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Information Acquisition and Sociality Among Migratory Birds

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INFORMATION ACQUISITION AND SOCIALITY

AMONG MIGRATORY BIRDS

by

Zoltán Németh

Abstract of a Dissertation
Submitted to the Graduate School
of The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy

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ABSTRACT

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Information use is a key feature of adaptive behavior: the better informed an individual, the better it is able to adjust its behavior to meet the demands of a variable world. Therefore, most animals attempt to reduce environmental uncertainty by gathering information when it is available. However, tracking unpredictable ecological factors may carry costs as individuals invest valuable time and energy in the process of information acquisition. Social learning (i.e., use of social information inadvertently produced by other individuals) enables the individual to gain rapid and more complete assessment of its novel environment. This process may be particularly important for animals under time and energetic constraints, such as migrating birds that land at unfamiliar stopover sites to replenish depleted energy stores. Migration is an ideal context in which to examine how animals respond to multiple, simultaneous constraints (informational, time and energetic) because a successful migration depends on making appropriate decisions quickly under novel circumstances.

In this dissertation, I investigate the mechanisms of information acquisition in the context of migration with particular attention to social learning. My research was organized around the following questions: (a) When are long-term spatial memories encoded during the life of a first-year migratory songbird? (b) Is the seasonally high degree of sociality observed during migration an indication of the increased value and use

of social information in a stopover setting? (c) Can social learning speed up the familiarization process with a novel foraging environment? (d) Does the degree of social information use vary between seasons?

I found evidence of relatively low investment in long-term spatial memory formation during migration in free living migratory thrushes. However, social affiliation reduced the novelty response in captive migrants and sped up the acquisition of a novel foraging technique. Interestingly, birds in migratory disposition were slower on a social learning task than birds in non-migratory condition. Finally, as indicated by the change in flocking propensity and space use, the value and use of social information seemed to decline over the course of the stopover period. These findings suggest that social learning plays an important role in the decision-making process during migration.

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CHAPTER I

SYNOPSIS

Informed decision-making contributes to fitness (McNamara & Dall, 2010), yet,

questions about the ecological and evolutionary consequences of information use has

only recently been addressed empirically (Schmidt, Dall, & van Gils, 2010). In general,

organisms that live in seasonal or heterogeneous environments face a higher degree of

uncertainty throughout their annual cycle and benefit from the ability to associate

environmental cues with attributes of risks and resources (i.e. learn what, where, when

and who to avoid or eat) and use them to reduce time and risks when sampling the

environment (Shettleworth, 1998). It is reasonable to expect that certain life history

stages with particularly high energy demand may select for better cognitive performance

if cognition correlates with the ability to secure resources. For example, bird migration is

one of the energetically most expensive seasonal behaviors and requires frequent and

rapid replenishment of depleted energy stores to fuel migratory flights (Blem, 1980).

Even though migratory birds are capable of flying long distances, sometimes over several

days without stopping (Gill et al., 2009), most nocturnal migratory landbirds select a

stopover site at the end of each night to rest and refuel during the daylight hours

(Alerstam, 1993; Berthold, 2001). These repeated refueling stops often take place in an

unfamiliar landscape where migrants must compete for limited resources with other

migrant and resident birds while coping with unfavorable weather events, loss of sleep

and risk of predation (Moore, 1999; Moore, Smith, & Sandberg, 2005). Moreover, the

lack of prior experience with migration and the diversity of novel habitats magnify the

challenges young, hatch-year migrants face when completing their first migration. The

unfamiliar and unpredictable nature of *en route* conditions make these marathon journeys particularly challenging and perhaps it is not surprising that the migration phase is associated with the highest mortality estimates within the annual cycle of a migratory songbird (Sillett & Holmes, 2002).

Given the time, energy and information constraints at stopover sites, one would expect that migratory birds employ efficient cognitive strategies to compensate for the lack of prior information about stopover sites when making decisions in response to novel habitat features and food types. Cognitive processes (e.g. exploration and learning) are likely to contribute to the successful completion of migration by increasing the chance of a rapid assessment of resources and predation risk (Cimprich, Woodrey, & Moore, 2005). When settling in a habitat with unpredictable spatial distribution of optimal resources, the initial exploration or "discrimination phase" (Ward, 1987) may carry costs in the form of time away from foraging while increasing the risk of predation, an especially serious problem for a fat-depleted, energetically stressed migrant. A foraging migrant, however, may supplement personal sample information (i.e., *private information* gained on its own) with socially acquired cues provided inadvertently by other foraging individuals (*inadvertent social information*) (Danchin, Giraldeau, Valone, & Wagner, 2004; Valone & Templeton, 2002; Wagner & Danchin, 2010). The combination of private information with social information obtained from observing the location and successful or unsuccessful sampling activities of others improves the speed and accuracy with which an individual assesses habitat quality (Rafacz & Templeton, 2003; Smith, Benkman, & Coffey, 1999; Templeton & Giraldeau, 1996; Valone, 1989). Thus social learning enables the individual to more completely assess an unfamiliar

