

Spatial Neophilia and Spatial Neophobia in Resident and Migratory Warblers (*Sylvia*)

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Received: 10 July 2008

Initial acceptance: 8 October 2008

Final acceptance: 13 January 2009

(J. Kotiaho)

doi: 10.1111/j.1439-0310.2009.01632.x

Abstract

Residents and migrants use their environment very differently – the former remain in a given habitat throughout the year, whereas the latter are repeatedly confronted with unfamiliar environments. The difference in ecology may influence decision-making processes whether, when and to which extent to explore an unfamiliar environment. We have investigated spatial neophobia and spatial neophilia – two important novelty reactions that may underlie decision-making – in two closely related warbler species, the resident Sardinian warbler and the migratory garden warbler. Individuals of both species could access an unfamiliar room from a familiar cage. We assessed the conflict between the motivation to enter the novel room (spatial neophilia) and the motivation to avoid it (spatial neophobia) as the frequency and duration of perching on the dowel in the cage, which led to the unfamiliar room before entering it. Furthermore, we measured the latency to enter the novel room and compared the number of individuals of each species entering the room. The combination of the parameters measured allowed assessing the degree of both neophobia and neophilia. Finally, the time spent on each branch in the novel room was taken as a measure for spatial exploration. The migrants perched less often and spent less time on the dowel leading to the room, and entered the novel room quicker than the residents. Additionally, more migrants than residents entered the room. The migrants' decision to enter the novel room can best be explained with a combination of low spatial neophobia coupled with high spatial neophilia, whereas the residents' decision-making is best explained with high spatial neophobia coupled with high spatial neophilia. The differences in neophobia support the migrant-neophobia hypothesis. When in the room, the migrants spent less time on each branch than the residents, possibly indicating that the former collect less spatial information than the latter.

Introduction

Most animals live in changing environments and have to collect environmental information to reduce uncertainty and assess variability of the distribution

and quality of resources like food, mates or territories (Schwagmeyer 1995; Reed et al. 1999; Bruinzeel & van de Pol 2004) or the occurrence of predators (Edelaar & Wright 2006) for decision-making. However, little is known about the factors underlying

decision-making and how they are modulated under different environmental conditions. Animals assess their environment by relying on information collected individually ('personal information'; Day et al. 1998; Göth & Proctor 2002; Mettke-Hofmann & Gwinner 2003) or socially ('social information'; e.g. Swaney et al. 2001; Coolen et al. 2005). With respect to personal information, there are two simultaneously occurring basic behavioural reactions – approach and avoidance – when confronted with novel situations like an unfamiliar food source or habitat. The expression of each reaction varies independently from each other (Wood-Gush & Vestergaard 1993; Mettke-Hofmann et al. 2002). For example, an individual can be highly neophilic (attracted to novelty) and at the same time highly neophobic (repelled by novelty; two-factor model, Greenberg & Mettke-Hofmann 2001), resulting in an ambivalent behavioural response (e.g. common ravens, Heinrich 1988). Both reactions have a heritable component which in great tits (*Parus major*) is 54% and 19%, respectively (Drent et al. 2003; Van Oers et al. 2004). Novelty reactions are elicited as soon as a situation deviates from what has been experienced before (Berlyne 1966; Corey 1978), e.g. when encountering a new prey type or unfamiliar sites during dispersal or migration (Greenberg & Mettke-Hofmann 2001).

Object-related neophilia and neophobia differ between species in relation to their ecology and migratory strategy (Mettke-Hofmann et al. 2002, 2005b; Mettke-Hofmann 2006). When confronting parrots and songbirds with a change (a novel object) in their familiar environment, resident species explored the novel object more than closely related non-resident species (Mettke-Hofmann et al. 2005b; Mettke-Hofmann 2006). The results supported hypotheses derived from cost/benefit considerations (Mettke-Hofmann et al. 2005b; Mettke-Hofmann 2006). Shortly, residents benefit more when exploring changes in their familiar environment than migrants as the former remain in their territory year-round and can use the information later on whereas the latter stay in each area for only limited periods of time and cannot use the collected information in the long term. With respect to neophobia reactions, residents were less neophobic than migrants to feed from a familiar food dish with novel objects beside it under captive settings (Mettke-Hofmann et al. 2005a) and in the field (Mettke-Hofmann C., Hamel P. B., Winkler H. & Greenberg R., unpubl. data). Again, lower neophobia to approach changes in the familiar environment helps residents

to utilize resources ('get-away' hypothesis; Mettke-Hofmann et al. unpubl. data). However, how do residents and migrants react when confronted with a novel environment? There is increasing evidence that spatial and object-related information is learned and processed differently. For example, the hippocampal formation is an important brain region for processing spatial information. Damage to this region does impair spatial learning but not object-related learning (e.g. Sherry & Vaccarino 1989; Hampton & Shettleworth 1996). Furthermore, the right eye system shows a preference for object-specific cues, whereas the left eye system for spatial cues (Clayton & Krebs 1994). Finally, species that rely to a different degree on spatial information (e.g. food-storer and non-storer) differ in the kind of information stored – spatial or object-related (Brodbeck 1994).

