Chapter 6

LEARNING AND COGNITION IN RESIDENT AND MIGRANT BIRDS

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ABSTRACT

Nearly all bird species experience some kind of environmental variability—predictable or unpredictable—and have evolved a variety of mechanisms to cope with it. In pronounced seasonal environments, these are on the one hand, migratory behaviour to avoid periods of food scarcity and on the other hand, residency by relying on or switching to resources that are still available. Migrants have evolved an entire suit of adaptations for their migratory way of life such as morphological (e.g., pointed wings), physiological (e.g., premigratory fattening), hormonal (e.g., lower melatonin production), and behavioural ones (e.g., migratory restlessness). However, little attention has been paid to adaptations in cognitive abilities. Migrants and residents differ strongly in the way they use environments. Migrants encounter a variety of unfamiliar habitats while on migration where they spent only short periods of time. Nonetheless, they have to get familiar with these sites to find food, shelter, and avoid predation. Residents, in contrast, live in the same area throughout the year but must cope with seasonal changes, e.g., in food abundance and distribution. Because of these differences, it is expected that migrants and residents have evolved specific learning and memory abilities that help them to optimize knowledge about their environment. I will first review the evidence for such adaptations in the context when changes in the familiar environment of an individual occur which may be particularly important for a resident to keep updated about newly emerging resources. Then I will focus on cognitive adaptations when individuals are confronted with a novel environment, which is an important aspect for migrants. The chapter will close with a discussion about the consequences of different cognitive abilities on population development in the face of increasingly faster changing environments.

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INTRODUCTION

Birds form a very successful family—they are found from the North Pole to the South Pole in nearly every imaginable habitat from deserts, to scrublands, to tropical rainforests, in lowlands and mountains, and even in the ocean. Despite this broad range of habitats, all or at least most of these habitats have one thing in common—they undergo, though to different degrees, predictable (seasonal) or unpredictable changes in resource availability and distribution. In northern latitudes these changes are strongly seasonal, whereas in southern latitudes changes are often less predictable but fluctuate with rainfall [Alerstam 1993]. Birds and other animals have evolved strategies to cope with this environmental variation. In principle, there are two main reactions to environmental variability—an individual can either decide to stay or to leave. When an individual is able to stay in a changing environment, it often has to find new resources and has to use different feeding techniques over the course of the year. For example, many songbirds such as tits (Paridae) switch from an insectivorous diet in summer to a granivorous or frugivorous diet in winter [Gosler & Clement 2007]. A totally different strategy is to leave the breeding ground to spend periods of unfortunate conditions somewhere else. Under predictable conditions, these movements are often migrations from the breeding ground to a specific wintering ground and back again. Under unpredictable conditions, movements are often nomadic and the birds follow the availability of resources.

Birds like other animals constantly collect information about their environment to reduce uncertainty about food availability and distribution, competitors, and predators [Inglis et al. 2001; Dall & Johnstone 2002]. As information gathering is time and energy consuming, animals do not collect as much information as possible but as much as is necessary depending on the costs and benefits of information gathering. Costs and benefits are likely to differ for residents and non-residents. For example, residents need a detailed knowledge about their territory/home range and have to track changes in their environment to discover newly emerging resources in due time. Non-residents, in contrast, leave the habitat before or when conditions deteriorate and recently collected information cannot be used later. Gould [1974] defined the value of information as the difference in payoff between a decision of an informed and an uninformed individual. From the viewpoint of a resident, one may expect that it pays to be well informed about changes in the environment in order to discover new resources in time. From the viewpoint of a non-resident, it may pay little to be informed about changes in the current environment as they leave the area and this information cannot be used any longer [Mettke-Hofmann et al. 2005b].