environment (Galef & Giraldeau, 2001; Galef & Laland, 2005; Hoppitt & Laland, 2008; Kendal, Coolen, van Bergen, & Laland, 2005; Valone, 1989, 2007), which may be particularly important for migrants under time, energetic and information constraints (for a more detailed treatment of social information use in the context of migration along with testable predictions see Chapter II).

The interplay of different constraints (i.e., time, energy and information) acting simultaneously on a migratory bird during passage creates an ecological context within which the study of information use can provide insights into how migratory birds cope with the seasonally increased uncertainties during migration. In this ecological setting, social learning is expected to provide unique benefits by supplementing private sampling information of a foraging migrant with inadvertent social information, which should lead to reduced uncertainty and faster risk and resource assessment (Galef & Giraldeau, 2001; Moore & Aborn, 2000; Németh & Moore, 2007). In this dissertation, I test this general hypothesis while seeking answers to the following questions: (a) Is long-term spatial memory formation relevant for the development of the global navigation map in migratory songbirds? If so, when are long-term spatial memories encoded during the life of a first-year migratory songbird? (b) Is the seasonally high degree of sociality observed during migration an indication of the increased value and use of social information in a stopover setting? (c) Can social learning speed up the familiarization process with novel foraging environments? (d) Does the degree of social information use vary between seasons in a migratory songbird? I addressed these questions with a combination of field and laboratory studies.

Chapter III. Long-Term Memory Formation and Migration

Long-distance navigation (i.e. global navigation) is aided by a number of well studied mechanisms in migratory animals (e.g. magnetic compass, use of celestial and olfactory cues, use of polarized light), and these traits show remarkable similarities across taxonomic groups (Rozhok, 2008). Although, spatial memory is thought to play an important role in homing and navigation on a local scale, the role of long-term memory in assisting global navigation in migratory animals have been questioned (Bingman & Cheng, 2005). However, the hippocampal formation of the brain, the region primarily responsible for long-term memory formation (Sherry & Vaccarino, 1989), contains an increased number and density of neurons after migratory experience, presumably, in response to the cognitive demand associated with migration (Healy, Gwinner, & Krebs, 1996). This neuroanatomical response suggests that long-term memory may have a more significant role in migration than previously thought.

I examined this problem by assessing long-term memory formation at different life history stages during the first year in the life of migratory songbirds representing two thrush species (*Turdinae*), the long-distance migrant Veery (*Catharus fuscescens*) and the shorter distance migrant Wood Thrush (*Hylocichla mustelina*). To indicate the intensity of long-term memory deposition through the hippocampal formation, I measured the amount of CREB (cyclic AMP response element binding protein) expressed in this brain region during the different stages. CREB-responsive transcription is central in the formation of long-term memory in a wide variety of taxa from Drosophila, through Aplysia to mice (Yin & Tully, 1996), thus it is reasonable to expect that the amount of CREB expressed in each life history stage correlates with the intensity of long-term

memory formation in the individual. Among the different stages that were sampled (first migration [fall], return migration [spring], and nesting [summer]), the first fall migration showed the lowest while the nesting season produced the highest amount of CREB in the samples in both species. Also, the two species differed significantly in the amount of CREB expressed across the seasons with the lower amounts showed in the longer-distance migrant Veery.

These findings suggest that that learning and long-term memory formation may be less relevant during migration relative to the breeding season. However, the results seem to support the idea that in order to develop a global navigational map that enables the migrant to compensate for displacements, migrants first have to experience and spend time at the wintering grounds (Thorup et al., 2007). Thus, depositing long-term spatial memory during the first migratory trip may have little value without a spatial reference point at the wintering destination.