Recently, Mettke-Hofmann & Greenberg (2005) proposed the migrant-neophobia hypothesis which states that migrants should be less neophobic than residents to enter a novel environment at least during migration. Migrants are repeatedly confronted with novel habitats while on migration, in which they stay for relatively short periods of time. Even though they may possess an innate template of their habitat, they have to explore unfamiliar sites to find food, shelter and so on (Mettke-Hofmann & Greenberg 2005). Many migrants act to maximize migration speed (Alerstam & Lindstrom 1990). Strong neophobic reactions to land in an unfamiliar environment (spatial neophobia) increase travel time and also prolong the time to get familiar with the new site. Reduced spatial neophobia may help to overcome hesitancy to enter an unfamiliar habitat, e.g. a stopover site. Residents, in contrast, are seldom confronted with novel habitats and being more neophobic helps them to avoid dangerous situations. The migrant-neophobia hypothesis, therefore, predicts the opposite from what has been found when investigating novelty reactions to changes in the familiar environment (Mettke-Hofmann et al. 2005a).

As in the novel-object situation, a novel environment not only elicits neophobic but also neophilic reactions. From a cost/benefit approach one may expect that migrants benefit more from both, being less repelled to enter novel environments (low spatial neophobia) and more attracted to novel environments (high spatial neophilia) than residents (two-factor model, Greenberg & Mettke-Hofmann 2001). As outlined above, a lower spatial neophobia may help to reduce hesitancy to enter an unfamiliar environment (migrant-neophobia hypothesis). However,

an individual also needs the motivation to enter a novel environment (spatial neophilia). As migrants are repeatedly confronted with unfamiliar environments they should be more interested in novel space. Residents do not face this challenge and may even risk losing their territory when engaging in spatial neophilia. Hence we expected migrants to show low spatial neophobia and high spatial neophilia, whereas residents to show high spatial neophobia and low spatial neophilia.

In this study, we investigated spatial neophobia (migrant-neophobia hypothesis) and spatial neophilia in two closely related warbler species – the migratory garden warbler and the resident Sardinian warbler. Both species live in comparable habitats and have a similar food spectrum (Glutz v. Blotzheim 1991; Shirihi 1996). However, they differ conspicuously from each other with regard to seasonal migration: The garden warbler breeds in Europe and migrates several thousands of kilometres to winter south of the Sahara (Glutz v. Blotzheim 1991). In contrast, the subspecies of the Sardinian warbler we have tested is a year-round resident of Israel (Abramsky & Safrieli 1980).

In an earlier study, spatial assessment was compared between these two species (Mettke-Hofmann & Gwinner 2004) in a small room (100 × 80 × 120 cm, H × W × L) that was decorated with silk plants. Besides testing how spatial neophobia and neophilia influence decision-making to enter an unfamiliar room (which has not been tested before), the current study allowed further investigating whether the earlier findings on spatial assessment can be confirmed in a different setting.

Novelty reactions play a crucial part in how animals deal with unfamiliar situations as these reactions determine whether and when an individual will approach and learn about the novel situation (Seferta et al. 2001). Understanding under which ecological circumstances animals approach or avoid novelty leads to a better picture about the evolutionary forces that have shaped species differences in learning and decision-making.

Methods

Subjects

Fourteen hand-raised garden warblers (from six nests) and 22 hand-raised Sardinian warblers (from 10 nests) were available for the experiment. All birds had been collected in southern Germany (garden warblers) and Israel (Sardinian warblers) as nes-

tlings about 2.5 yr prior to the experiment. After hand-raising, birds were kept in groups of six in aviaries (1 × 2 × 2 m) under simulations of their respective natural photoperiods. At the time of testing, photoperiods ranged from 1254 to 1226 h light in the garden warblers and from 1254 to 1212 h in the Sardinian warblers according to the changing photoperiod during that time of the year (Sep–Oct). Photoperiods were adjusted weekly. Aviaries were structured with twigs and branches to provide various opportunities for perching as well as refuges. A special insectivorous diet (Gwinner et al. 1988), a pollen mixture (Mettke-Hofmann et al. 1997), live mealworms and water were daily provided *ad libitum*. Minerals and vitamins were provided once a week. The birds had been subjected to a memory retention test a year before (Mettke-Hofmann & Gwinner 2003).