Non-residents face other challenges. While on the move, they are repeatedly confronted with unfamiliar habitats with which they have to become familiar to find food and avoid predation [Aborn & Moore 2004]. As a consequence, non-residents may benefit more from being able to explore an unfamiliar environment quickly and efficiently in order to find new resources than to assess a known area in detail which will soon be abandoned. This may not be the case for residents as they seldom leave their familiar area. A detailed knowledge about resource distribution and availability in the home range is pivotal for survival, whereas knowledge about new sites may be marginal. Taken together, from a cost/benefit approach one would expect differences in environmental assessment between residents and non-residents. Similarly, one may expect differences in what is stored or how long information is stored.
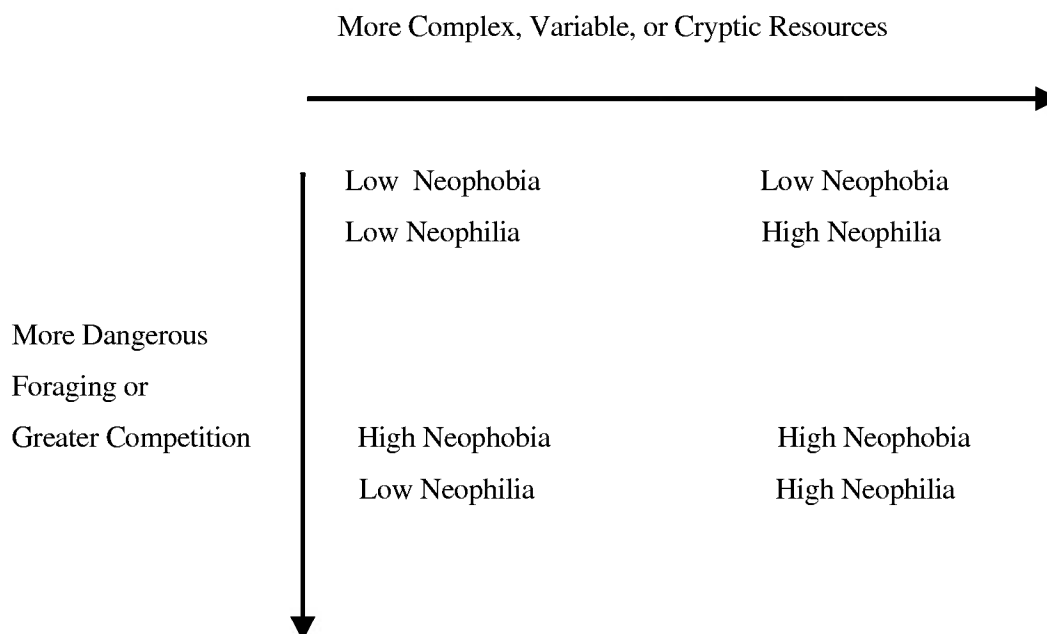
More Complex, Variable, or Cryptic Resources

	Low Neophobia	Low Neophobia
	Low Neophilia	High Neophilia
More Dangerous Foraging or Greater Competition	High Neophobia	High Neophobia
	Low Neophilia	High Neophilia

Figure 1. The two-factor model for neophilia and neophobia The two-factor model shows how environmental factors favour different combinations of neophobia and neophilia. Adapted from Greenberg & Mettke-Hofmann 2001 (with permission of Curr. Orn.).

Gathering of information, its processing, and storing is ultimately related to the underlying neurobiological networks. I will review the available information with respect to differences in environmental assessment, learning, and memory in residents and non-residents and address the accompanying differences in the brain.

HOW DO BIRDS COLLECT INFORMATION?

Birds collect information either by exploring the environment on their own [personal information; Day et al. 1998, Göth & Proctor 2002, Mettke-Hofmann & Gwinner 2003] or by observing other individuals [social information; Swaney et al. 2001, Coolen et al. 2005]. When birds explore on their own, two behaviours are primarily involved when novelty is encountered. Individuals can either be attracted to novelty (neophilia) or repelled by novelty (neophobia) resulting in approach or avoidance of the novelty, respectively. An individual experiences a situation as novel whenever it deviates from what it has experienced before [Berlyne 1966, Corey 1978]. This may be a change in the familiar environment (e.g., a tree turning into flowers) or an encounter with a novel environment [Greenberg & Mettke-Hofmann 2001]. Approach to and avoidance of novelty are two independent behaviours that are simultaneously elicited but to different degrees depending on the situation [Wood-Gush & Vestergaard 1993, Mettke-Hofmann et al. 2002]. In great tits (Parus major), approach and avoidance reactions have been shown to have a heritable component of 54% and 19%, respectively [Drent et al. 2003, van Oers et al. 2004].
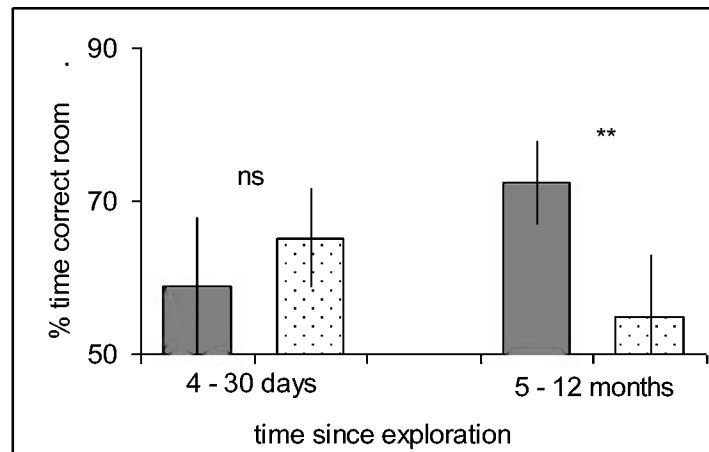
ANOVA: F=2.909, P<0.05, species x groups F=6.179, P<0.02
Gray: residents, dotted: migrants, ns: not significant, ** p<0.01
After Mettke-Hofmann & Gwinner 2003

Figure 2. Memory persistence in resident Sardinian warblers and migratory garden warblers. The percent time spent in the room that had contained food during exploration (correct room) is shown for Sardinian and garden warblers after two different delays.