Chapter IV. Sociality and Information Acquisition during Stopover

Social Learning Theory (Boyd & Richerson, 1988) predicts that social information should be favored over individual sample information when individual sampling is (a) costly or risky, or (b) the outcome of individual sampling is uncertain. Stopover conditions during passage satisfy these conditions, therefore to test this prediction I assessed flocking behavior at two different stages during a migrant's stopover during spring migration at the northern coast of the Gulf of Mexico. These periods differed in the amount of knowledge a migrant likely had about the stopover site. This measure is only a surrogate variable to assess the potential for social learning in a field setting as I assumed that in order to obtain social information a migrant would have

to maintain a relatively close proximity to others (i.e., become temporarily part of a foraging aggregation or flock). I found that migrants were more likely to flock soon after arrival than later when presumably gained more information about local conditions. Flocking behavior of radio-tracked Hooded Warblers (*Wilsonia citrina*) also supported these results, while movement data from this species showed that the daily area used by these migrants declines as they transition from an early exploratory/social phase to a more sedentary/solitary period by the end of the stopover period. Moreover, energetic condition was only a weak predictor of flocking behavior suggesting that regardless of energy stores, most migrants benefit from access to social information after arrival at a stopover site. On the other hand, data collected on the foraging behavior of Hooded Warbler, Black-and-white Warbler (*Mniotilta varia*) and Tennessee Warbler (*Vermivora celata*) revealed that flocking individuals compromise their foraging and/or movement rate, presumably, to maintain contact with the flock (Hutto, 1988).

These results suggest that there is a temporal shift in the value and use of social information during stopover. Early benefits of social information use may be outweighed by the costs an 'informed' migrant must pay to maintain access to this type of information in the latter part of stopover. For example, these costs could manifest in the form of lower food intake rate, a particularly costly price for a fattening migrant.

Chapter V. Social Facilitation and Neophobia

Upon encountering a novel place, object or food item, individuals usually exhibit two types of behavioral responses: (a) fear and aversion (i.e. neophobia), and/or (b) curiosity and attraction (i.e. neophilia) towards novelty (Corey, 1978). While neophilia and the tendency to explore novelty facilitate information acquisition in an unfamiliar

environment, neophobia generally hinders this process of familiarization and must be overcome by the individual before acquiring a new food item or learning a new foraging behavior (Greenberg, 2003). Because flocks may act as a source of information during migration, one would expect that (a) individual migrants reduce their feeding neophobia in a social setting and that (b) the neophobic response of the entire flock converges upon that of the least neophobic individual (Greenberg & Mettke-Hofmann, 2001). I tested these predictions by presenting captive, hatch year Indigo Buntings (*Passerina cyanea*) with a series of novel objects under both solitary and flocking conditions and measured the intensity of their neophobic response as a latency to approach and feed from their feeder.

The study demonstrated that Indigo Buntings reduce object neophobia in a social setting, which finding is consistent with other studies that show mitigating effects of social facilitation on feeding neophobia in resident, highly social birds (Coleman & Mellgren, 1994; Soma & Hasegawa, 2004) as well as in social mammals (Forkman, 1991; Visalberghi, Valente, & Fragaszy, 1998). However, the results did not support the prediction that feeding latencies of flock members will converge upon the least neophobic member's novelty response. Nevertheless, the degree of neophobia animals exhibit in unfamiliar situations have a demonstrated negative effect on their problem solving ability (Seferta, Guay, Marzinotto, & Lefebvre, 2001; Webster & Lefebvre, 2001). Thus lowering the emotional response to novelty does not only speed up the familiarization process with novel features of the immediate environment but it facilitates the learning of new behaviors, innovation or simply the recognition of new food items

(Greenberg, 2003), any of which can be important when an individual is under time and energetic stress.

Chapter VI. Use of Social Information in Problem Solving: A Seasonal Comparison

In Chapter IV, I demonstrated that landbird migrants prefer social foraging during the early period of stopover, which behavior could be a vehicle to obtain social information for a more complete and rapid assessment of the unfamiliar stopover habitat. However, it is unclear whether the increased use of social information is a seasonal adaptation for migration or given the opportunity and proper conditions (i.e., uncertainty or costly/risky conditions for individual sampling) birds in non-migratory condition would prefer the use of social information as well. In this chapter, I present a study that examined this question. More specifically, I tested whether migratory disposition (i.e., *Zugunruhe*) would influence the birds' use of social information and performance on a social learning test.