Experimental Design

The present experiment took place in Sep/Oct, during the naturally occurring autumn migration period of the garden warblers. Autumn was selected because differences in novelty reactions and environmental assessment should be greatest when the migrant has to deal with unfamiliar environments and the resident remains in its familiar ground. Only those garden warblers that were in migratory disposition were tested (see below), excluding the possibility of seasonal variation in exploration (Mettke-Hofmann 2006) related to actual migration.

Experiments were carried out in two experimental rooms (320 × 175 × 300 cm) with four and five artificial trees, respectively (Fig. 1). The number of trees differed because of a difference in arrangement of the heating system between the two rooms. However, the difference in the number of trees allowed having the same distance (approx. 1 m) between neighbouring trees in both rooms. The trees were 170 cm tall with four perches of 50 cm length each. The upper two perches were positioned opposite to each other 10 cm below the tip of the main trunk. The lower two perches were positioned perpendicular and 30 cm below the upper perches. In one corner of each room was a cage (home cage; 75 × 40 × 40 cm) which was kept at a height of 1 m from which the experimental bird could enter the room. The cage had three perches, two elevated on the right and left side and one near the bottom in the middle of the cage which led directly to the cage door. Garden and Sardinian warblers were equally distributed between the two experimental rooms.

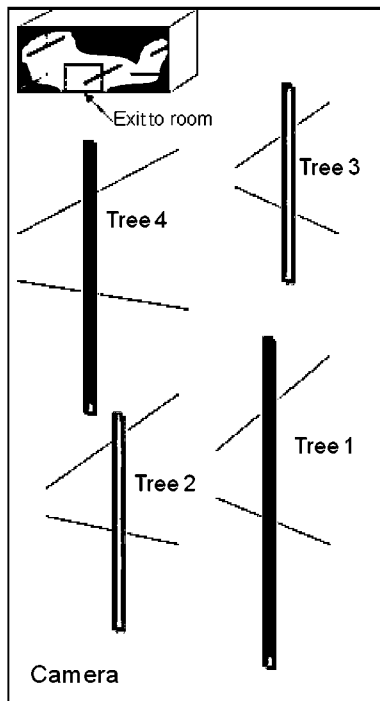


Fig. 1: Schematic drawing of the experimental room (not to scale; design follows Verbeek et al. 1994).

Experimental Procedure

For the experiment, birds of both species were caught in the aviaries and kept in individual cages (75 × 40 × 40 cm) in the holding room for 1 wk to be habituated to the cage. In the experiment an identical cage served as a familiar home cage. In the cage, nocturnal activity of the garden warblers was measured with passive infrared detectors (Conrad Electronic, Hirschau, Germany). After 1 wk, garden (only those that exhibited nocturnal activity; Gwinner 1996) and Sardinian warblers were caught in the morning and transferred to the home cage in one of the two experimental rooms. Food and water were provided ad libitum in the home cage. After a 30-min habituation phase one of the experimenters opened the door of the home cage. The experimental bird had 45 min to leave the home cage. If it left the home cage it was allowed to explore for 30 min. A video camera recorded the behaviour in the home cage and the experimental room. After this, the bird was caught and transferred to the holding aviaries.

Statistical Analyses

Before testing for spatial neophobia and neophilia we tested whether kinship had an influence on

these traits. Ideally, kinship would be included in the general analysis. However, except one garden warbler nest and four Sardinian warbler nests contributing three young, nests were represented with one or two young only, which is an insufficient sample size within groups. We, therefore, statistically compared only those nests with more than one young by using a one-way ANOVA. Statistical testing of this point was restricted to the garden warblers and here to: (a) the latency to enter the room; (b) the number of branches visited in the room; and (c) the latency to reach the last branch in the room because only these variables met the assumptions required for a one-way ANOVA. However, all variables were visually compared between siblings of both species.

Behaviour in the home cage

Based on the two-factor model (Greenberg & Mettke-Hofmann 2001), four main combinations of spatial neophilia and neophobia can be distinguished: (a) low spatial neophobia coupled with high spatial neophilia; (b) high spatial neophobia coupled with high spatial neophilia; (c) low spatial neophobia coupled with low spatial neophilia; and (d) high spatial neophobia coupled with low spatial neophilia. Our experimental design allowed distinguishing between these combinations.

