

Personality traits in resident and migratory warbler species

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Summary

Animals are often confronted with environmental challenges and the way in which they cope with these challenges can have important fitness consequences. There is increasing evidence that individuals differ consistently in their reaction to the environment (personality traits). However, little is known about whether different life-styles (e.g., resident or migratory) influence personality traits and if so, in what manner.

We compared neophobic and exploratory behaviours, both of which play an important role in personality traits, between two closely related species, the resident Sardinian warblers and the migratory garden warblers, at two different times during the year. Neophobia was tested by placing a novel object, a mop, beside the feeding dish and measuring the latency to feed (neophobia score). Exploration was tested by offering another novel object, a tube, attached to a perch at a neutral location and measuring latency to approach and investigate the tube (exploration score). Both tests were carried out at the end of the breeding season and repeated ten months later in spring. The Sardinian warblers showed consistent behavioural reactions over time. Furthermore, neophobia and exploration scores were negatively related. The garden warblers neither behaved consistently over time nor was there a correlation between neophobia and exploration. Overall, Sardinian warblers were less neophobic and more explorative than garden warblers. The different reactivity may be due to a different frequency distribution of the individuals of the two species along a reactivity axis.

It can be concluded that the Sardinian warblers have personality traits. The situation is less clear in the garden warblers. Possibly, different life-styles require different organisation of behaviours.

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Introduction

Throughout life animals are confronted with social and non-social challenges in their environment, such as interacting with other animals or adjusting to changes in food distribution. Decisions about how to react to these challenges can have important fitness consequences at present and in the future, and may crucially affect whether or not an individual will survive. In recent years, evidence has accumulated that individuals have evolved different behavioural and physiological strategies to react to a great variety of challenges (e.g., Hessing et al., 1994; Wilson, 1998; McIntyre et al., 2003). These strategies, which are called coping styles (Koolhaas et al., 1999), personality traits (Budaev, 1997) or temperament (Visser et al., 2002), are characterised by the following patterns: a given individual usually uses the same strategy over time and often behavioural reactions are correlated across contexts (Wilson et al., 1994; Boissy, 1995). Furthermore, individual differences have a genetic component (Dingemanse et al., 2002; Drent et al., 2003; van Oers et al., 2004). Personality traits are often divided into different dimensions along which behaviours vary. Two important personality dimensions are approach and avoidance (Elliot & Thrash, 2002). The first dimension describes the willingness or motivation of an individual to approach and explore environmental challenges (often referred to as extraversion; Budaev, 1997), whereas the second describes how hesitantly an individual reacts to challenges (often referred to as neuroticism; Budaev, 1997). Several studies indicate that these two dimensions are mutually independent (Budaev & Zhuikov, 1998; Coleman & Wilson, 1998). From an evolutionary point of view it is thought that different personality traits are adaptive under different environmental conditions (Brick & Jakobsson, 2002; Dingemanse et al., 2003) which may be present in local microhabitats or may occur in temporal succession.

Because studies on personality traits concentrate on individual differences within species, little is known about the extent to which the range of behavioural reactions in one species overlaps with the range of reactions in another species. Comparative studies indicate that species differ in their exploratory (approach) and neophobic (avoidance) behaviours in relation to their ecological requirements and life-style (Greenberg, 1983; Mettke-Hofmann et al.,

2002; Mettke-Hofmann et al., 2005). For example, resident parrot species investigate novel objects in their familiar environment on average earlier than closely related nomadic species (Mettke-Hofmann et al., 2005). Similar results were found in closely related passerine species, depending on whether they have a resident or migratory life-style (Mettke-Hofmann, in prep.). As in the personality studies, exploration and neophobia were found to be influenced by different motivations and to be independent of one another (Wood-Gush & Vestergaard, 1991, 1993). In the above-mentioned studies, species' means were compared but no record was kept of individual reactions. Dingemanse (2003) postulated that species may not only differ in average personality but also in the trait frequency distribution, depending on the environment.

