. After correcting for habitat quality, we found that birds that bred in nest boxes exposed to higher levels of human disturbance showed decreased fitness. In areas with higher disturbance levels, the clutch sizes were smaller and the chicks were lighter and had smaller tarsi, possibly caused by an increased perceived predation risk due to increased human disturbance. These results, combined, suggest an apparent miss-match between settlement choices and the consequences of subsequent disturbance levels for chick feeding. From our results, it is not clear whether birds gain higher benefits from choosing high-quality areas compared to the possible costs of ending up in high-disturbance areas, or if fast and slow explorers choose different strategies with similar fitness outcomes. These results are intriguing; however, in order to confirm these patterns and to separate effects of habitat quality and human disturbance, experimental studies are necessary.

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Author contributions

Utku Urhan: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Visualization (lead); Writing - original draft (lead); Writing - review and editing (lead). Kim Platjouw: Conceptualization (supporting); Investigation (equal); Methodology (supporting); Writing - review and editing (supporting). Peter P. de Vries: Data curation (supporting); Investigation (supporting); Software (supporting); Visualization (supporting); Writing - review and editing (supporting). Eva Serrano Davies: Conceptualization (supporting); Data curation (supporting); Investigation (supporting); Methodology (supporting); Project administration (supporting); Supervision (supporting); Writing - original draft (supporting); Writing - review and editing (supporting). Kees van Oers: Conceptualization (supporting); Data curation (supporting); Formal analysis (supporting); Funding acquisition (equal); Investigation (supporting); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Visualization (supporting); Writing - original draft (supporting); Writing review and editing (supporting).

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.79cnp5j5k (Urhan et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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