ORIGINAL PAPER

Migratory and resident blue tits *Cyanistes caeruleus* differ in their reaction to a novel object

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Abstract Individuals differ consistently in their behavioural reactions towards novel objects and new situations. Reaction to novelty is one part of a suit of individually consistent behaviours called coping strategies or personalities and is often summarised as bold or shy behaviour. Coping strategies could be particularly important for migrating birds exposed to novel environments on their journeys. We compared the average approach latencies to a novel object among migrants and residents in partially migratory blue tits *Cyanistes caeruleus*. In this test, we found migrating blue tits to have shorter approach latencies than had resident ones. Behavioural reactions to novelty can affect the readiness to migrate and short approach latency may have an adaptive value during migration. Individual behaviour towards novelty might be incorporated among the factors associated with migratory or resident behaviour in a partially migratory population.

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Introduction

The reaction of individuals, faced with new and uncertain situations differ consistently between individuals in a range of species, such as mice *Mus musculus*, rats *Rattus novegicus* (Benus et al. 1987), pumpkinseed sunfish *Lepomis gibbosus* (Wilson et al. 1993), three-spined sticklebacks *Gasterosteus aculeatus* (Giles and Huntingford 1984; Tulley and Huntingford 1987), the poecilid *Brachyraphis episcopi* (Brown et al. 2005) great tits *Parus major* (Verbeek et al. 1994) and Sardinian warblers *Sylvia melanocephala momus* (Mettke-Hofmann and Greenberg 2005; Mettke-Hofmann et al. 2005a). Such consistent differences in suites of behaviours have been termed coping strategies, behavioural syndromes, shy-bold continuum or personalities and reflect different strategies in coping with new information (Wilson et al. 1993; Drent et al. 2003; Greenberg and Mettke-Hofmann 2001; Sih et al. 2004).

Behavioural responses to novelty are one aspect of the complex suites of individually consistent behaviours called coping strategies. In birds, behavioural responses to novelty have mainly been investigated in two different contexts: exploratory behaviour in a novel environment and approach to a novel object. Individuals spending more time on a slow and thorough exploration of a new environment are also slower in approaching a novel object and these birds can be labelled as shy, slow or reactive. Bold, fast or proactive individuals, on the other hand, are fast and superficial explorers of a new environment and approach novel objects

faster (Benus et al. 1987; Wilson et al. 1993; Verbeek et al. 1994; Koolhaas et al. 1999).

Migratory birds are annually exposed to novel environments during migration as well as when arriving at stopover and wintering sites. Thus, how an individual reacts to a novel environment or object could be an important trait, particularly for young birds on their first migratory journey. In interspecific comparisons, residents show higher flexibility in foraging behaviour, which seem to enable them to cope better with seasonal variation (Sol et al. 2005). Residents have also been shown to be more exploratory than migratory or nomadic species (Mettke-Hofmann et al. 2005a, b). For instance, resident Sardinian warblers spent more time on exploration of novel objects than did the migratory garden warbler, as residents would benefit more from extensive knowledge of their environment than would migrants spending only part of their time there (Mettke-Hofmann 2007).

Among partial migrants, individuals can change from being migrants to becoming residents with increasing age (Schwabl 1983; Heldbjerg and Karlsson 1997; Able and Belthoff 1998). Hence, partial migrants need adaptations for both migration and residency, potentially making the association between behavioural response and migratory strategy particularly interesting. Furthermore, in a within-species comparison of a non-migratory population, resident great tits with more extensive natal dispersal distances were faster explorers than those dispersing shorter distances (Dingemanse et al. 2003).

The aim of this study was to investigate the possible association between the latency to approach a novel object and migratory strategy (resident versus migrant) in a partial migrant, the blue tit *Cyanistes caeruleus*. In line with findings in the inter-specific comparison between resident Sardinian and migratory garden warblers mentioned above, we hypothesise that migratory blue tits are slower explorers of the novel object than residents and test the prediction that approach time to the novel object is longer in migrants than in residents.