In the present study personality traits of two closely related passerine species, the Sardinian warbler (*Sylvia melanocephala momus*) and the garden warbler (*S. borin*), were investigated. The two species are closely related (Blondel et al., 1996; Shirihai et al., 2001) and have similar habitat and feeding preferences (Glutz von Blotzheim, 1991; Shirihai, 1996). However, they differ in their migratory behaviour. The garden warbler is a long-distance migrant, breeding in Europe and over-wintering south of the Sahara (Glutz von Blotzheim, 1991). The subspecies of the Sardinian warbler we have tested is a year-round resident in Israel (Abramsky & Safriel, 1980). Residents and migrants are confronted with different environmental challenges. Migrants encounter a variety of unfamiliar habitats and food sources and stay in a particular area for relatively short periods of time. Residents, in contrast, stay in the same area throughout the year and have to cope with seasonal changes in food abundance and distribution. The two species are already known to differ in their exploratory behaviour. Among the resident Sardinian warblers more individuals approached a novel object in their familiar aviary than was the case for the migratory garden warblers, and individuals of the former species spent more time within reach of the novel object than did those of the latter species (Mettke-Hofmann, in prep.). In the study reported here, we were interested in whether specific behavioural reactions in the two species are part of the personality syndrome and if yes, whether these traits differ between the species as an adaptation to different environmental challenges. Behavioural traits were investigated (1) by confronting the birds with a novel object beside the feeding dish and (2) by offering the same individuals another novel object at a neutral location in the familiar environment. In the first situation, the motivation to feed conflicts with the motivation to avoid the novel object

(neophobia). Therefore, in this situation neophobia is measured (Greenberg & Mettke-Hofmann, 2001; Mettke-Hofmann et al., 2002). In the second situation, the individual is not forced to approach and the intrinsic attractiveness of novelty can be tested. Here both approach and avoidance behaviour may be elicited. However, if the bird approaches the object this is motivated by the interest of the individual in the novel object (Mettke-Hofmann et al., 2002). This kind of experiment was also used in other studies on personality traits to test for exploration (e.g., Verbeek et al., 1994). Experiments were repeated ten months later to test for consistency of behavioural reactions.

Materials and methods

Subjects

Overall, 13 adult garden warblers and 15 adult Sardinian warblers were tested. Individuals of the two species were collected as nestlings in Germany and Israel, respectively. The garden warblers originated from seven nests, the Sardinian warblers from nine nests. No more than two siblings (four nests in each species) were tested from the same nest, except one nest in each species which contributed three siblings. Unrelated individuals originated from two and four nests in the garden and Sardinian warbler, respectively. After hand-rearing, they were kept in groups of six to seven birds per species in structured aviaries (2 × 1 × 2 m). Each species experienced its natural photoperiods, which were adjusted weekly. At the time of testing (both experiments) photoperiods were 16:38 / 7:22 hours (light/dark) for the garden warblers and 14:52 / 9:08 hours for the Sardinian warblers. All birds were three and a half years old. The Sardinian warblers consisted of ten females and five males, the garden warblers of four males, three females and six birds of undetermined sex (which were presumably females because they never sang).

All individuals had participated in a spatial memory test (Mettke-Hofmann & Gwinner, 2003) and a spatial exploration test (Mettke-Hofmann, Manthey, Schlicht, Schneider & Werner, in prep.).

Preparation for the experiment

The first part of the experiment took place in July after the breeding season of the birds. During that time garden warblers in the field are still

in their breeding area. Both species were in moult. Earlier experiments in both species have shown that moult does not influence exploration (Mettke-Hofmann et al., in press; Mettke-Hofmann, in prep.). One week before the experiment birds were transferred from the group aviaries to individual cages (75 × 40 × 40 cm) for habituation. One day prior to the experiment birds were moved to the experimental cages (65 × 50 × 60 cm). At that time they were weighted and their moult state was checked (for details see Mettke-Hofmann et al., in press). Experiments took place in two separate rooms with four experimental cages in each, located against the wall opposite to the door. The cages had three sides closed and a front side with bars and contained four perches. Food and water were provided ad libitum. The food was offered at the front side on a platform (16 × 11.5 cm). Only individuals of one species were in each room at a given time. In order to test all birds, those of each species were divided into four groups of four birds each (last group only the rest) and the groups were tested consecutively. Within species consecutive groups were allocated to different rooms. Experiments started at 8 o'clock in the morning.

Procedure

The experiment consisted of two tests, a neophobia test and an exploration test. In the neophobia test a novel object, a cotton mop (8 cm in diameter, Figure 1a, b), was introduced along with the food supplied as part of the daily morning routine. The object was placed on the platform beside the feeding dish and remained there until the bird had fed or for maximally 45 minutes. In the exploration test another novel object, a tube with holes that was attached to a perch (7.6 cm long and 2.2 cm in diameter, Figure 1c) was introduced into the cage by exchanging one of the normal perch dowels in the cage for the perch with the object attached. The object remained in the cage for 60 minutes. Although the two objects used differed to quite an extent from each other, qualitative differences in reaction are unlikely due to these differences because a variety of studies have shown that it is novelty and not the specific size, texture or shape of an object that elicits approach and exploration or avoidance (for a discussion of this point see Greenberg & Mettke-Hofmann, 2001). Furthermore, in earlier studies the cotton mop was used in an identical neophobia experiment with parrots eliciting strong neophobia (Mettke-Hofmann et al., 2002), whereas in a similar exploration experiment like in this study it elicited thorough exploration (Mettke-Hofmann et al., 2005).