REACTION TO CHANGES IN THE FAMILIAR ENVIRONMENT

Neophilia

As outlined above, residents should pay a lot of attention to their surrounding and track changes in their familiar territory or home range to be informed about forthcoming feeding options, whereas this may be less important for non-residents as they leave the area when conditions change. This proposition was tested in ten closely related parrot species—six nectarivorous lorikeets (Loriini) and four granivorous broad-tailed parrots (Platycercini). Within each tribe, species differed in their movements ranging from resident species to species with resident and nomadic individuals to nomadic species [Mettke-Hofmann et al. 2005b]. Neophilia was tested by hanging three novel objects over a neutral perch (no food or water nearby) in the familiar aviary of the birds. The latency to first approach and touch one of the objects, the number of objects touched as well as the time spent exploring was taken as a measure of neophilia. In this situation, neophilia and neophobia are equally likely to be elicited. However, when a bird approaches and investigates the novel objects this should be primarily driven by neophilia (the interest of the bird in the novel) as the bird is free to approach the objects [Mettke-Hofmann et al. 2005b]. Closely related species tend to behave more similarly than less closely related ones. Therefore, phylogenetic relationships were considered. The resident species touched the novel objects earlier and also explored more objects than the nomadic ones. Furthermore, the species depending on a high proportion of fruits in their natural diet explored earlier and more than the species with a low proportion of fruits in their diet [Mettke-Hofmann et al. 2005b] confirming earlier findings from a study on 61 parrot species that species depending to a high degree on difficulty to find food are more

explorative [Mettke-Hofmann et al. 2002]. Differences in reaction to a novel object in the familiar cage were also found in two closely related songbird species, the resident Sardinian warbler (Sylvia melanocephala momus) and the migratory garden warbler (S. borin). More individuals of the resident species approached the novel object and spent more time near the object than individuals of the migratory one [Mettke-Hofmann 2006]. In another study, resident Sardinian warblers explored the novel objects significantly earlier than migratory garden warblers [Mettke-Hofmann et al. 2005a]. All three studies support the prediction that resident species should pay more attention to changes in their familiar environment than non-resident ones. The former have to find sufficient resources under changing environmental conditions in their familiar area to persist in this area throughout the year. Higher neophilia and increased exploration helps them to find newly emerging resources. Non-residents abandon the area when conditions worsen and the costs of exploration may outweigh the benefits of it [Mettke-Hofmann et al. 2005b].

Residents are also known to be more innovative than migrants. Sol et al. [2005] searched the literature for notes reporting novel or opportunistic food types and feeding techniques in resident and migratory temperate Palaearctic birds. After adjustment of the data for research effort, resident species had more feeding innovations than long-distance migrants. More importantly, residents were particularly innovative in winter [Sol et al. 2005]. As a consequence, residents are more flexible in their foraging behaviour than migrants. The greater flexibility, particularly in winter, allows them to exploit a variety of food resources at a time when feeding conditions are difficult. In the long-term, this secures year-round residency. The above mentioned higher neophilia in residents as compared to migrants may be a keystone to support innovations [Ramsey et al. 2007]. A high motivation to approach and investigate novelty may ultimately lead to the discovery of new edible resources or the development of new feeding techniques. In contrast, the lower neophilia in migrants constrains contact with novelty and subsequently the occurrence of innovations and may force migrants to move to areas that allow continuation of their common foraging techniques.

Innovation rate is known to correlate with brain size. In mammals, behavioural innovations, social learning and tool use are positively correlated with the relative size of the neocortex and striatum [Reader & Laland 2002]. Likewise, in birds feeding innovations are correlated with the size of the neostriatum-hyperstriatum ventrale complex [Timmermans et al. 2000]. With respect to differences in brain-size between residents and migrants Sol et al. [2005] compared absolute brain size which is a good approximation for the size of the neostriatum-hyperstriatum ventrale complex. The more innovative resident species had larger brains than the less innovative migratory species. Similar results were found by Winkler et al. [2004] which measured skull dimensions and forebrain size. Residents had higher skulls which is a good predictor of telencephalon size and also had larger forebrains.