As a bird's novelty behaviour is influenced at the same time both by its neophilia and its neophobia, it is difficult to measure neophilia and neophobia separately despite the fact that both novelty reactions are intrinsically independent. With our experimental design we attempted at identifying associations of high or low neophilia and neophobia by combining two measures. On the one hand, we assessed the conflict between the motivation to enter (spatial neophilia) and avoid the novel room (spatial neophobia). For this we counted the frequency and measured the duration of perching on the lower dowel which directly led to the open cage door until the bird entered the novel room. The birds usually prefer the elevated perches and garden and Sardinian warblers do not differ in the use of the lower perch in their home cage (C. Mettke-Hofmann unpubl. data). Perching on the lower perch indicates interest in the novel environment (spatial neophilia). However, spatial neophobia may hinder the bird from immediately entering the novel environment and it may jump back and forth between the upper and lower perch. Thus, repeated and prolonged perching on the lower perch indicates a conflict

between the motivation to enter the novel environment (spatial neophilia) and to avoid it (spatial neophobia). This measure was already successfully used to distinguish conflicting behaviour when confronted with novel objects (Mettke-Hofmann et al. 2006). The higher the frequency/duration of perching on the lower perch is before entering the novel room the larger the conflict between spatial neophobia and spatial neophilia. Differences in this value between the two species were tested with a t-test. The comparison was restricted to birds that had been tested in one of the experimental rooms (garden warbler $n = 7$, Sardinian warbler $n = 12$) because data of the other room were lost during data backup because of computer failure (the data that are still available were collected with a videotape system). Both variables were log-transformed to reach normally distributed data.

On the other hand, we measured the latency to enter the novel room which was the time between the opening of the door of the home cage and the bird flying into the experimental room. This measure has generally been accepted as representing novelty reactions rather than escape behaviour as the animal is free to enter the novel room or stay in the cage (Corey 1978; Fernandez et al. 2002; King et al. 2003). Birds that did not enter the room received a latency of 45 min. We compared latencies of all birds ($n = 36$) as well as of only those that had entered the experimental room ($n = 25$). Latencies of the two species were compared with the Wald test (Genstat 1993) which allowed including the two rooms as a random factor. To reach normally distributed data latencies were rank-transformed.

Each of the two measures alone – the frequency/duration to perch on the lower perch and the latency to enter the novel room – do not allow determining the contribution of neophobia and neophilia to the decision to enter the room. However, the combination of both does. Individuals having:

(a) *low spatial neophobia and high spatial neophilia* are highly motivated to enter the novel environment and are not very afraid of it. Therefore, they are expected to have a low frequency and short duration of perching on the lower perch as there is little conflict between the decision to enter the novel room and to avoid it. Furthermore, they are expected to enter the novel room quickly as they are motivated to do so (spatial neophilia) and are not hindered by high spatial neophobia.

(b) *high neophobia and high neophilia* are highly motivated to enter the novel room but are also afraid to do so resulting in a high frequency and

long duration of perching on the lower perch (high conflict between the motivation to enter and avoid the novel room). The latency to enter the novel room is expected to be moderate to long as a consequence of the high neophobia.

(c) *low neophobia and low neophilia* are not very interested in entering the novel room but are also not afraid of it. Because of the low interest in the room individuals will seldom perch on the lower perch and will also spend short times on this perch (no conflict). Latency to enter the novel room will be long (no interest).

(d) *high neophobia and low neophilia* are not very interested in the novel room but are also highly afraid of it. Again, individuals are expected to show a low frequency and short duration of perching on the lower perch. Latencies are expected to be long.

Combinations (c) and (d) cannot be distinguished with our approach but all other combinations are separable. Independence between the variables mentioned above was tested with Spearman test (because of low sample sizes; garden warbler $n = 7$, Sardinian warbler $n = 12$). Furthermore, we compared the number of individuals entering the experimental room between the two species (crosstabs; $n = 36$).

Differences in latencies might be related to the activity of a bird. Earlier studies, however, have shown that neophilia/neophobia latencies and activity are never correlated, neither in the warblers (Mettke-Hofmann & Gwinner 2004; Mettke-Hofmann et al. 2005a) nor in a variety of parrot species (Mettke-Hofmann 2000; Mettke-Hofmann et al. 2005b). Thus, latencies were expected to represent a measure of novelty reaction.

Behaviour in the room

Initially, we had three measures of spatial exploration (following Verbeek et al. 1994). We measured the time elapsed between entering the room and landing on the last new branch; calculated the percentage of available branches visited; and calculated the mean duration spent on each branch until the last new branch was reached. However, as these variables were correlated with each other in the garden warbler (Spearman corr.: r^2 range 0.61–0.84, $p < 0.05$), we restricted these analyses to the mean time spent on each branch. Data were log-transformed.

Not all individuals that had entered the experimental room proceeded in assessing the room. Some landed on the ground and did not return to the perches. These birds were excluded from the spatial

assessment analysis. A Wald test with the variable room as a random factor was used to test for differences in spatial exploration between those garden ($n = 11$) and Sardinian warblers ($n = 7$) that had investigated the experimental room. All analyses were performed with SPSS 14.0 except for the Wald test which was conducted with Genstat.