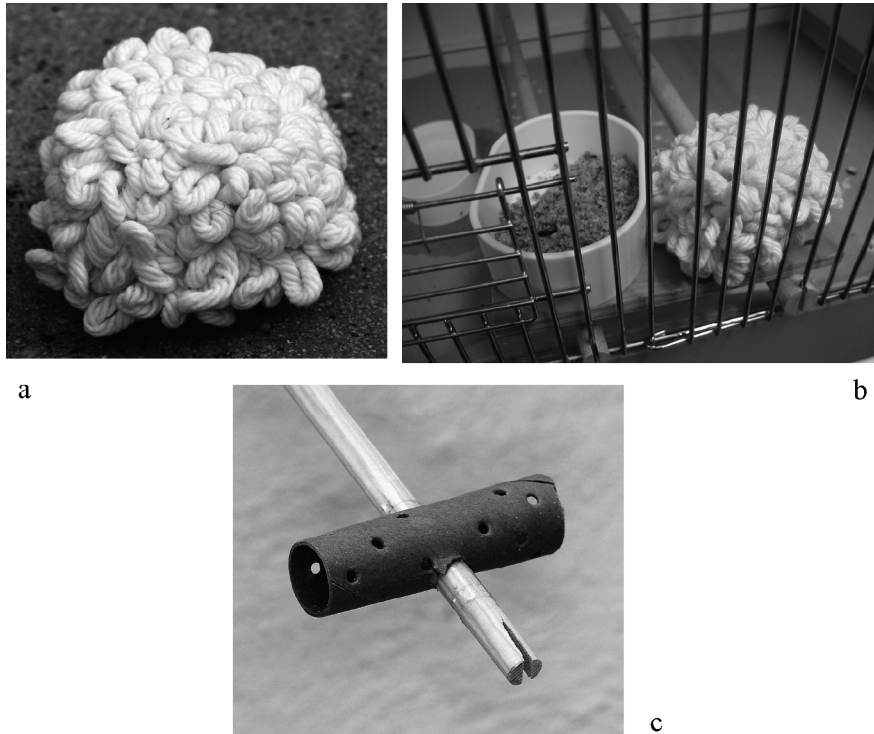


Figure 1. Novel objects used in the neophobia test and the exploration test: (a) cotton mop used in the neophobia test, (b) mop beside feeding dish, (c) tube attached to a perch in the exploration test.

Observations were made from outside through a one-way window. Before each test the activity of the birds was recorded for 10 minutes. For every 30 seconds of observation the activity level of the subjects was recorded (calm: the bird quietly perched without changing location and engaged in minimal preening or other activity; active: the bird changed perch usually three times or less, moderate feeding and/or preening behaviour; very active: multiple location changes, and/or agitated preening and stretching behaviour).

Neophobia tests always started at 8:00 a.m., exploration tests at 9:00 a.m. Individual birds experienced both tests on consecutive days. Always two birds in a group started with the neophobia test, whereas the other two started with the exploration test. In both tests observation started with introduction of the object. In the neophobia test every 30 seconds we recorded the activity of the birds as well as the latency to feed and whether the mop was

approached or touched. In the exploration test, we recorded the activity and whether the tube was approached within reach or touched during each 30 seconds of observation. Objects were immediately removed after the test.

The entire experiment was repeated 10 months later in May, at the beginning of the breeding season of both species. Nine garden warblers and 11 Sardinian warblers participated in this second part of the experiment. During that time none of the birds was in moult but the garden warblers still showed nocturnal activity (Gwinner, 1996; nocturnal activity was measured in the habituation cages with passive infrared detectors — Conrad Electronic, Germany). The second part of the experiment was prepared and performed in the same way as the first one. However, this time we additionally measured the latency to feed without objects (reference value) on the exploration day before the start of this experiment. Reference data are available for nine Sardinian warblers and eight garden warblers. In the second part of the experiment, the same objects were used and the birds experienced the objects in the same order and in the same room as before.

