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# Personality predicts spatial responses to food manipulations in free-ranging great tits (*Parus major*)

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**Personality differences measured under standardized lab-conditions are assumed to reflect differences in the way individuals cope with spatio-temporal changes in their natural environment, but few studies have examined how these are expressed in the field. We tested whether exploratory behaviour in a novel environment predicts how free-living individual great tits (*Parus major*) react to a change in food supply. We temporarily removed food at feeding stations during two summers and recorded the behavioural response of juvenile birds to these food manipulations using radio-tracking. When challenged by an abrupt change in food supply, fast-exploring individuals more rapidly switched to different foraging areas at longer distances from the feeder. This study is the first to show that personality traits predict the spatial response to experimentally induced changes in their natural environment.**

**Keywords:** personality; spatial behaviour; *Parus major*

## 1. INTRODUCTION

Recent laboratory experiments have revealed within-species variation in levels of aggressiveness, boldness, social tolerance or exploration that are consistent across time and contexts (Sih *et al.* 2004). Such between-individual differences in suites of correlated behaviours are referred to as animal personality (Gosling 2001) or temperament (Réale *et al.* 2007), and are generally assumed to reflect differences in the way individuals cope with changes in their natural, social or physical environment. In support of this hypothesis associations between personality traits and fitness parameters have been shown to vary according to spatio-temporal changes in predation pressure, food availability or social conditions (reviewed in Dingemanse & Reale 2005). However, experimental tests on how such differences are expressed in the field remain scarce.

One behavioural mechanism that has been proposed is that individuals with different personality may use environmental information in a different way. For example, maze experiments in rodents have shown that proactive individuals more easily build up routines in food-searching, while reactive individuals behave more flexibly to changes in maze structure, suggesting personality-related differences in awareness to environmental stimuli (Benus *et al.* 1990). Similarly, in captive great tits (*Parus major*), experimental changes in food-distribution showed that 'bold' individuals more easily formed routines in foraging behaviour, whereas 'shy' individuals behaved more flexibly and were more likely to sample other available food resources (Drent & Marchetti 1999).

In this study we performed a field experiment to test whether personality differences in great tits predict variation in spatial response to changes in food availability. We used exploration score as a measurement of personality variation (Verbeek *et al.* 1996). We manipulated food availability by temporarily emptying artificial feeding stations, and monitored the behaviour of birds with different exploration scores before and after the manipulation by means of radio-tracking. We expected the spatial response to reflect differences in behavioural flexibility for switching to other available (natural) food resources and predicted slow and thorough explorers to respond by moving to nearby areas with other, but known, natural food resources and fast and superficial explorers to leave the area of the feeder in search for other food resources. We made, however, no *a priori* predictions on what time scale such changes would occur as for example, the personality differences in routine behaviour described by Drent & Marchetti (1999) were based on very brief (5 min) observations in small aviaries. To minimize possible prior residence effects affecting the spatial response (Sandell & Smith 1991), we used first-summer birds shortly after independence.

## 2. MATERIAL AND METHODS

### (a) *Study area and trapping methods*

The study was conducted in 2007 and 2008 in a small-scale landscape with scattered woodland fragments in northern Belgium (51°08′ N, 4°32′ E). This area contains 17 fragments of mature forest surrounded by residential areas and agriculture. We installed two feeding stations at 1 km distance (F1 and F2) in the central part of the study area at the end of June, when most juveniles had become independent. Feeding stations were continuously baited for at least four weeks with peanuts until the food manipulation started. In July we caught juvenile great tits using mist nets. Juveniles not banded in the nest in the study area were considered immigrants.

### (b) *Exploration test*

After ringing and measuring we transported the birds to the laboratory where they were tested for exploratory behaviour the next morning. Following Dingemanse *et. al.* (2002), exploratory behaviour was measured by entering each bird separately into a sealed room (4.0 × 2.4 × 2.3 m) containing five artificial trees and calculated individual exploration scores as the total number of flights and hops made within two minutes after entering the room. All birds were released near their site of capture within 24 h after capture. A larger dataset from this population show that our exploration score is repeatable ($n = 224$, $r = 0.42$, unpublished data).