Neophobia

The above section discussed how neophilia, innovation, and brain size may be linked with resident or migratory behaviour. In this section, neophobia reactions will be compared between residents and migrants. Like with neophilia, cost/benefit considerations are likely to determine neophobic reactions. On the one hand, an individual may benefit from being neophobic by avoiding dangerous situations. On the other hand, neophobia incurs the cost of

missing out opportunities. For example, slower learning of a food task in Zenaida doves (Zenaida aurita) as compared to pigeons (Columba livia) was caused by higher neophobia of the former [Seferta et al. 2001]. Depending on the costs and benefits an individual experiences in its environment neophobia reactions are expected to vary. In a given environment, residents and non-residents are exposed to the same uncertainties and dangers. However, depending on their life-style, resident or non-resident, costs and benefits of the same threat may be differently rated. For example, as residents are restricted to a relatively small area throughout the year the costs of missing out opportunities e.g. discovery of a novel food source may weight more than the benefit of being protected from dangerous situations. Non-residents, in contrast, are not bound to a given area and protection from danger may be weighted higher than lost opportunities as they move away when conditions deteriorate. Furthermore, as migrants spend only a limited time in each area they are overall less informed and familiar with each of the environments than residents. Therefore, residents are expected to be less neophobic than non-residents when changes in the familiar environment occur [Mettke-Hofmann, C., Hamel, P. B. & Greenberg, R. subm.].

An ideal test to elicit neophobia reactions in the familiar environment is to place a novel object beside the feeding dish and measure the difference in time it takes an individual to feed with and without the novel object. In this situation, primarily neophobia is elicited as the animal is in conflict between the motivation to feed and the motivation to avoid the novel object. Usually, no neophilia is elicited [Mettke-Hofmann et al. 2002, 2005b]. There are two studies available that have investigated neophobia in residents and non-residents. In one study, neophobia was compared between resident Sardinian warblers and migratory garden warblers in captivity [Mettke-Hofmann et al. 2005a]. Latency to feed was measured in the familiar cage without (control) and with an object placed beside the feeding dish. The difference in time to feed was taken as a measure of neophobia. The Sardinian warblers hesitated significantly less to feed in the presence of a novel object than the garden warblers [Mettke-Hofmann et al. 2005a]. The second study compared neophobia reactions of 8 New World blackbird species/subspecies (Icteridae) in the field in relation to their migratory behaviour (ranging from pure residents to mixed populations of residents and migrants to pure migrants) and ecological plasticity [Mettke-Hofmann, C., Hamel, P. B. & Greenberg, R. subm.]. In winter, the blackbird species form mixed-species foraging flocks. The blackbirds were attracted to feeding locations and after a habituation period to the locations, neophobia was tested by placing novel objects around the feeding location. Migratory behaviour was a strong predictor of neophobia reactions between species as well as between resident and migratory populations of the same species. Again, residents needed less time to resume feeding in the presence of novel objects than migrants [Mettke-Hofmann, C., Hamel, P. B. & Greenberg, R. subm.]. Both studies support the expectation that residents should be less neophobic to approach changes in the familiar environment than migrants.

Taken the results from the neophilia and neophobia studies together residents seem to be more neophilic and less neophobic than non-residents when confronted with changes in their familiar environment. Both, high neophilia and low neophobia help residents to find new resources in time. The former attracts individuals to novelty and favours exploration, the latter reduces avoidance reactions resulting in fast assessment of changes in the familiar environment. Non-residents are more likely to have low neophilia and high neophobia. Therefore, they show only little interest in changes in their environment but also strong

avoidance reactions. As a consequence, non-residents collect only limited information about environmental changes.

Correlated Behavioural Traits

The examples mentioned thus far primarily report on mean differences in novelty reactions between species. However, little is known about how these differences are realized on the individual level. Are there differences in the frequency distribution of high and low neophilia between species or are the differences clear-cut with all individuals of one species being very neophilic and the one from another all showing low neophilia? Furthermore, are some combinations of novelty reactions more likely to occur than others? Intuitively one may expect that high neophilia is coupled with low neophobia.

As mentioned before, neophilia and neophobia are two independent reactions to novelty. Experiments have shown that the two behaviours can be found in all kind of combinations [Mettke-Hofmann et al. 2002]. In their extremes, there are four possible combinations – (1) high neophilia coupled with low neophobia, (2) low neophilia coupled with high neophobia, (3) high neophilia coupled with high neophobia, and (4) low neophilia coupled with low neophobia [Figure 1, two-factor model by Greenberg & Mettke-Hofmann 2001]. The first two combinations include what we would intuitively expect. When neophilia is high and neophobia is low the individual approaches and investigates the novel. Likewise, when neophilia is low and neophobia is high the individual stays away from the novel. The two latter combinations seem to be counterintuitive but demonstrate that the two behaviours are independent from each other. An individual can be highly attracted to novelty (high neophilia) but at the same time highly afraid of it (high neophobia) which leads to an ambivalent behaviour e.g. the animal switches between approach and avoidance [Heinrich 1988]. Finally, an individual can be neither attracted to (low neophilia) nor afraid of novelty (low neophobia) resulting in disinterest and no exploration.