Analyses

The two species and the two parts of the experiment were analysed separately. Because of small sample sizes and unequal variances nonparametric tests were used (Spearman correlations if not indicated otherwise).

Before testing for correlations within and between behavioural traits we tested whether kinship has an influence on exploration and neophobia. Statistical testing of this point was restricted to the data of the exploration experiment because only these data met the assumptions required for a one-way ANOVA. Additionally, exploration and neophobia values were visually compared between siblings. Furthermore, we tested for differences in exploration and neophobia between sexes by use of the Mann-Whitney *U* test.

In the first part of the experiment, we were interested in whether neophobia and exploration were correlated. Latency to feed (neophobia test) was measured as the time elapsed between introduction of the food together with the object and the first 30-second period in which the bird fed. Latency to feed will further be referred to as neophobia score. Likewise, in the exploration test latency to approach and latency to touch the tube were measured as the time elapsed between introduction of the object and the first 30-second period with approach within reach of or tactile contact with the object. Birds

that did not approach or touch the object within the 60-minute period were each assigned a latency of 60 minutes. An exploration score was calculated for each individual as the mean of the two latencies. Latency to feed can be a function of how afraid an individual is of the novel object beside the feeding dish. However, differences in latencies can also be caused by different activity levels. The same applies to exploration latencies. Latency to explore can be a function of how interested an individual is in changes in its environment or it may depend on the activity level of the individual. Therefore, we calculated activity scores from the data collected directly before each test. For each bird, mean activity was calculated from the frequency of each activity class. Furthermore, body mass may influence the neophobia reaction (lean birds may approach earlier). Therefore, in a first step we tested for an association between neophobia score, activity and body mass with a Spearman correlation. Likewise, in the exploration test we tested for an association between exploration score and activity. In a second step, it was tested whether neophobia and exploration scores were correlated.

The second part of the experiment was conducted to test for consistency of behavioural reactions over time. Neophobia scores in the first and second part of the experiment were compared. Moreover, we subtracted the latency to feed without objects (reference value) from the neophobia score assessed in the second part of the experiment and re-run the correlation between the first neophobia score (not corrected for latency to feed without object) and the second neophobia score (corrected value) to test whether consideration of latency to feed without object changes the correlation. Furthermore, exploration scores in the first and second part of the experiment were compared.

Finally, we tested for species differences. Because sample size was larger here and data normally distributed, we used *t*-tests. Neophobia and exploration scores were compared between the two species. Furthermore, the two species were compared for their latency to feed without objects.

Results

First of all, in both species there was behavioural variation in the neophobia score, ranging from one and two minutes to 16 and 43 minutes in the Sardinian and garden warblers, respectively. Likewise, the exploration score varied from six minutes in the Sardinian warblers and 17 minutes in the garden warblers to 60 minutes in both species. The mop presented beside the

feeding dish never elicited exploratory behaviour, indicating that in this situation the novel object only elicited avoidance reactions.

Kinship seems to have no influence on the exploration score neither in the Sardinian warbler (One-way ANOVA: $df = 8$, $F = 0.337$, $p > 0.5$) nor in the garden warbler ($df = 6$, $F = 0.415$, $p > 0.5$). Likewise, visual inspection of the distribution of the data between related individuals revealed very different neophobia and exploration scores. Furthermore, we could not find a significant influence of sex on neophobia (Mann-Whitney U test: Sardinian warbler: $N = 15$, $z = -0.185$, $p > 0.5$; garden warbler: $N = 7$, $z = 0.000$, $p = 1$) or exploration (Sardinian warbler: $z = -0.492$, $p > 0.5$; garden warbler: $z = -0.441$, $p > 0.5$). Therefore, data of females and males were pooled.

Activity was correlated neither with the neophobia score (Sardinian warblers: $N = 15$, $r = 0.368$, $p > 0.05$; garden warblers: $N = 13$, $r = 0.000$, $p > 0.05$) nor with the exploration score (Sardinian warblers: $r = -0.194$, $p > 0.05$; garden warblers: $r = -0.042$, $p > 0.05$). Furthermore, body mass did not correlate with the neophobia score (Sardinian warblers: $r = 0.170$, $p > 0.05$; garden warblers: $r = -0.142$, $p > 0.05$). Thus, latency to feed as well as latency to approach and investigate the objects is the outcome of an active decision process.