I presented naïve Indigo Buntings ("observers") with a novel feeder that had to be manipulated to gain access to the seeds inside. The correct feeding technique was presented by a trained "demonstrator". While buntings in migratory and non-migratory condition showed no difference in the latency to approach the novel feeder in the presence of the demonstrator, buntings in migratory disposition were slower and less successful in extracting seeds from the novel feeder. In addition, migratory buntings had significantly higher baseline plasma corticosterone levels but hormone titers did not predict performance on the social learning test.

Although the function and causal mechanism of this compromised cognitive performance is unclear, it is possible that the high energetic demand and, as a

consequence, the intense fuel deposition associated with migration may indirectly influence the migrant's ability to quickly learn a new foraging technique via social information. In a heightened motivational state, birds in migratory disposition may narrow their attention to the food while ignoring contextual or social information; ultimately, resulting in poor social learning performance. However, the slower tendency to learn from others may be compensated by the increased amount of time migrants spend in flocks during migration.

Conclusions

This dissertation is organized around a series of studies that investigate the role of information, and particularly social information, in the ecology of landbird migration. Although numerous questions remain to be answered by further research, certain observations can be made based on the findings of this dissertation research:

1) The relatively low investment in long-term memory formation during migration as well as the narrowed attention for contextual cues under a heightened motivational state seen in captive migrants magnifies the importance of a compensatory mechanism to reduce uncertainty during passage.

2) Social learning is a good candidate for this compensatory mechanism. By maintaining close proximity to other foraging migrants or residents, a newly arrived migrant may vicariously exploit the sampling behavior of others and obtain a more complete picture of the unfamiliar habitat in a timely manner, an important benefit during a period of time and energetic stress. I demonstrated some of these benefits: (a) social affiliation reduces novelty response in migrants as well as (b) speeds up the acquisition of a novel foraging behavior. However,

social information is inherently less accurate than private information and access to social information can often be costly as it requires flock membership. Thus the value of social information is context dependent so a newly arrived, naive migrant may be more likely to pay the costs (e.g., competition and compromised movement and foraging behavior) associated with flock membership than a more informed migrant preparing for departure. This shift in the value and use of social information was also demonstrated in a field setting.

3) Considering all the potential costs and benefits associated with the use of social information in the context of migration, together with the findings of this dissertation research, I would argue that social learning plays an important role in the ecology of landbird migration. Perhaps one of the most exciting aspects of *en route* social information use is largely unique to migration: the aggregation of large number of migrants from a wide range of breeding populations with a variety of experiences, foraging skills and diet preferences. This diversity provides the raw material for learning. One could easily imagine the abundant learning opportunities at stopover sites where large flocks of migrants with diverse skill sets refuel. These can be as simple as recognizing a potentially edible food item, joining in on the food discoveries of others, being warned about the approach of a dangerous but previously unknown predator or as complex as learning a new foraging technique. As a result, a relatively inexperienced migrant is not only able to adjust to local conditions and increase food intake rate in a timely manner but could potentially exploit a wider range of resources and increase its foraging efficiency with each subsequent stopover. A similar

mechanism, called "skill pool effect", was proposed by Giraldeau (1984) to

describe the effect of within-population differences in foraging repertoire in

single-species foraging flocks.

Finally, another, more and more relevant implication of *en route* social

information use deserves mentioning. Local conditions at stopover sites have been

changing in unpredictable ways over the continental scale due to rapid global climate

change (Bairlein & Hüppop, 2004). Information transfer by social learning can speed up

the adjustments to the changing global environment (Helm, Piersma, & Van der Jeug,

2006) provided that the changes are not too severe and migratory bird populations still

have individuals who can successfully cope with them and serve as behavioral templates

for others.