Housing, maintenance and experimental conditions were in agreement with the legal requirements of Germany. Licences for the collection and keeping the garden warblers were obtained from the Regierungspräsidium Freiburg. Licences for the collection and export of the Sardinian warblers were granted by the 'Israel Nature and National Parks Protection Authority' and licences for import and keeping these birds from the Bayerisches Staatsministerium für Arbeit und Sozialordnung, Familie, Frauen und Gesundheit.

Results

Kinship had no influence on the latency to enter the room in the garden warbler (one-way ANOVA: $df = 5$, $F = 1.704$, $p = 0.239$) or to reach the last branch in the novel room ($df = 4$, $F = 1.273$, $p = 0.376$). However, the number of branches visited was more similar among siblings than unrelated garden warblers ($df = 4$, $F = 4.677$, $p = 0.047$). Visual inspection of all variables in both species revealed very different reactions between related individuals except the variable 'time spent on the lower dowel'. In the Sardinian warbler, related individuals spent similar amounts of time on the lower dowel. We, therefore, calculated means of siblings for the variable 'time spent on the lower dowel'. For all other variables we used individual values because of the low impact of kinship on reactions.

Behaviour in the Home Cage

In the home cage, we measured the frequency and duration of perching on the lower perch as well as the latency to enter the novel room. The three variables were not correlated with each other (Spearman corr.; frequency vs. duration: garden warbler: $n = 7$, $r = -0.001$, $p = 0.998$, Sardinian warbler: $n = 12$, $r = 0.075$, $p = 0.818$; frequency vs. latency: garden warbler: $n = 7$, $r = 0.397$, $p = 0.378$, Sardinian warbler: $n = 12$, $r = 0.323$, $p = 0.305$; duration vs. latency: garden warbler: $r = 0.214$, $p = 0.645$, Sardinian warbler: $r = 0.325$, $p = 0.303$).

The garden warblers perched significantly less often and for a shorter period of time on the lower

perch than the Sardinian warblers (Fig. 2; t-test; frequency: $t_{19} = -2.931$, $p = 0.009$; duration: $t_{19} = -2.993$, $p = 0.008$). These data were confirmed when only considering birds that had finally entered the novel room (frequency: $t_{13} = -2.644$, $p = 0.023$; duration: $t_{13} = 2.278$, $p = 0.044$). Considering an influence of kinship on the variable 'time spent on the lower perch' we repeated the test with means of siblings. The significance dropped to a nearly significant value which was possibly due to the low sample size in the garden warbler (garden warbler $n = 5$, Sardinian warbler $n = 9$, $t_{14} = -2.131$, $p = 0.054$).

Furthermore, garden warblers had significantly shorter latencies to enter the experimental room than Sardinian warblers (Wald test: $df = 1$, $n = 36$, $\chi^2 = 8.94$, $p = 0.003$). However, when considering latencies of only those birds that finally entered the experimental room latencies did not differ between the two species ($df = 1$, $n = 25$, $\chi^2 = 1.70$, $p = 0.192$). Finally, 13 of 14 garden warblers but only 12 of 22 Sardinian warblers entered the novel room (Fig. 3; crosstabs: $df = 1$, $\chi^2 = 5.918$, $p = 0.015$).

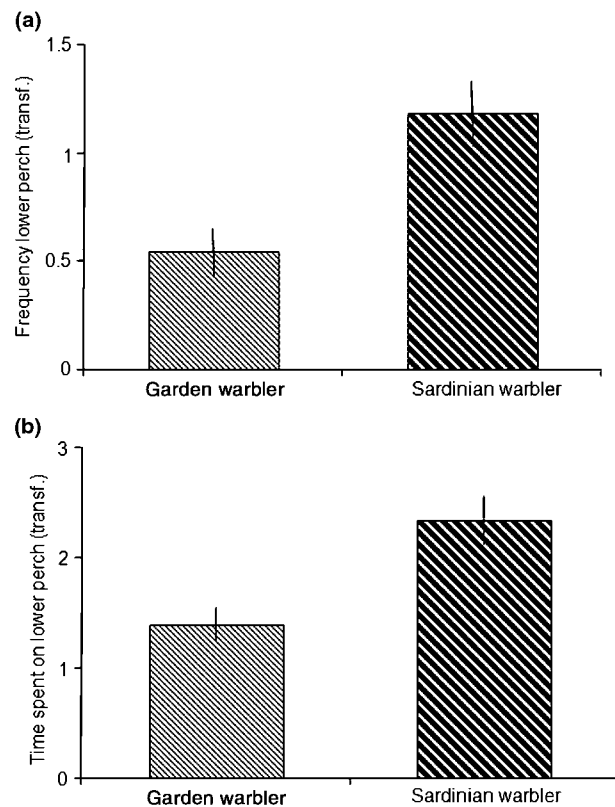


Fig. 2: Spatial neophobia. Mean frequency (a) and duration (b) \pm SE of perching on the lower perch in the cage are shown for garden and Sardinian warblers.