### (c) *Spatial behaviour*

In 2007 and 2008 we fitted 18 and 20 individuals, respectively, with radio-tags, equally divided over experimental feeding sites FI and F2 and stratified by exploration score (range 0–31). A backpack harness was used to attach the radio-tag to the birds. The weight of the radio-tags was 0.75 g (4% of the average body mass) and lasted for 35–45 days (Model 1035, Advanced Telemetry Systems, Isanti, USA). We located the birds 2–6 times per day between 8.00 and 20.00, with a time interval of at least 1 h. We collected 25 locations per individual during the pre-experimental period and on average 30 locations after we removed the food (range 17–37 locations).

### (c) *Experimental protocol*

Spatial behaviour was recorded from the 10th of August in both 2007 and 2008. Food was subsequently removed from two experimental feeders but not synchronously. Experimental feeders were emptied

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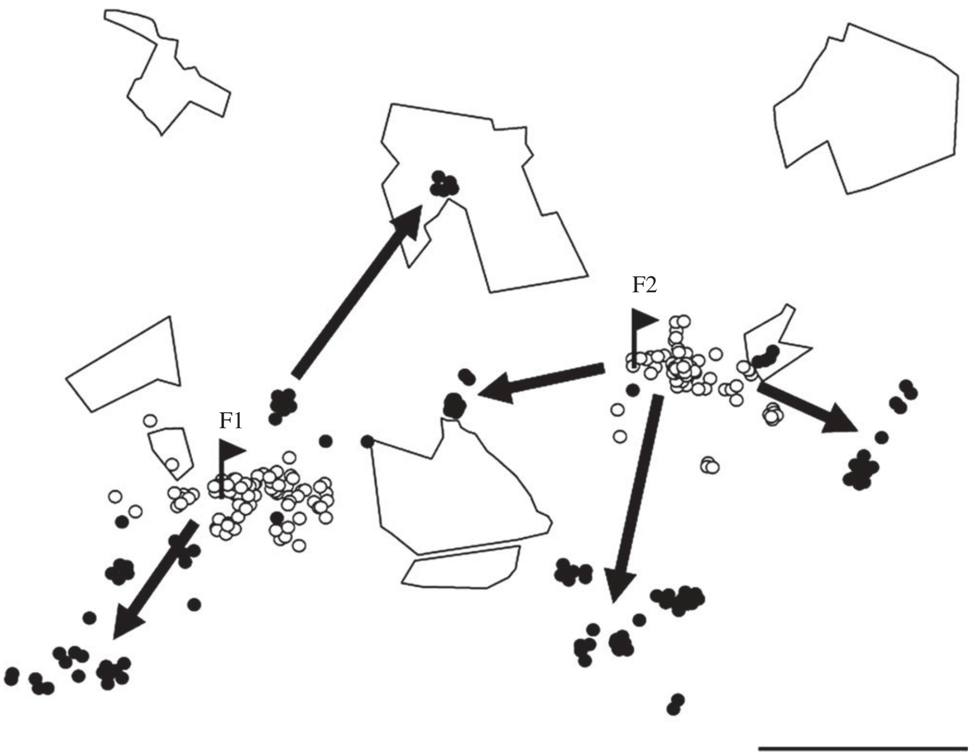

Figure 1. Examples of spatial response of fast (filled circles) and slow explorers (open circles) to the removal of food at artificial feeding stations F1 and F2 (flags). Each black arrow represents a fast explorer. At both F1 and F2 the locations of two slow explorers are shown.

Table 1. Results from a GLM analysis on relationship between exploration score and distance to the feeding-tables before and the after the food manipulation.

| | distance before manipulation | | | | increase in distance after manipulation | | | |
|---|---|---|---|---|---|---|---|---|
| variable | d.f. | *F* | *p* | effect ± s.e. | d.f. | *F* | *p* | effect ± s.e. |
| exploration score | 1,28 | 0.27 | 0.61 | −0.01 ± 0.01 | 1,31 | 2.97 | 0.09 | 0.03 ± 0.02[a] |
| dispersal status | 1,29 | 0.67 | 0.42 | −0.16 ± 0.19 | 1,32 | 7.50 | 0.01 | −0.74 ± 0.27 |
| year | 1,31 | 9.71 | 0.004 | 0.54 ± 0.17 | 1,28 | 0 | 0.94 | 0.02 ± 0.27 |
| area | 1,31 | 12.76 | 0.001 | 0.62 ± 0.17 | 1,29 | 0.08 | 0.79 | −0.08 ± 0.27 |
| sex | 1,30 | 1.39 | 0.25 | −0.21 ± 0.18 | 1,30 | 0.52 | 0.47 | 0.21 ± 0.29 |

[a] Significant if entered in the model without dispersal status ($F_{1,32} = 6.24$, $p = 0.018$, effect ± s.e. = 0.04 ± 0.015), see text for details.