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CHAPTER II

INFORMATION ACQUISITION DURING MIGRATION: A SOCIAL PERSPECTIVE

Migration is a life history strategy evolved to facilitate the exploitation of seasonally abundant but distant resources (Dingle, 2006; Rappole, 1995). The cost migrants pay to gain access to these resources can be measured in time, energy and mortality (Alerstam, Hedenström, & Åkesson, 2003). Indeed, most mortality seems to occur during the migration phase of the annual cycle (Sillett & Holmes, 2002) suggesting that migration is a significant population limiting factor (Newton, 2006). This may not be a surprise considering the multitude of challenges migrants face *en route*: aside from navigating across vast continents and coping with adverse weather conditions, migrants must meet the high energy demand of long-distance travel under unpredictable conditions (Moore, Gauthreaux, Kerlinger, & Simons, 1995; Moore, Smith, & Sandberg, 2005). That is, a migrant's fitness is dependent upon the timely and safe acquisition of resources at unfamiliar stopover sites. This conundrum poses an interesting and so far largely overlooked problem: how do migrants acquire information to reduce risks and uncertainties associated with unfamiliar stopover sites? Moreover, what is adequate information under the simultaneous constraints of time minimization and energy requirements? The information migratory birds use to make decisions about resources and sources of stress during stopover and the manner in which they do so is poorly understood (e.g. Moore & Aborn, 2000). The development of the ecology of information use (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Giraldeau, 1997) and the recent advancement in our understanding of the role of social interactions in information acquisition (Bonnie & Earley, 2007; Danchin, Giraldeau, Valone, & Wagner, 2004;

Giraldeau, Valone, & Templeton, 2002; Hoppitt & Laland, 2008; Kendal, Coolen, van Bergen, & Laland, 2005; Laland, 2004; Seppänen, Forsman, Mönkkönen, & Thomson, 2007; Valone, 2007) allow us to explore these questions in more detail.

Risks and uncertainties associated with novel surroundings can be reduced by gathering and continuously updating information about the immediate environment. After landfall, migrants can sample resources directly, through their personal experience (asocial learning), and/or acquire information by observing others' location and behavior (social learning) (Moore & Aborn, 2000). Asocial learning allows migrants to gather accurate, up to date information although the sampling process requires significant time and energy investment and may lead to delayed refueling and increased exposure to predators. Social learning, on the other hand, may provide a shortcut to become informed by relying on readily available social information obtained vicariously through other migrants while the observer may stay in the relative safety of a foraging flock or in cover. By using social information, a migrant searching for profitable resources after landing can reduce the risk of predation and time associated with direct sampling. The performance and location of other foraging migrants potentially provides the same, if not more, information content to a migrant than asocial, direct sampling: e.g., location and quality of food resources, type of novel food sources and the appropriate foraging technique to access them, location of predator and the current level of predation risk at a site (Galef & Giraldeau, 2001; Galef & Laland, 2005).

Although social learning can be viewed as a cognitive mechanism to speed up the assessment of risk and resources, social information is potentially less reliable than privately acquired information mainly due to its second-hand nature (Giraldeau et al.,

2002). The cost of relying on socially obtained information when making decisions during the stopover may outweigh its benefits if, for example, a migrant distances itself in space or time from the source of the information and the information becomes outdated (Seppänen et al., 2007). This cost can become pronounced if conditions vary rapidly on a temporal or spatial scale. Moreover, the value of social information may depend on how closely the observer's foraging ecology is related to that of the demonstrator's (source of information). Heterospecifics, especially those in different foraging guilds, may provide less useful information about resources and foraging techniques than conspecifics. On the other hand, seasonal changes in behavior such as foraging and diet plasticity can reduce this ecological distance among heterospecifics and consequently promote social information use (Seppänen et al., 2007). Finally, even if the socially acquired information is up to date and accurate, the effort of keeping it updated (e.g., in a variable environment) by joining and following a foraging flock may become costly if it results in increased competition and/or forces the migrant into a sub-optimal foraging pattern (Hutto, 1988). Ultimately, the use of private versus social information by migrants can be viewed as a trade-off between accuracy and cost, while the migrant's preference will likely depend on the interplay between its internal state and the external ecological context.

To better understand information use when migrants stopover, and more specifically, what factors influence whether a newly arrived migrant relies more heavily on social information or personal sampling to explore and assess its stopover site, we turn to models developed in anthropology. Boyd and Richerson (1985, 1988) identified two main conditions under which individuals should prefer the easily accessible but

potentially less reliable social information over the costly but more accurate personal sampling information. Their models predict that individuals rely more heavily on social information (a) when personal sampling information would be too costly ("*copy when asocial learning is costly*" social learning strategy [Laland, 2004]), or (b) when their personal sampling information leaves them uncertain as to what to do ("*copy when uncertain*" social learning strategy [Laland, 2004]). For example, European starlings (*Sturnus vulgaris*) cue on foraging conspecifics to determine whether to remain at or leave a foraging patch when information about patch quality is difficult to acquire by personal sampling thus using social information in a consistent manner with the "copy when asocial learning is costly" strategy (Templeton & Giraldeau, 1996). If, however, the location of food is predictably associated with contextual cues in an environment, starlings are less likely to rely on social information than in another environment where these cues are unpredictable, lending importance to the "copy when uncertain" strategy (Rafacz & Templeton, 2003).