In the first part of the experiment, a negative correlation between the neophobia score and the exploration score was found in the Sardinian warblers (Figure 2a; $N = 15$, $r = -0.564$, $p < 0.05$). Individuals with short latencies to feed in the neophobia test hesitated for a long time to approach and explore the tube on the perch. In contrast, the two variables did not correlate in the garden warblers (Figure 2b; $N = 13$, $r = 0.197$, $p > 0.05$).

We tested for consistency of both behavioural traits by comparing reactions in the first and the second part of the experiment. In the Sardinian warblers both traits, the neophobia scores (Figure 3a; $N = 11$, $r = 0.604$, $p < 0.05$) and the exploration scores (Figure 3b; $N = 11$, $r = 0.786$, $p < 0.01$), were correlated between the two parts of the experiment. In contrast, the garden warblers showed no correlation for either the neophobia scores (Figure 3c; $N = 9$, $r = 0.201$, $p > 0.05$) or the exploration scores (Figure 3d; $N = 9$, $r = 0.168$, $p > 0.05$). Consideration of the latency to feed without objects (reference value) in the second part of the experiment changed the correlation between the first and the second part of the neophobia experiment only marginally (Sardinian warbler: $N = 9$, $r = 0.748$,

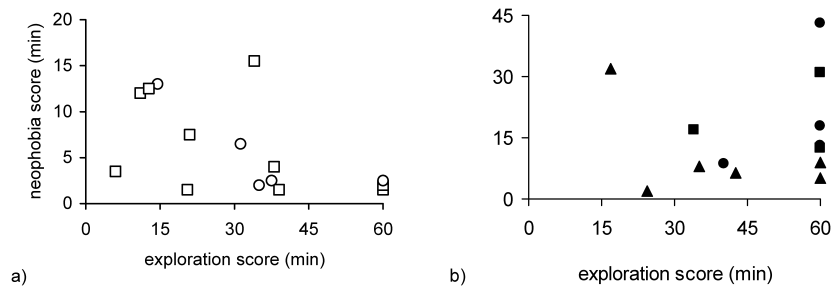


Figure 2. Correlation between neophobia score and exploration score in Sardinian and garden warblers. The neophobia score is plotted against the exploration score of each individual; (a) Sardinian warblers, (b) garden warblers. Circles: males, squares: females, triangles: undetermined sex.

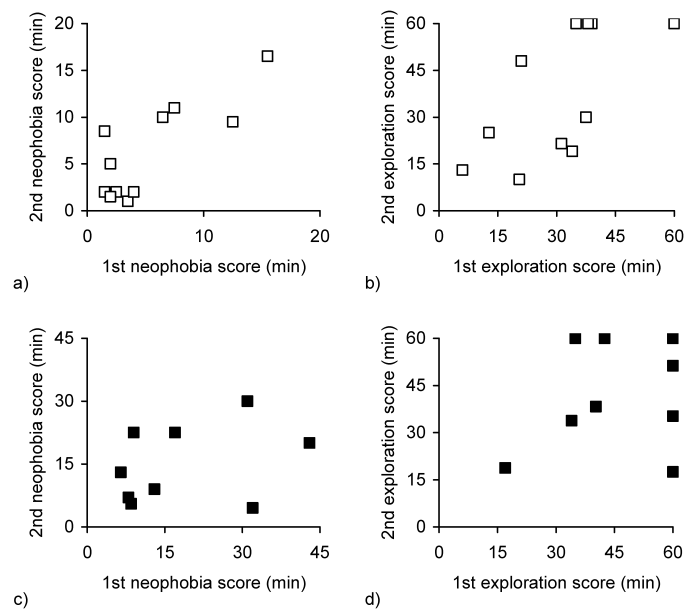


Figure 3. Consistency of behavioural traits over time in Sardinian and garden warblers. Neophobia scores in the first and second part of the experiment are plotted against each other, as are the exploration scores: (a) and (b) Sardinian warbler, (c) and (d) garden warbler.

$p < 0.05$; garden warbler: $N = 8$, $r = 0.214$, $p > 0.05$) indicating no influence of the reference value on the neophobia reaction. Indeed, in both species reference values were very low (Sardinian warbler: mean = 0.72 min; garden warbler mean = 0.38 min).