Table 2. Results from a GLM analysis on relationship between exploration score and individual intercepts and slopes of the change in distance over an 8 day period after the food manipulation.

| | intercept | | | | slope | | | |
|---|---|---|---|---|---|---|---|---|
| variable | d.f. | *F* | *p* | effect ± s.e. | d.f. | *F* | *p* | effect ± s.e. |
| exploration score | 1,32 | 5.84 | 0.02 | 0.02 ± 0.01 | 1,28 | 0.05 | 0.83 | 0 ± 0 |
| dispersal status | 1,29 | 0.22 | 0.64 | −0.07 ± 0.14 | 1,32 | 10.35 | 0.003 | −0.14 ± 0.04 |
| year | 1,31 | 0.93 | 0.34 | 0.11 ± 0.12 | 1,29 | 0.33 | 0.58 | −0.02 ± 0.04 |
| area | 1,30 | 0.76 | 0.38 | 0.11 ± 0.13 | 1,30 | 0.64 | 0.43 | −0.03 ± 0.04 |
| sex | 1,28 | 0.03 | 0.87 | 0.02 ± 0.14 | 1,31 | 0.68 | 0.42 | 0.04 ± 0.04 |

on the 20th (F1) and 24th (F2) of August 2007, and on the 18th (F2) and 22nd (F1) August of 2008. After eight days the feeders were again refilled. Emptying and refilling feeders always occurred in the evening while birds were roosting.

### (**d**) ***Statistical analyses***

We obtained data from 34 individuals. Spatial behaviour in the eight days before and after the manipulation was quantified by the median distance per day to the feeder and by the 50 and 95 per cent kernel areas, calculated by the fixed kernel contour method using RANGES7 software (Anatrack Ltd. http://www.anatrack.com). To quantify individual differences in the rate of change in spatial behaviour we regressed the distance from the feeder against time (i.e. 8 days) using a general linear mixed model with individual as 'subject' (random effect), and extracted individual intercepts and slopes using the restricted maximum likelihood (REML) method (i.e. best linear unbiased predictors). We used general linear models (GLMs) with normal errors to test for the relationships between spatial behaviour and exploratory behaviour. To test for relationships in the pre-manipulation period, we used the absolute measures characterizing spatial behaviour, whereas after the removal of food we tested for the effect of 'treatment' (i.e. differences in spatial measurements before and after the manipulation, and slopes and intercepts of individual distance against time regressions). Normality of residuals was tested using Shapiro–Wilk test and distances were log-transformed to improve normality. Exploration score was used as a continuous variable in all analyses. We included sex, dispersal status (immigrant or locally born), year and area as fixed effects in the models. Analyses were performed using SAS v. 9.2 software.

## 3. RESULTS

Average home range sizes pre-manipulation were 0.81 ha ± 0.47 s.d. for the 50 per cent contours (range 0.13–1.89 ha), and 3.57 ha ± 2.0 s.d. for the 95 per cent contours (range 0.61–7.49 ha). Median distance per day to the feeder was 30 m ± 23 s.d. (range 12–85 m). Removing the food at feeding stations had a large impact on the spatial behaviour of the birds. Birds increased their average home range sizes both for the 50 per cent contours (2.2 ha ± 0.88 s.d. range 0.65–3.94 ha) and the 95 per cent contours (8.6 ha ± 4.3 s.d. 2.7–21 ha) and were found at considerably larger distances from the feeder (median daily distance 265 m ± 171 s.d. range 40–634 m; all paired *t*-test comparisons $p < 0.001$).

In the pre-manipulation period, home range sizes and distance to the feeders differed between years and areas ($p < 0.01$ for both variables), but were unrelated to exploration score, dispersal status or sex of the birds ($p > 0.08$ for all variables in all 3 models).