Although Boyd and Richerson developed their models with humans in mind, the assumptions and predictions of their models have been applied to other organisms as well and were used to create a theoretical foundation for social learning studies (e.g. Galef & Laland, 2005; Giraldeau, 1997; Kendal, Coolen, van Bergen, & Laland, 2005; Laland, 2004). We use them here to propose a predictive framework to study information use in migratory birds. Herein, we put forward eight testable predictions about ecological factors that may promote social information use during migration. These predictions are organized under two hypotheses: (a) "costly information hypothesis", which refers to the "copy when asocial learning is costly" strategy and (b) "uncertainty hypothesis", which

refers to the "copy when uncertain" strategy generated by Boyd and Richerson (1985, 1988).

<div align="center">Hypotheses and Predictions</div>

Costly Information Hypothesis

Migration is associated with a set of ecological conditions under which social information should be favored when available due to its lower costs. Migrating birds are under time and energetic constraints (Alerstam, 1993; Hutto, 1985; Loria & Moore, 1990; Wang & Moore, 2005), so any factor that causes delay in refueling and departure from a stopover, e.g., predation risk (Cimprich, Woodrey, & Moore, 2005), can be viewed as increasing the costs of information acquisition and should promote social information use in migrants (Nocera, Taylor, & Ratcliffe, 2008).

Prediction 1: Migration strategy. Migration strategy (e.g. short- or long-distance, partial or obligate, time- or energy-minimized, nocturnal or diurnal) likely has significant influence on what type of information is valued at certain stages of migration. Long-distance migrants, for example, may be under stronger selection to minimize migration time than short-distance migrants (Alerstam, 2003; Alerstam & Lindström, 1990), thus we should expect that the incentive for timely refueling would increase tolerance to risk using less accurate information (c.f. Metcalfe & Furness, 1984; Moore, 1994). Because migration speed seems to increase with migration distance (Alerstam, 2003; Ellegren, 1993), speed may be a good predictor of social information use: the faster the migration (either at the species, population or individual level) the higher the likelihood that a migrant uses social information when available to reduce time and risks associated with environmental assessment after landing (see also *Prediction 5*).

Prediction 2: Habitat requirements. The likelihood that a migrant can find suitable

stopover sites during passage is largely determined by the migrant's ecological tolerance

toward different habitat types and the availability of the preferred habitat type across the

landscape (Buler, Moore, & Woltmann, 2007; Moore et al., 1995). For example,

palearctic marsh warblers (*Acrocephalus sp.*) prefer reed beds as stopover habitat,

however the availability and distribution of this type of habitat is scarce and patchy

across the landscape. Thus, the likelihood of randomly encountering reed beds at the end

of a migratory flight is low. The value of revisiting or finding high quality stopover sites

in these species is likely high and the incentive to learn and remember the location of

previously used high quality reed beds or use social information (e.g. conspecific vocal

cues) during habitat selection to locate such habitat should also be high. The relatively

high stopover site fidelity rate (Cantos & Telleria, 1994; but see Catry et al., 2004) and

the high responsiveness to conspecific vocal cues (Mukhin, Chernetsov, & Kishkinev,

2008) in some of these species relative to habitat generalists seem to support this

prediction.

Prediction 3: Foraging ecology. Diet and the distribution of food resources determine

foraging strategies and consequently the cues and information that foragers use to locate

resources (Moore & Aborn, 2000). Despite the important role of foraging and diet

plasticity during passage (Graber & Graber, 1983; Loria & Moore, 1990; Martin & Karr,

1990; Parrish, 2000; Wang & Moore, 2005), omnivorous migrants use patchily

distributed locally abundant resources such as fruits, nectar or seeds, whereas strictly

insectivorous migrants feed only on insect prey, which is usually more evenly distributed.

The two types of resource present migrants with different economic decisions (Brown,

1964; Crook, 1965). The importance of extra eyes in finding patchily distributed food and the difficulty of monopolizing them should promote social foraging and the long term use of social information in omnivores (Greenberg & Salewski, 2005). On the other hand, the likelihood of finding evenly distributed food may not increase substantially if a foraging insectivorous migrant joins another but competition may. Making this distinction may be useful when one would like to understand the source and the value of information used by refueling migrants (Németh & Moore, 2007).