Methods

The blue tit is a common species in deciduous forests in large parts of Europe. In most of its breeding range, it is resident but in the northern parts, i.e. Scandinavia, it is a partial migrant that is frequently captured during autumn migration (Heldbjerg and Karlsson 1997). The study was conducted during September and October 2005. The total number of investigated blue tits was 135, consisting of 81 migrants and 54 residents. Only juvenile female blue tits were used in the experiments.

Migratory blue tits were captured at the migratory passage site of Falsterbo (55° 23′ N, 12° 49′ E), southwestern Sweden.

This is a location where large numbers of migratory blue tits are passing during a short migratory period (Nilsson et al. 2006). There are only two pairs of local blue tits at the site and they are ringed before the migrating blue tits start to arrive. Resident blue tits were captured at an inland site in an area close to Lake Krankesjön in south Sweden (55° 42′ N, 13° 28′ E), 50 km northeast of Falsterbo. See also Nilsson and Sandell (2009) for a description of the study approach comparing migrants and residents from these study sites. At both sites, birds were mist netted, sexed and aged according to Svensson (1992) and their mass and wing length was measured. Among the birds captured at the inland site, some were previously ringed in the area (17 out of 55), thus confirming that they were resident individuals. Previously unringed birds captured at the inland site are of unknown origin and this group might consist of residents and migrants from more northerly populations. However, by comparing the proportion of unringed birds during the summer (before any migratory movements are initiated) with the proportion of unringed birds during autumn (1999–2005), we estimate that the majority of birds classified as residents in the study area (76.4%; unpublished data) originate from there. Hence, we have classified all birds from the inland site as residents, noting that this group may contain a small minority of immigrants that contribute to increased variation in this group and, thus, make our analyses conservative.

Birds were kept in individual cages, measuring $0.45 \times 0.30 \times 0.48$ m, with at least three perches and with free access to water and food consisting of mealworms, *Tenebrio* sp. Caged birds could hear other caged birds, but not see them. The small size of the cages made it possible for all individuals to visit all parts of the cages (own observations) before introducing the novel object (see below). To minimize the time in captivity during a time constrained life stage, birds were captured in the morning and tested in the afternoon before they were released at the site of capture or transferred to the activity recording experiments (see below).

Behavioural tests were conducted similarly to Verbeek et al. (1994). The novel object was a pink panther rubber toy, which was curled around a perch. The tested bird could not see the observer after the novel object was inserted into the cage and the behaviour of the blue tits towards the new object was recorded during the first 2 min. Measured variables were approach time, i.e. the time for a first visit on the perch with the attached novel object, the total number of visits to the perch with the novel object, total time that the bird spent on the perch with the novel object, and the time for the second visit on the perch with the novel object. Visits to the perch did not include tactile contact with the novel object. Birds that never visited this perch were assigned an approach time of 120 s. Birds that never visited the perch a second time were given a second

approach time of 120 s. The same observer (ALKN) conducted all tests.

Measurements of the activity of migratory and resident blue tits were also performed during September and October 2005. Not all birds included in the novel object tests were kept for overnight record of activity, as we only had access to eight cages with activity detectors (same type of cages as were used above). In total, we have activity records of 100 of the individuals that were included in the exploration test. Birds were inserted into individual cages in the evening with ad lib food and water. Recording of activity ended at 1320 hours the next day. Activity was measured with an individual detector (same as is commonly used in burglar alarms in houses) in the cage, which was switched on as the bird moved. Recordings were made in 20-min bouts, thus activity was estimated as the mean number of movements per 20 min. As birds showed no activity during night, recordings from 0500 until 1320 hours were used in the analysis.

The measured behavioural variables were correlated with Spearman's rank correlation for investigating their mutual dependency and approach time was selected for further analysis. As approach time was Poisson-distributed, the variable was square-root transformed and used as the response variable in a general linear model. Standardised residuals from a linear regression of body mass in relation to wing length were used as a measure of condition corrected for body size, while wing length was used as a measure of size. Approach time (square-root transformed) was entered in a general linear model as the dependent variable and date of the test, condition, wing length and migratory strategy (migrant or resident) as independent variables. As we were interested in the relation between behavioural response and whether an individual was migratory or resident, we included all two-way interactions with migratory strategy. Approach times (square-root transformed) between groups were compared in a t test performed under the condition of unequal variances. Statistical analyses were conducted in R.