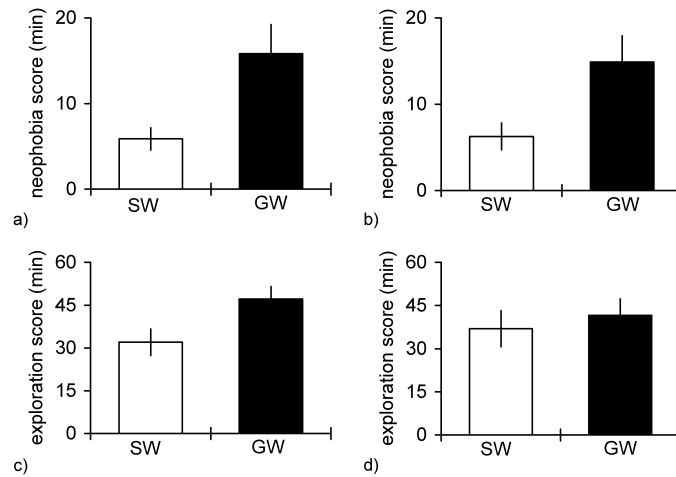


Figure 4. Species comparison. Mean values and SD-errors are given for Sardinian and garden warblers: (a) first part of the neophobia test, (b) second part of the neophobia test, (c) first part of the exploration test, (d) second part of the exploration test. SW: Sardinian warblers, GW: garden warblers.

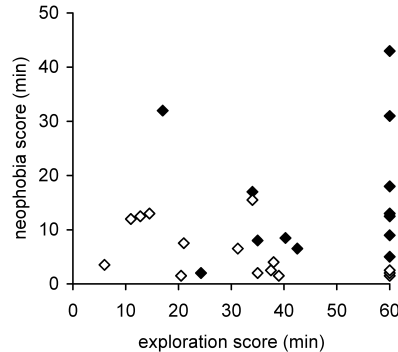


Figure 5. Distribution of individual reactions of both species along the same reactivity axis. Individual neophobia scores and exploration scores of both species in the first experiment are plotted against each other. White: Sardinian warblers, black: garden warblers.

Finally, reactions of the two species were compared. In both parts of the experiment, Sardinian warblers had on average significantly lower neophobia scores than the garden warblers (Figure 4a; 1st part: $df = 26$, $t = 2.729$, $p < 0.05$; Figure 4b; 2nd part: $df = 18$, $t = 2.524$, $p < 0.05$). Moreover, latency to feed without objects (reference value) did not differ between the two species (t -test: $df = 15$, $t = -0.983$, $p > 0.05$). Furthermore, in the

first part of the exploration experiment the Sardinian warblers explored on average significantly earlier than the garden warblers (Figure 4c; $df = 26$, $t = 2.345$, $p < 0.05$). In the second part of the exploration experiment, no species differences were found between the exploration scores (Figure 4d; $df = 18$, $t = 0.543$, $p > 0.05$). In Figure 5 individual neophobia scores and exploration scores of both species in the first part of the experiment are plotted against each other to show how the individual reactions of the two species are located along the same reactivity axis.

Discussion

In this study we investigated whether in garden and Sardinian warblers different behavioural reactions to challenges can be seen as part of the personality syndromes and thus indicate personality traits and whether these traits differ between the two species. We tested this by confronting the birds with a neophobia-eliciting situation and an approach-eliciting situation.

In both species, behavioural reactions varied considerably between individuals. Moreover, in the Sardinian warblers these variations were consistent over time (Figure 3a). Individuals that had low or high neophobia scores in the first part of the neophobia test behaved similarly in the second part of the neophobia test ten months later. Likewise, repeated exposure to a novel object attached to a perch resulted in individually consistent exploration scores (Figure 3b). This is in accordance with consistency of behavioural reactions over time, including exploration and neophobia in many other species ranging from fish (Budaev, 1997), to birds (Dingemanse et al., 2002; van Oers et al., 2004), to mammals (Reale et al., 2000; van Erp van der Kooij et al., 2002). It is likewise an important prerequisite for the existence of personality traits (Boissy, 1995; Koolhaas et al., 1999). Furthermore, in the Sardinian warblers behavioural reactions in the two contexts were correlated, though negatively (Figure 2a). Correlated behavioural reactions across context are usually interpreted as an indication for personality traits (Hessing et al., 1993; van Erp van der Kooij et al., 2002). Intuitively, a negative correlation of the two behavioural traits might be puzzling. However, individuals with a long latency to feed in the neophobia test (high neophobia score) and a short latency until they approached and investigated the object in the exploration test (low exploration score) reacted very strongly to