After the removal of food the increase in home ranges sizes was unrelated to exploration score or other variables ($p > 0.1$ for all variables in both models). The increase in median daily distance from the feeders, however, was positively related to exploration score (table 1, figure 1). Because immigrants had higher exploration scores compared to locally born birds ($F_{1,33} = 4{,}65$, $p = 0.039$), the relationship between exploration score and increase in median distance to the feeders was confounded by dispersal status, with immigrants moving further away compared to locally born birds (table 1).

Analyses of the rate in change in distance over time (average intercept = 4.72 ± 0.1, average slope (days) = 0.13 ± 0.03, both $p < 0.001$) revealed significant between-individual variation in both intercepts ($\sigma^2$ (s.e.) = 0.19 (0.07), $p = 0.002$) and slopes ($\sigma^2$ (s.e.) = 0.02 (0.001), $p = 0.005$). Exploration score was positively related to the intercepts of these movements, while immigrants had higher slopes (table 2, figure 2). This illustrates that, in general, fast explorers typically responded by a quick shift to other areas, while immigrants had a general tendency to gradually shift further away from the feeder.

## 4. DISCUSSION

We show that the exploration behaviour of great tits tested in laboratory conditions is related to their spatial response in the field to an experimental change in food availability. After removing food at feeding stations, all birds increased their home range size, but slow-exploring individuals remained relatively close to the feeder, whereas fast-exploring individuals quickly changed to foraging areas further away. To our knowledge, this study is the first to show that personality traits predict how individuals respond on a spatial scale to experimentally induced changes in their natural environment.

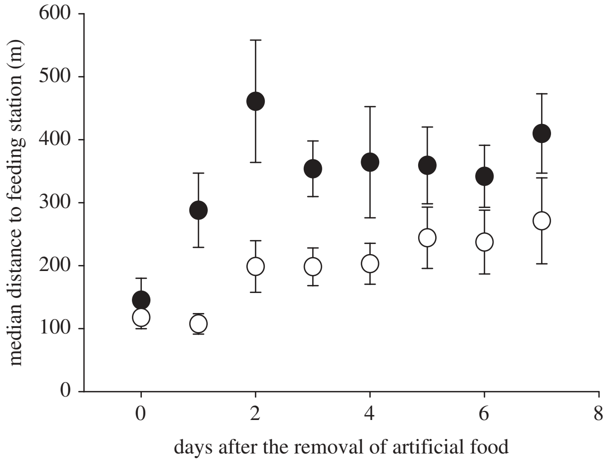

Figure 2. Difference between fast and slow explorers in median daily distance to the feeding stations after the food manipulation. Filled dots represent fast explorers ($n = 15$ range in exploration score 11–31) and open dots slow-explorers ($n = 19$ range in exploration scores 0–7). Note that in the analysis exploration score was used as a continuous variable and that distance was log-transformed.

The observation that fast explorers had a higher tendency to move away from the area of the feeder supports the idea of personality differences in the use of environmental information, as it suggests that fast and slow explorers had different knowledge about other locally available food resources, whereby slow birds switch to alternative food within or close to their pre-experimental home-range. However, the differences cannot easily be interpreted in terms of flexibility in behaviour, because fast explorers responded by rapid shifts to new foraging areas within one or two days after the manipulation, while slow explorers did this more gradually and on a smaller spatial scale. Furthermore, fast explorers did not show a more pronounced increase in home range, suggesting they tended to move to areas they already knew prior to the presence of artificial food rather than searching over wider areas. Fast and slow explorers may therefore not differ in the spatial extent of their foraging activities on a short time scale (i.e. home range size), but in the way they use past and current information to deal with changes in their current environment.

Few studies have studied the link between personality and space use, but those that did reported similar tendencies for proactive individuals to have a more explorative foraging strategy (Wilson & McLaughlin 2007) or move over larger distances (Boon *et al.* 2008). While these studies linked this variation to more general components of personality such as activity level and risk-taking behaviours, our results highlight the importance of experimental work in revealing how and when such personality differences are expressed. Furthermore, given recent findings showing relationships between personality variation and natal dispersal (Dingemanse *et al.* 2003; T. van Overveld 2009, unpublished data) and our finding that (fast) immigrants had a general tendency to move further away, such studies may also help to reveal how personality differences in reaction to environmental changes are linked to population dynamics in general.

Experiments in this study were done in accordance with University procedures concerning animal ethics.

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