Results

Approach time to the perch with the novel object was strongly correlated to the other variables of approach behaviour, such as total number of visits to the perch (Spearman's rank correlation: $r_s=-0.63$, $N=135$, $P<0.001$), total time at the perch ($r_s=-0.65$, $N=135$, $P<0.001$), and time to the second visit to the perch ($r_s=0.63$, $N=135$, $P<0.001$). In accordance with Verbeek et al. (1994), we decided to use only approach time for further analyses. The distribution of approach times are illustrated in Fig. 1.
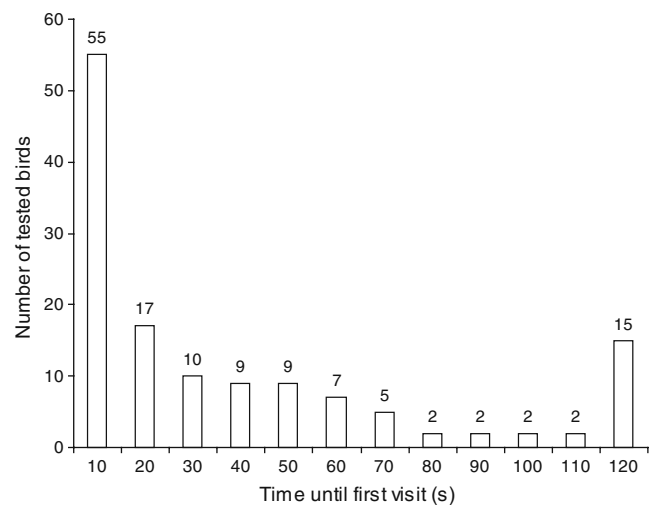
Fig. 1 The distribution of blue tits on 10 s intervals in approach times towards a novel object. Number of individuals within each time category is shown above the *bars*. The category 120 s includes individual with an approach time of 120 s or longer

We found no statistically significant difference in mean activity between migrants and residents (average number of movements per 20 min (±SE): migrants=91.2± 2.7; residents=91.8±3.1; t test: $t=0.16$; df=94.3; $P=0.87$). The mean level of activity did not explain any significant part of the variation in approach time to the novel object ($F=0.01$, $df=1$, $P=0.91$). Thus, birds with different approach times did not differ in activity.

Migratory strategy emerged as the only significant variable able to explain part of the variation in approach time in the model (Table 1). Migrants approached novel objects faster than residents (Fig. 2; average for migrants= 30.1 s and for residents=47.3 s; $t=2.45$, $df=91$, $P=0.016$). It should be noted that this test is conservative as more resident than migratory individuals (eight and five, respectively) did not approach the novel object within the 2 min

Table 1 The variation in approach time that could be explained by wing length, date of the test, condition and migratory strategy (migrant or resident)

	Estimate	T	P
Wing length × migratory strategy	0.003	0.006	1.00
Wing length	−0.046	−0.193	0.85
Date of the test × migratory strategy	−0.039	−0.612	0.54
Condition × migratory strategy	−0.859	−0.747	0.46
Date of the test	0.024	0.812	0.42
Condition	0.993	1.808	0.07
Migratory strategy	1.165	2.282	0.024

Non-significant variables were removed stepwise from the model and estimated slopes and significance levels, P, are given. The only significant variable (migratory status) remaining in the final model is marked in bold. R^2 of the final model is 0.04
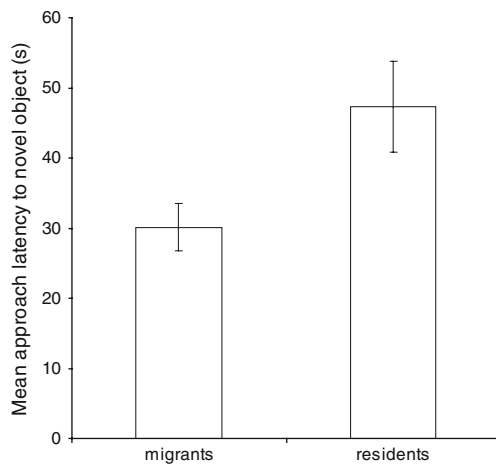
Fig. 2 Mean (±SE) approach latency to a novel object among migrant and resident blue tits. Sample size: residents=54; migrants=81. Maximum approach time was set at 2 min. Eight residents and five migrants failed to approach the novel object within this time and were given the approach time 120 s

of the test and thus were given the approach time 120 s. We also categorised the approach latency in short and long latencies (break point=60 s) and used the independent variables to explain the distribution of individuals in the two categories with logistic regression. Again, migratory strategy was the only variable explaining our results ($z=$ 2.51, $df=$134, $P=$0.012).