the environmental changes in both situations. In the neophobia test, this resulted in long latencies to feed because the novel object presented beside the feeding dish elicited avoidance reactions (neophobia; Greenberg & Mettke-Hofmann, 2001). In the exploration test, mainly neophilia (approach and exploration) was elicited (Mettke-Hofmann et al., 2002). Thus, a strong reaction to the novel object was reflected in an early approach. Conversely, individuals with a short feeding latency (low neophobia score) and a long latency until exploration (high exploration score) reacted only weakly to the changes, i.e., they showed little neophobia but also weak interest in the novel object in the exploration test. A negative correlation of behavioural traits was possible because different and independent motivations (Wood-Gush & Vestergaard, 1993; Mettke-Hofmann et al., 2002) were activated in the two situations. Studies using factor analyses have categorised approach motivation (boldness) and avoidance motivation (anxiety) on different personality dimensions (e.g., Mather & Anderson, 1993; Budaev, 1997; Elliot & Thrash, 2002). A negative correlation between behavioural traits across contexts was also found in bighorn ewes (*Ovis canadensis*) in which boldness, measured as the trappability of an individual, and docility during handling were compared (Reale et al., 2000). Taken together, the reaction of the Sardinian warblers was consistent over time and across contexts, indicating the existence of personality traits. However, although Sardinian warblers showed consistent reactivity across environmental challenges, the expression of behaviours differed situation-specifically depending on the personality dimensions involved.

In the garden warblers, the neophobic and exploratory reactions were not consistent over time (Figure 3c, 3d), nor was there a correlation of the two behavioural traits across contexts (Figure 2b). Several interpretations are possible, as follows. First, sample size might have been too small to detect significant correlations. In the Sardinian warblers, correlations within and between contexts ranged from 0.56 (between contexts) to 0.79 (within the exploration score), which is rather high (Reale et al., 2000; van Erp van der Kooij et al., 2002). Therefore, significant correlations were found even though sample size was small. However, weaker correlations might not be detectable with small sample sizes.

Second, season may have influenced reactions. The first experiment was carried out after the breeding season when the garden warblers were in moult, whereas the second experiment was done during the spring migration period

of the garden warblers. The different stages may have altered reactivity of the birds. Moulting is unlikely to have changed reactions at least in the exploration experiment because earlier studies in the garden warblers have shown that exploration does not change with moulting (Mettke-Hofmann et al., in press; Mettke-Hofmann, in prep.). Alternatively, migration may have altered reactions. In the garden warbler, mean latencies to explore and duration of exploration vary across the year. Exploration is highest in spring at the onset of the breeding season, whereas it persists on a low level for the rest of the year (Mettke-Hofmann, in prep.). Analysis of these data on an individual basis revealed no consistent reaction over the year (even when exactly the same phases were compared; Mettke-Hofmann, unpubl.), supporting the results of the present study. Nearly no data exist about consistent individual behaviours in other migratory species. Sih et al. (2003) investigated larvae of the sunfish-salamander (*Ambystoma barbouri*), which drift from pool to pool in order to survive until metamorphosis. The authors found behavioural correlations across situations, indicating that personality traits can exist in non-resident species. Similarly, in the migratory rainbow trout (*Oncorhynchus mykiss*) individual boldness and learning ability were correlated (Sneddon, 2003). However, in both studies this correlation was found within a specific developmental stage so that nothing can be said about behavioural correlations across different developmental stages (e.g., moving larval stages vs. resident adult stages or migratory and resident phases in the trout). Clearly, more research including different stages is required.

Third, several studies did not find behavioural correlations across contexts, although within contexts behaviours were consistent over time (e.g., Coleman & Wilson, 1998; Reale et al., 2000). It is argued that selection pressure may act differently in each situation, resulting in situation-(context-) specific reactions that are not necessarily correlated. Context-specific reactions may be present in the garden warblers as well. Context specificity can explain the lack of correlation between contexts and even within behavioural traits at different stages of the annual cycle (given that stationary and migratory stages are experienced by an individual as different contexts).

Finally, it is possible that garden warblers do not have personality traits. The various environments encountered may require very flexible behaviours. However, the observed consistency of behavioural traits in other species with migratory periods (Sih et al., 2003; Sneddon, 2003) makes this relatively unlikely.

Although we cannot clarify which of the explanations or combinations of them relate to the garden warblers, the garden warblers' reactions are likely to differ from those of the Sardinian warblers. Differences may exist only in the strength of correlations, but more profound differences in individual reactivity between the two species are possible. Clearly, more research is needed to confirm these results.