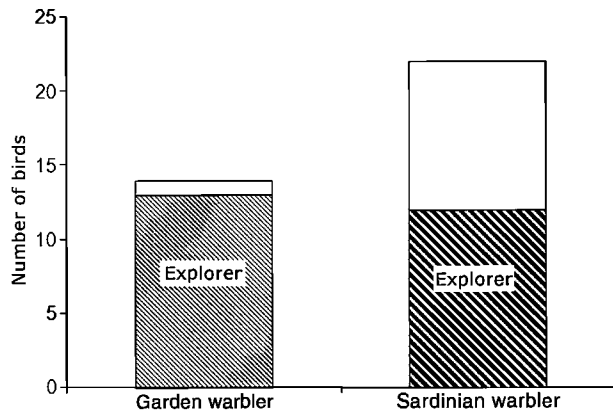


Fig. 3: Number of birds entering the room (spatial neophilia). The total number of garden and Sardinian warblers tested (white) and the number of birds entering the unfamiliar room (explorer; grey) are shown.

Behaviour in the Room

The garden warblers spent on average significantly less time on each branch than the Sardinian warblers (Fig. 4; Wald test: $df = 1$, $n = 18$, $\chi^2 = 6.43$, $p = 0.011$). After the birds had reached the last new branch they all soon became inactive and perched on a branch until the end of the experiment.

Discussion

The study compared spatial neophobia and neophilia as well as spatial assessment of a novel environment in a migratory and a resident species. Before starting with the main discussion we will shortly expand on the applicability of this two-species study on residents and migrants in general. Differences in cognitive abilities between residents and migrants have been documented in a variety of species. For example, it has been shown in several songbirds that migrants have a better spatial memory than residents (Cristol et al. 2003; Mettke-Hofmann & Gwinner 2003; Pravosudov et al. 2006) which is accompanied by differences in the hippocampal formation (Healy et al. 1996; Cristol et al. 2003; Pravosudov et al. 2006). Furthermore, novelty reactions to environmental change differ with life-style not only in the two warbler species (Mettke-Hofmann 2006) but also in New World blackbirds which were tested in the wild (Icteridae: Mettke-Hofmann C., Hamel P. B., Winkler H. & Greenberg R., unpubl. data) and in parrots (Mettke-Hofmann et al. 2005b). Moreover, the two species in investigation have a very similar ecology with respect to foraging and habitat

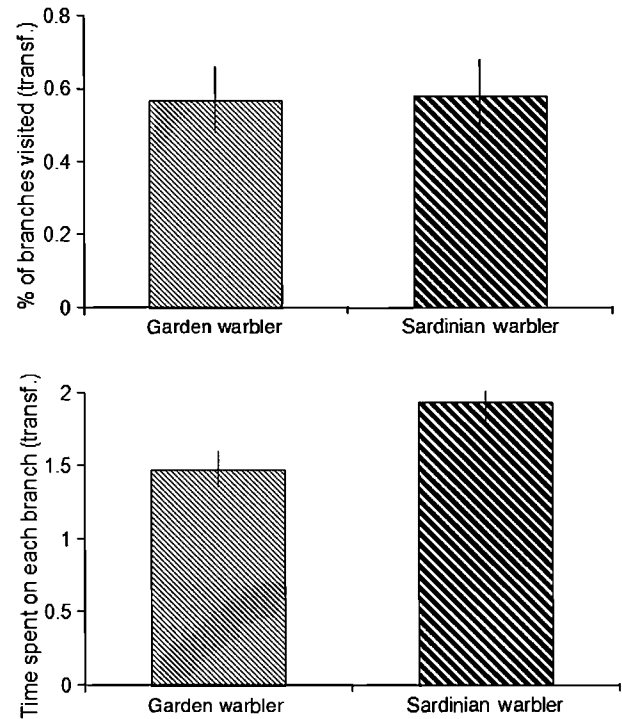


Fig. 4: Spatial assessment. Mean time spent on each branch \pm SE are shown for garden and Sardinian warblers.