Discussion

Contrary to our hypothesis, migratory blue tits approached novel objects faster than residents did. Thus, individuals that can be assumed to find themselves in new environments are faster explorers than individuals staying in more well-known surroundings. Differential activity between migrants and residents cannot explain the higher number of fast-approaching migrants, as migrants and residents showed the same level of activity. This is the first time behavioural responses to novel objects have been evaluated in relation to migratory strategy within the same species and is in line with the finding that individuals with longer natal dispersal distances are predominantly bold (Fraser et al. 2001; Dingemanse et al. 2003). However, by comparing migratory and sedentary species, Mettke-Hofmann (2007) and Mettke-Hofmann et al. (2005a, b) found that migratory species were more reluctant to approach a novel object (longer approach time) than resident species. In contrast to these studies, migratory blue tits approached the novel object faster than residents. However, the blue tit is an exception among migratory species as it belongs to a phylogenetic cluster of mainly sedentary species. Several features of the migratory behaviour in blue tits, such as

diffuse directions, slow migration speed and short distances as well as occasional breeding at the wintering areas, also indicate that blue tits are at one of the extreme ends of a spectrum of migratory performance (Nilsson et al. 2008). These migratory behaviours indicate that migratory blue tits continuously explore passed areas for wintering opportunities and their behaviour may be more similar to the natal dispersal observed in resident great tits (Dingemanse et al. 2003) than to migrating warblers (Mettke-Hofmann 2007). Also, blue tits differ from migrating warblers by being diurnal migrants (Heldbjerg and Karlsson 1997) and thereby having the opportunity to continuously forage en route. However, the migratory blue tits are a heterogeneous group originating from a range of populations in southernmost Sweden and local adaptive regimes might also be influencing the outcome of the novel object experiments. An alternative explanation, based on time of captivity being comparatively short in our experiment, might be that our results reflect spatial exploration rather than object-related exploration. In line with this, Mettke-Hofmann et al. (2009) conducted an inter-specific comparison and found that migratory garden warblers entered a novel room faster than resident Sardinian warblers.

Personalities have been shown to have a heritable component (van Oers et al. 2004, 2005). Although the genetic component is moderate (van Oers et al. 2005), it is tempting to suggest that the behavioural reactions we studied are among the causes and not the consequences of the difference in migratory behaviour between individuals. It cannot be excluded however, that the observed differences in approach latency are the result of phenotypic plasticity and a consequence of migratory strategy. The results of this study indicate that behavioural reactions may be an important element warranting further research, which might be added to the complex set of factors like genetic propensity, age, sex and dominance, which are associated with migratory or stationary behaviour among partial migrants.

Exploratory behaviour affect social status in aviary flocks of great tits with shy birds having on average a higher dominance score than bold birds (Verbeek et al. 1999). Defeated bold great tits could not avoid further challenges from the winner because of the confinement, while the shy birds coped better with defeat and therefore did not loose as much in social status. However, in pair-wise confrontations, bold great tits won more interactions. Verbeek et al. (1996) therefore suggested that bold great tits did better on their own which corresponds well with the more extensive natal dispersal distances in this group. Thus, the shorter approach latencies among migrants might indicate that these birds are similar to bold great tits. They might therefore be confined to lower quality habitats and thereby their propensity to migrate might be higher than for blue tits with longer approach

latencies. Another possibility is that the adaptive value of short approach latencies is higher for birds on migration (Mettke-Hofmann and Greenberg 2005) as they are confronted with novel environments en route, and this fast approach reaction may form part of the migratory syndrome (Piersma et al. 2005) in the migrant-resident dichotomy of behavioural phenotypic flexibility.

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