There is increasing evidence that individuals differ consistently and predictably in their behavioural and physiological reactions to a wide range of environmental challenges (termed personality traits, coping styles, or temperament; [e.g. Budaev 1997, Koolhaas et al 1999, Visser at al. 2002]). This also includes reaction to novelty. The above mentioned study on resident Sardinian warblers and migratory garden warblers [Mettke-Hofmann et al. 2005a] not only investigated differences in neophilia and neophobia between the two species but also whether these two behaviours were correlated with each other on the individual level (indicating personality traits). Neophilia and neophobia were each tested at two different time points – after the breeding season and in spring – to test for consistency of the two behaviours which is another important prerequisite for personality traits [Boissy 1995, Koolhaas et al. 1999]. Novelty reactions were repeatable over time in the resident Sardinian warbler but not in the migratory garden warbler. Furthermore, in the former neophilia and neophobia were negatively correlated with each other, whereas no correlation was found in the latter [Mettke-Hofmann et al. 2005a]. Thus, it seems that in the Sardinian warbler novelty reactions are part of a personality trait with high and low reacting individuals. High reacting individuals showed a strong reaction in both the neophilia-eliciting and the neophobia-eliciting situation but in opposite directions. They readily approached and explored a novel object at a neutral location but showed strong avoidance reactions when a novel object was placed beside the

feeding dish. Low reacting individuals showed only a weak reaction to the changes and waited long to explore the novel object but readily resumed feeding in the presence of the novel object beside the feeding dish. No such correlations were found in the garden warbler. At the moment it is unclear whether these differences are related to the resident or migratory life-style of the species. One possibility is that year-round residency may favour the evolution of correlated behaviours, whereas the encounter of different habitats may favour more flexible behaviour. However, more research is needed here.

REACTION TO NOVEL SPACE

Spatial Neophilia and Neophobia: The Decision to Enter an Unfamiliar Room

Non-resident species are repeatedly confronted with novel environments when on the move, even though many migratory species show a predisposition for specific habitat types [Moore et al. 1990, Baierlein 1983]. Stopover times are often short and many migrants act to maximize migration speed [Alerstam & Lindstrom 1990]. Nonetheless, migrants have to collect at least some information to assess food availability and predation pressure. A fast assessment whether a site is suitable or not would speed up migration considerably. However, before a site can be assessed it has to be approached and entered. Like in the novel object situation in which a change in the familiar environment elicites both neophilia and neophobia does a novel environment elicit approach and avoidance. While on migration, a high motivation to enter unfamiliar sites (in combination with a specific habitat preference) would attract migrants to possible stopover sites (high spatial neophilia). At the same time, a low hesitancy to enter the unfamiliar site (low spatial neophobia) would speed up migration [Mettke-Hofmann, et al. 2009]. Residents are only seldom confronted with novel environments and high spatial neophobia may protect them from entering unfamiliar terrain and encountering dangerous situations. At the same time, they may have little interest to explore new sites (low spatial neophilia).

Currently, there is only one study available that investigates how spatial neophobia and neophilia may influence decision-making to enter a novel environment in relation to residency and migratoriness [Mettke-Hofmann et al. 2009]. Sardinian and garden warblers were kept in a cage from which they had access to an unfamiliar room. It was measured how often and how long the birds perched on the dowel leading to the novel room and the time to leave the cage. The dowel leading to the novel room was located near the bottom of the cage and was only rarely used when the door was closed. Repeated and prolonged perching was taken as a measure for a conflict between the motivation to enter the novel room and the motivation to avoid it. Among the birds that finally entered the novel room, resident Sardinian warblers perched more often and for a longer time on the lower dowel before entering the novel room than migratory garden warblers. Latencies to enter the room were short for both species [Mettke-Hofmann et al. 2009]. The results indicate that individuals of both species that entered the novel room were motivated to explore the novel room (short latencies, spatial neophilia) but avoidance reactions (spatial neophobia) were stronger in the residents as compared to the migrants as the former had a larger conflict between approach

and avoidance of the novel room than the latter. This conflict arises when an individual is, on the one hand, motivated to enter the novel room and, on the other hand, afraid of it (high spatial neophilia coupled with high spatial neophobia). Thus, other than predicted residents were interested to explore a novel environment but at the same time were also very hesitant to do so. This latter result supports the 'migrant-neophobia' hypothesis [Mettke-Hofmann, C., Hamel, P. B. & Greenberg, R. subm.] which predicts that migrants should be less neophobic to enter a novel environment than residents [Mettke-Hofmann & Greenberg 2005]. Migrants benefit largely by having low spatial neophobia as it reduces hesitancy to enter an unfamiliar site which speeds up migration. High spatial neophobia in residents, in contrast, protects them from dangerous situations outside their familiar territory. The high spatial neophilia in at least some of the residents (see below) let assume that knowledge about unfamiliar but nearby sites is important. However, the same study found that overall fewer resident individuals than migratory ones finally entered the novel room and that the former had overall longer latencies than the latter [Mettke-Hofmann et al. 2009]. This is in concordance with the expectation that migrants may be more motivated than residents to enter a novel environment (spatial neophilia).