Before discussing the between-species differences a few words should be said about problems arising from such a comparison with respect to the investigation of personality traits. Holding and experimental conditions may influence behavioural reactions in the two species differently. The same holding conditions may favour a specific personality trait in one species and another in another species. Although we believe this scenario as less likely it cannot be excluded at the moment. Alternatively, one may expect that irrespective of the species one personality trait does better in captivity than another. This would shift the reaction to challenges to one or the other extreme making the discovery of species differences more difficult. As a consequence, the differences found in the Sardinian and garden warbler may not represent the entire breadth of differences in reactivity. Thorough studies about the influence of holding conditions on individual survival with particular personality traits across species are needed as well as more comparative studies in the field. Furthermore, the same challenges may mean different things to different species. However, Gosling & John (1999) showed that similar factors occur across species and that species differences in these factors are meaningful with respect to personality traits. Moreover, species comparisons allow us to examine the origins and adaptive significance of specific traits (Gosling, 2001). Another factor that may cause species differences in our study is the female biased sample in the Sardinian warbler which contrasts with the more balanced sex ratio in the garden warbler. However, we could not find differences in neophobic and exploratory reactions between sexes rendering this variable as a possible explanation for species differences relatively unlikely. Furthermore, sex did not play a role in other studies on neophobia and also on exploration in more than 25 parrot species (Mettker, 1993; Mettke-Hofmann et al., 2005) and the Sardinian warbler (Mettke-Hofmann, in prep.).

Direct comparison of the two species revealed differences in their mean reactivity. At both time points of testing, the Sardinian warblers were less neophobic and fed much earlier in the presence of the novel object than the

garden warblers (Figure 4a, 4b). This is surprising because migrants might have been expected to be less neophobic, particularly during the migratory period. Lower neophobia would be advantageous in making the birds less hesitant to come into an unfamiliar stopover site (Mettke-Hofmann & Greenberg, 2005). However, in the present study, object neophobia was tested. Possibly, hesitancy to enter a novel environment and to overcome neophobia to a novel object in the familiar environment are two distinct processes.

In the exploration experiment, the Sardinian warblers were at least in the first part of the experiment more explorative than the garden warblers (Figure 4c). This corroborates earlier findings in garden and Sardinian warblers (Mettke-Hofmann, in prep.) and several resident and nomadic parrot species (Mettke-Hofmann et al., 2005). Exploration of changes in the familiar environment is advantageous for a resident species that has to cope with seasonal changes, for example in food abundance and distribution, whereas it pays less to explore changes in the environment for a migrant that stays for relatively short periods in each area (Mettke-Hofmann, in prep.). Through exploration residents can discover new food resources comparatively quickly. These differences in object exploration go along with other differences in cognitive abilities between residents and migrants like the speed of assessment of a novel environment which is faster in migrants than in residents (spatial exploration; Mettke-Hofmann & Gwinner, 2004) or spatial memory persistence which is longer in migrants than in residents (Cristol et al., 2003; Mettke-Hofmann & Gwinner, 2003). These differences seem to be related to the different life-styles — resident or migratory — rather than to general differences in cognitive abilities (Mettke-Hofmann & Gwinner, 2003, 2004; Mettke-Hofmann & Greenberg, 2005). Species differences disappeared in the second exploration test (Figure 4d). This was mainly due to the shorter exploration latencies in the garden warblers, which is consistent with the seasonal variation in exploration (Mettke-Hofmann, in prep.).

The question remains: how were the individuals of both species distributed along a reactivity axis? Did individuals of the two species cluster at the opposite ends of the axis or were they intermixed? This is shown in Figure 5. In the neophobia test, the Sardinian warblers were concentrated in the lower part of the diagram (see data points along the y-axis), expressing relatively low neophobia. The garden warblers, in contrast, were distributed over the entire range, and thus included highly neophobic as well as less neophobic individuals. In the exploration test, both species covered nearly

the entire range of reactions (see data points along the x-axis) but the garden warblers were missing on the left side of the diagram (no rapidly exploring individuals) and concentrated more on the right side of the diagram (slow exploration). It should be mentioned that the exploration test was terminated after 60 minutes and therefore, the distribution is truncated at this point. Altogether, there was large overlap between individual reactions of the two species, suggesting more differences in frequency distribution than in the overall distribution. However, more data are needed to confirm this pattern.

In conclusion, the resident Sardinian warblers had strong correlations within the same behavioural trait over time as well as between different traits, indicating the existence of personality traits. The results in the migratory garden warblers are less clear and require further testing. Finally, there is the possibility of differences in frequency distribution in reactivity rather than of overall differences in reactivity between the two species.

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