requirements as well as social organization, making it unlikely that these factors are responsible for the species differences. Finally, generalization from hand-reared birds to wild birds may be problematic. However, neophilia and neophobia have a substantial heritable component (Drent et al. 2003; Van Oers et al. 2004). Furthermore, earlier studies on parrots originating from the wild or from captivity yielded consistent results in neophobia and neophilia reactions (Mettke-Hofmann et al. 2002, 2005b). The object neophobia results from the warbler study (Mettke-Hofmann et al. 2005a) were confirmed by a comparison of eight blackbird species in the wild (C. Mettke-Hofmann et al. unpubl. data). Last but not least, experiments on memory persistence in hand-raised (Mettke-Hofmann & Gwinner 2003) and wild-caught (Scriba M., Mettke-Hofmann C. & Rattenborg N. unpubl. data) garden and Sardinian warblers that included spatial exploration of two novel rooms revealed identical behaviour of the captive-reared and wild-caught birds in the novel rooms making a strong influence of rearing experience unlikely. Therefore, the differences found are probably an adaptation to a resident or migratory life-style. However, more data from a larger set of species are needed.

Behaviour in the Home Cage

In the home cage we tested in how far spatial neophobia and spatial neophilia influence decision-making to enter a novel environment. Before entering the novel room the resident Sardinian warblers perched more often and for a longer time on the lower perch than the migratory garden warblers (Fig. 2), indicating that the residents had a larger conflict between attraction to and avoidance of the novel room than the migrants. Furthermore, fewer individuals of the Sardinian warbler entered the novel room than of the garden warbler (Fig. 3) and latencies to enter the room were longer in the former than in the latter, although this difference disappeared when only considering birds that entered the room. The results indicate that the decision to enter the novel room in the garden warblers was influenced by low spatial neophobia coupled with high spatial neophilia as they showed little conflict between attraction to and avoidance of the novel room and entered the novel room quickly. The decision of the Sardinian warblers, in contrast, was influenced not only by high spatial neophobia but also high spatial neophilia, as they showed a much stronger conflict between attraction to and avoidance of the novel room than the garden warblers. The results support our expectation that the migratory garden warblers are highly motivated to enter a novel environment and are also little afraid to do so, whereas the resident Sardinian warblers are much more neophobic to enter the novel room. However, contrary to expectations the Sardinian warblers seem to be similarly interested in the novel room as the garden warblers.

The lower spatial neophobia in the garden warblers when compared with the Sardinian warblers is in concordance with the migrant-neophobia hypothesis (Mettke-Hofmann & Greenberg 2005). Migrants that are repeatedly confronted with unfamiliar environments, e.g. on migration, benefit from being less hesitant to enter a novel environment as it speeds up the process of environmental assessment and hence, the speed of migration. Residents, in contrast, are seldom confronted with novel environments and a heightened spatial neophobia protects them from encountering dangerous situations outside their territory. However, although low spatial neophobia favours a rapid assessment of an unfamiliar surrounding, an individual still needs to be motivated to finally enter a novel environment (spatial neophilia). This was the case in the garden warbler as nearly all individuals rapidly entered the novel room

(Fig. 3). In contrast, only half of the tested Sardinian warblers entered the novel room. However, if they did so they entered the room as fast as the garden warblers. The latter result corroborates earlier findings in the two species (Mettke-Hofmann & Gwinner 2004) and indicates that the individuals of both species that were willing to enter the novel room showed high spatial neophilia although the reasons for its adaptiveness may differ (e.g. territory assessment in the residents, stopover site assessment in the migrants). From a cost/benefit approach it was expected that residents gain little when entering a novel environment unless they search for a new territory (Mettke-Hofmann & Greenberg 2005). The results show that collecting information about the surrounding environment may be of more importance for a resident than originally thought. Knowledge about neighbouring territories, resources and competitors has been shown to be advantageous when occupying territories or searching for mates (Stamps 1987; Schwagmeyer et al. 1998; Bruinzeel & van de Pol 2004). Therefore, residents may show the same degree of spatial neophilia as migrants.

Taken together, the migrants showed low spatial neophobia and high spatial neophilia favouring a rapid entering of a novel environment, whereas the residents showed not only high spatial neophobia but also high spatial neophilia resulting in a conflict to enter or avoid a novel environment which finally leads to a longer latency to enter an unfamiliar site.