To summarize, preliminary results on resident Sardinian warblers and migratory garden warblers show that the residents have higher spatial neophobia to enter an unfamiliar room than the migrants and that the former on average are also less interested to enter a novel environment (spatial neophilia) than the latter. However, it should be mentioned that the results are based on a two-species comparison. Clearly, more studies are needed to confirm the findings.

Assessing a Novel Environment

Several studies are available that compare the spatial assessment of residents and migrants. An often used design is to measure how long it takes an individual to visit a given number of trees and how many branches of each tree are inspected in the novel environment [Verbeek et al. 1994]. The more branches are visited and the longer the exploration the more accurate should be the assessment. Interestingly, the Sardinian warblers that finally entered the novel room spent more time on each branch than the garden warblers [Mettke-Hofmann et al. 2009]. Similar results were found by Dingemanse et al. [2003] in great tits (Parus major). Young tits were captured in the wild, their spatial assessment tested in the lab after which they were released again to measure their natal dispersal distance later in the year. Tits that later turned out to settle near their place of birth spent more time on each branch and needed more time to reach the last tree than tits that dispersed further [Dingemanse et al. 2003]. An interesting parallel in exploratory behaviour was found in flying squirrels (Pteromys volans). Young flying squirrels can be categorized in long-distance and short-distance natal dispersers, and philopatric individuals that settle within the mother's home range [Selonen & Hanski 2006]. Long-distance dispersers which could not reach their future breeding site during exploration trips had fewer exploration trips prior to dispersal than short-distance dispersers and philopatric individuals which settled within the range of their exploration trips. It seems that the short-distance dispersers and philopatric individuals can use the information for future settlement decisions, whereas long-distance dispersers may gain little from exploring the natal area as they will move away [Selonen & Hanski 2006]. The same explanation may

hold for the long and short dispersing great tits. Finally, in the warbler study when adult residents decide to leave their territory it may be to collect information about new breeding sites and a thorough exploration of the new site is essential to learn about the short-term and particularly long-term suitability of the new site. The purpose of spatial exploration in a migrant is likely to be different. While on the move, a migrant only needs to fulfil current metabolic needs and a rough overview about food availability and predation pressure at a given site may be sufficient even if it is only a suboptimal habitat [Moore et al. 1990]. A thorough spatial exploration in residents versus a superficial spatial exploration in migrants is supported by the following finding [Mettke-Hofmann & Gwinner 2004]. Resident Sardinian Warblers moved only over short distances in a novel room exploring a particular corner for a long time, whereas migratory garden warblers moved over larger distances covering the room in a shorter period of time than the residents. Surprisingly, the migrants found food earlier than the residents possibly as a consequence of their faster movement pattern which increased the likelihood to encounter easy to find food [Mettke-Hofmann & Gwinner 2004]. Observations in the field further support that newly arrived migrants move only little (often below 500 metres) before selecting a site for refuelling [Aborn & Moore 1997, Chernetsov 2005, Matthews & Rodewald 2006, van Riper III et al. 2006]. Furthermore, movement patterns indicated only little information gathering [Aborn & Moore 1997]. To conclude, residents may explore a novel site thoroughly to allow long-term settlement decisions, whereas migrants may explore a novel site superficially to allow short-term settlement decisions.

Exploring an unfamiliar site on its own (personal information) is time consuming and can also be dangerous when predation risks are high. An easier and safer way to get familiar with a site may be to join more experienced individuals (conspecifics or heterospecifics). The use of social information is known from at least some migrants. Nemeth and Moore [2007] studied flocking behaviour of Nearctic-Neotropical passerine migrants stopping over in a coastal habitat after passage of the Gulf of Mexico shortly after arrival (afternoon) and the next morning. A larger percentage of newly arrived insectivorous migrants was feeding in flocks as compared to those present for a longer time. Joining flocks has several advantages; firstly, an uninformed bird looking for other feeding birds is immediately led to a suitable site without wasting time to assess various sites on its own. Secondly, while moving with the flock a bird can satisfy its metabolic needs and with little extra effort learn about the environment. Finally, the flock gives safety from predators. However, flocking also increases competition and may outweigh the advantage of flocking when the bird is more familiar with the site resulting in decreased flocking behaviour the next morning. A high flocking tendency which persisted throughout the stopover time was also found in granivorous migrants [Nemeth and Moore 2007] who often experience less competition than insectivorous species.

Overall, migrants seem to be little afraid but also highly motivated to enter an unfamiliar site. However, personal spatial exploration seems to be restricted to a minimum. Instead, at least some migrants may use social information to speed up the process of familiarization. Residents often hesitate to enter an unfamiliar site but when they decide to do so they explore it thoroughly.

Spatial Memory

Many migrants stopover at the same sites, use the same wintering area, and return to the same breeding site year after year often even settling in the same territory as the year before [e.g. Mikkonen 1983, Hansson et al. 2002]. Endogenous migration programs may guide birds to the rough area of the species' winter ground [e.g. Gwinner 1986] but learning also plays a role as displacement experiments with inexperienced (first year) and experienced (adult) migrants showed - adult birds compensated for displacement, whereas first-year migrants did not [Perdeck 1958]. Migrants are likely to learn about the spatial relationships between different stopover sites and winter sites and their suitability and may use this information to optimize or correct migration routes. Furthermore, postfledging exploration prior to departure familiarizes a young bird with its natal site and may also aim as a navigational target on its return [Baker 1993]. Remembering suitable stopover and winter sites until the next migration season reduces uncertainty and allows migrants to optimize the migratory journey. Furthermore, the ability to return to a site of successful reproduction reduces search time for new breeding sites and also increases the likelihood to be successful again. Therefore, one may expect that migrants have a long-lasting memory to remember suitable sites for stopover, over-wintering and reproduction after many months of absence. Residents are not challenged with prolonged periods of absence from their place of living. Moreover, updating information in a changing environment from time to time is likely to be better than relying on old, possibly outdated information [Inglis et al. 2001]. Indeed, studies on nine-spined sticklebacks (Pungitius pungitius) demonstrated that individuals relied less on personal information when it was collected a week ago than when collected more recently [van Bergen et al. 2004]. Resident Sardinian warblers and migratory garden warblers were again used to test whether migrants have a longer lasting memory than residents [Mettke-Hofmann & Gwinner 2003]. During the autumn migration period, individuals of both species were first allowed to explore two unfamiliar rooms – one with food, one without food – for eight hours. To test their memory persistence, individuals of each species were assigned to groups that were tested after different delays ranging from 4 days to 12 months. The time spent in each room, this time without food, was compared between the two species and among the different delays. Both species preferred the room that had contained food after short delays. However, only the garden warblers still preferred this room after long delays, whereas the Sardinian warbler performed about chance level (Figure 2 [Mettke-Hofmann & Gwinner 2003]). These differences in memory persistence were confirmed in resident and migratory subspecies of the dark-eyed junco (Junco hyemalis) with the migrants having a longer lasting spatial memory than the residents [Cristol et al. 2003]. Likewise, in white-crowned sparrows (Zonotrichia leucophrys) the migratory subspecies Z.l. gambelii showed a better spatial memory (measured as the number of visits required to find a formerly baited feeder) than the resident subspecies Z.l. nuttalli [Pravosudov et al. 2006].

The results are further backed up by differences in the hippocampal formation which is an important brain region for processing spatial information [e.g. Healy et al. 1994, Reboreda et al. 1996, Volman et al. 1997]. When comparing the relative size of the hippocampal formation between young, migratory inexperienced and adult, migratory experienced garden warblers Healy et al. [1996] found that the relative hippocampal size was larger in the latter than in the former. The change in size could be attributed to both age and migratory experience. No such changes were observed in the hippocampal formation of the Sardinian

warbler [Healy et al. 1996]. In migratory dark-eyed juncos, hippocampal neurons were more densely packed than in resident dark-eyed juncos [Cristol et al. 2003] and migratory white-crowned sparrows had larger hippocampal formations with more neurons than their resident counterparts [Pravosudov et al. 2006]. All three examples indicate that better spatial memory abilities co-occur with changes in the hippocampal formation that allow better processing of spatial information. It should be highlighted that the larger and/or more densely packed hippocampal formation in migrants [Healy et al. 1996, Cristol et al. 2003, Pravosudov et al. 2006] is in contrast to the overall smaller brain size reported for migrants as compared to residents [Winkler et al. 2004, Sol et al. 2005]. This discrepancy indicates that migrants depend and rely more heavily on spatial information than residents.

It seems that migrants have evolved hippocampi that help them to remember spatial information efficiently and for a long time to overcome constrains imposed by migration. Remembering high-quality stopover sites until the next migration season allows migrants to optimize their migration route. Furthermore, the ability to be site faithful even after a long period of absence increases familiarity with the site resulting in higher survival and breeding success [Bruinzeel & van de Pol 2004, Griffith et al. 2004, Vergara et al. 2006]. Residents do not need such a long lasting memory as they can update their information whenever necessary. Moreover, a long-lasting memory may be disadvantageous as residents have to keep track of recent changes in the environment and memory of old information may interfere with newly collected information [Mettke-Hofmann & Gwinner 2003].

CONSEQUENCES OF DIFFERENCES IN NOVELTY REACTIONS AND MEMORY PERSISTENCE IN RESIDENTS AND MIGRANTS

Studies about consequences of differences in novelty reactions are rare and require future investigation. I will summarize the few examples that are available and discuss possible consequences that still have to be confirmed.