The lower spatial neophobia in the migrants when compared with the residents is in contrast with the reactions when changes occur in the familiar environment. Here the migratory garden warblers reacted with stronger neophobia than the resident Sardinian warblers (Mettke-Hofmann et al. 2006; see also C. Mettke-Hofmann et al. unpubl. data for Icteridae). In the object neophobia test, a novel object is placed beside the feeding dish and the latency is measured to resume feeding. In the wild this may correspond to a situation in which the resident regularly feeds on a field in its territory and one day finds several scarecrows standing on this field. It could avoid the areas around the scarecrow but at the cost of losing substantial feeding ground. Low (object) neophobia allows the resident to rapidly test for the dangerousness of the situation and if this is low to exploit the resource further before other animals may take advantage of it. In the long run this helps residents to maintain year-round residency. In contrast, given that residents are usually not forced to leave their familiar sites, spatial neophobia protects them from encountering unfamiliar and

potentially dangerous sites. The situation is opposite in migrants. Consider again the example with the scarecrow. The object neophobia experiment requires that the bird is familiar with its environment, or else it cannot discover a change in it. In the scarecrow example this would mean that a migrant is already feeding on a field for a couple of days before it is confronted with scarecrows on this field. Other than a resident, the migrant is not bound to this particular site and may move somewhere else for foraging to avoid this potentially dangerous situation (C. Mettke-Hofmann et al. unpubl. data). With respect to spatial neophobia in migrants, we have already discussed the advantage of being less neophobic when entering an unfamiliar site while on migration.

Thus, depending on the context (novel environment, change in the familiar environment), residents and migrants may have evolved different reactions. As mentioned in the Introduction, spatial and object-related information is processed differently (Sherry & Vaccarino 1989; Clayton & Krebs 1994) and animals differ in the types of information stored depending on their ecology (Brodbeck 1994). The contrasting novelty reactions in relation to changes in the familiar environment (object-related) and to a novel environment as shown in this study add to these differences.

Behaviour in the Novel Room

Despite the fact that more migrants than residents were motivated to enter the unfamiliar room, the former did not explore more than the latter. In fact, the residents spent on average more time on each branch than the migrants (Fig. 4). This difference can be interpreted in two ways. First, the migratory garden warblers may be better adapted than the resident Sardinian warblers to collect spatial information in a short period of time, thus needing less time to collect the same amount of information as the latter. Secondly, by spending less time on each branch the garden warblers may have collected less information than the Sardinian warblers (Verbeek et al. 1994). With respect to the first scenario, although relative brain size (Sol et al. 2005) as well as relative forebrain size (Winkler et al. 2004) are smaller in migrants than in residents Pravosudov et al. (2006) showed that migratory white-crowned sparrows (*Zonotrichia leucophrys gambelii*) have a larger hippocampal formation relative to the rest of the telencephalon than resident conspecifics of the subspecies *Z. l. nuttalli*.

Likewise, migratory dark-eyed juncos (*Junco hyemalis hyemalis*) have more densely packed hippocampal neurones than resident dark-eyed juncos (Cristol et al. 2003). The hippocampal formation is a very important brain region for processing spatial information (e.g. Healy et al. 1996). Its relatively larger size in migrants despite the otherwise smaller forebrain emphasizes the importance of spatial information for migrants. Therefore, it is possible that migrants have faster learning abilities than residents. However, an increasing number of field studies show that migrants do not move much in a stopover site (often not more than 500 m; Aborn & Moore 1997; Chernetsov 2005; Matthews & Rodewald 2006; Van Riper et al. 2006) and in a pattern that would indicate little information gathering (high linearity and low turn bias; Aborn & Moore 1997). Aborn & Moore (1997) therefore, suggested that migrants have only a superficial knowledge about a stopover site. As migrants stay for only short periods in each site they do not need a detailed knowledge about the site. A rough overview about high- and low-quality stopover sites is sufficient. Differences in spatial assessment in garden and Sardinian warblers support this latter view (Mettke-Hofmann & Gwinner 2004). However, more research is needed to clarify these findings further. When residents investigate a new site it may be to find a new territory. They need detailed information not only about the current situation but also about the long-term suitability of a prospective territory (for a more detailed discussion of this point, see Mettke-Hofmann & Gwinner 2004). In line with this, residents spent more time than migrants exploring the novel room. The data confirm earlier findings on spatial assessment in these two species (Mettke-Hofmann & Gwinner 2004) which were derived from a much smaller room with intensive plant decoration.

To conclude, resident Sardinian warblers and migratory garden warblers differ in their spatial neophobia possibly as an adaptation to their life-style (migrant-neophobia hypothesis). During the migratory period, migrants are less neophobic to enter an unfamiliar environment than residents. This may help migrants to cope with the repeated confrontation with novel sites while on migration. However, the migrants spent less time to explore a novel environment than the residents as the former may only need a superficial knowledge about their environment. The differences found add to the differences in cognitive abilities already known in residents and migrants.

Acknowledgements

Part of the study was conducted during the Summer School 'Spatial Memory and Cognition'. We would like to thank the Max Planck Institute for Ornithology, Andechs, and the German Zoological Society for financial support of this Summer School. We also thank Barbara Helm for conducting the Genstat analyses.

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