Pigeons and Zenaida doves differ in their ability to learn a novel foraging task with the former being better than the latter [Lefebvre et al. 1996]. Other than originally expected, differences in social organisation (group-living vs. territorial) did not explain the differences in learning ability. Instead, neophobia reactions towards the novel feeding apparatus best explained the results [Seferta et al. 2001]. Strong neophobia reactions in the Zenaida doves prevented or delayed exploration of the novel apparatus. The example shows that neophobic reactions play a decisive role whether and when an individual approaches an unfamiliar situation. The study, however, does not show whether these differences translate into differential survival or reproductive success in the wild. Dingemanse et al. [2004] investigated fitness consequences of personality types (measured as the speed of assessment of a novel environment) in the great tit. Birds were captured, transferred to the laboratory for testing and afterwards released at the site of capture. Results showed that annual survival of the birds was related to their personality type (fast or slow exploration of the novel environment) but with opposite directions between sexes and years [Dingemanse et al. 2004]. Likewise, offspring recruitment into the next migration season was related to the personality trait of their parents with again opposite traits being successful in different years [Dingemanse et al. 2004]. This is one of the very few studies establishing a link between

environmental assessment and survival. Clearly, more such studies are needed to learn about the consequences of differences in novelty reactions, environmental assessment and memory.

How does this apply to differences in cognitive abilities in residents and migrants? From the above section one can predict that ultimately, novelty reactions (neophobia and neophilia) determine how an individual deals with environmental change. This is a very important aspect in an ever faster changing environment be it due to natural events such as climate change or human-induced such as conversion of forest to agricultural land. The ability to adapt to those changes gives an individual an evolutionary advantage. Residents are less neophobic and at the same time also more neophilic than migrants when encountering changes in the familiar environment. Moreover, residents explore novel environments thoroughly even though they initially hesitate longer to enter unfamiliar sites than migrants. Does the higher propensity to approach and thoroughly explore novel situations give residents an evolutionary advantage? Sol & Lefebvre [2000] showed that invasion success not only correlates with brain size but also with migratory strategy – migrants were least successful in colonizing new areas, whereas partial migrants (populations consisting of resident and migratory individuals, facultative migrants) were most successful. Furthermore, successful colonizers were also more innovative than unsuccessful ones. Finally, another study showed that residents are more innovative than migrants [Sol et al. 2005]. Novelty reactions are positively correlated with innovations [Ramsey et al. 2007]. For example, in carib grackles (Quiscalus lugubris) the number of different attempts to solve a foraging task (a measure of innovation) was closely associated with object neophilia [Reader 2003]. Therefore, low neophobia and high neophilia, i.e. a high propensity to rapidly approach and thoroughly investigate novel situations seems to benefit residents when invading new areas. A correlation between novelty reactions and invasion history was also shown by Martin & Fitzgerald [2005]. They compared neophobia reactions (novel object beside familiar food) and food neophobia (phobia to taste novel food) between two sparrow (Passer domesticus) populations – one still actively invading new sites, the other resident for 150 years. Both showed no neophobia in the presence of the novel object (they even approached the food bowl earlier than without object indicating neophilia) and the still invading population hesitated less to try and consume the novel food than the settled-in population [Martin & Fitzgerald 2005].

Beside a lower ability to occupy new areas population development at least of Palaearctic migrants is worse than in residents. Migrants decline much stronger in their established range than residents [Sanderson et al. 2006]. This is likely to be caused by a variety of factors such as problems associated with the winter quarter in Africa [Sanderson et al. 2006] or mismatch of breeding attempts and food availability due to climate change [Both et al. 2006]. However, another factor may be the inability of migrants to adapt to environmental change. For example, the migratory rusty blackbird (Euphagus carolinus) is the strongest declining songbird in the United States [Niven et al. 2004]. In a comparison of 8 closely related blackbird species and populations rusty blackbird showed the strongest neophobia reaction towards novel objects placed around a feeding location [Mettke-Hofmann, C., Hamel, P. B. & Greenberg, R. subm.]. Individuals of the species flew off more frequently and stayed away from the food source for a longer period of time than less neophobic blackbirds which likely has a negative influence on the species' energy budget in winter. Also, their stronger neophobia may prevent or at least delay exploitation of newly emerging resources. Strong neophobic reactions may also drive migrants out of areas with a high degree of environmental change.

On another front, the long-lasting memory of migrants may turn out to be a disadvantage in a rapidly changing environment. High-quality stopover sites can become unsuitable or disappear completely within a short period of time due to man-made habitat alteration or destruction, and habitat fragmentation may place the next available habitat out of reach of the migrant. A migrant relying on its memory may ignore sites earlier passed by to get to this one site which may have disappeared.

The above mentioned remarks are of course speculative, and comparisons of stable or even increasing migratory populations with those that are declining are warranted to support this possibility. However, until now many data indicate that residents are more flexible to react to environmental change than migrants.

CONCLUSION

The overview has shown that residents and migrants each have evolved specific adaptations to deal with environmental change and novelty. These adaptations include differences in neophobia and neophilia which may cause differences in innovation rate. Many of these behavioural adaptations are accompanied by neurological changes in the brain. The review has also flagged areas in which more research is needed such as investigating the consequences of differences in novelty reactions.

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