Prediction 4: Energetic condition. The amount of energy reserves a foraging bird has should influence its actual social foraging tactic in relation to its flock members, that is, whether to actively search for food (producer tactic) or to join in on others' findings (scrounger tactic) (Barta & Giraldeau, 2000). Lean House Sparrows (*Passer domesticus*) have been shown to prefer scrounging, which provides less variable feeding rates (Lendvai, Barta, Liker, & Bókony, 2004). This indicates that it pays to increase the use of social information to avoid starvation. In migrants, the importance of energy reserves is magnified therefore lean birds should prefer social information after landing to reduce the time and energy costs of exploration. Lean migrants show increased motivation to maximize food acquisition: they invest more in competitive interactions (Moore, Mabey, & Woodrey, 2003), diversify foraging behavior (Loria & Moore, 1990; Wang & Moore, 2005) and resume foraging sooner after exposure to a predator (Cimprich & Moore, 2006). This behavioral shift may significantly increase the risk of predation (Dierschke, 2003); thus, migrants in poor energetic condition should rely more heavily on social information to compensate for this increased risk (Barta, Liker, & Monus, 2004; Németh & Moore, 2007).

Prediction 5: Time of season. Migrants that are delayed in their departure from the breeding sites show higher travel speed (Ellegren, 1993) and may attempt to 'catch up' and reduce their lag behind their conspecifics traveling to the same general goal area (Drent, Both, Green, Madsen, & Piersma, 2003; Fransson, 1995). This increased time constraint should promote the use of social information.

Uncertainty Hypothesis

Environmental conditions can change very rapidly and often in unpredictable ways during migration, resulting in an ever-shifting ecological context in which migrants must make the appropriate decisions to meet the energetic demands of long distance travel. Even if a migrant obtained reliable, personal sampling information about the distribution and quality of food resources at an unfamiliar stopover site, the ecological context at any stopover site can quickly shift and the once accurate information becomes erroneous and outdated leaving the migrant uncertain about the success of its decisions. Several factors can increase uncertainty in the decision making process of a refueling migrant and here we focus on three of them.

Prediction 6: Endogenous control. A migrant's annual schedule is shaped by the interplay between its endogenous program and proximate factors such as daylength, temperature, food supply, weather and social interactions (Berthold, 2001; Gwinner, 1996; Gwinner & Helm, 2003; Helm, Piersma, & Van der Jeug, 2006). Depending on the rigidity of the endogenous program, social information may play a significant role in determining migration timing, orientation and habitat selection (Chernetsov, Berthold, & Querner, 2004; Terrill, 1987). In long-distance, nocturnal migrants, for example, a strict endogenous program may leave less room for the use of social information after the

initial exploratory period than in short-distance, partial or diurnal migrants. The latter ones may use social cues to find and track resources and maintain cohesive flocks during migration possibly to reduce predation risk and benefit from the navigational experience of conspecifics (e.g. Dolnik & Blyumental, 1967; Rabøl & Noer, 1973).

Prediction 7: Experience. Successful migration is dependent upon how well a migrant can cope with *en route* challenges (Alerstam & Lindström, 1990; Moore et al., 2005). Thus, familiarity and experience with a variety of stopover habitats, food types, foraging techniques and potential predators can ultimately lead to increased survivorship and successful migration (Moore et al., 2003; Woodrey, 2000). Young, inexperienced individuals are often socially subordinate to adults and forced to suboptimal, often riskier, foraging sites through interference competition (Ekman & Askenmo, 1984; Woodrey, 1995). This competitive disadvantage during fat deposition can result in higher mortality, longer stopovers due to lower fat deposition rates, or suboptimal departure fuel loads, which may be especially critical at sites near ecological barriers where migrants may concentrate (Alerstam, 1978; Moore et al., 1995). Furthermore, young, inexperienced migrants are more likely to make orientation errors than adult birds (Moore, 1984; Sandberg, Pettersson, & Persson, 1991) possibly because of the not yet developed navigational map in first time migrants (Thorup et al., 2007). Finally, a migrant's ability to "predict" weather conditions conducive to a successful flight may also depend on experience and flock members may be important sources of information in this context. In general, social learning speeds up the familiarization process with novel situations (Galef & Giraldeau, 2001) often by reducing neophobia in the inexperienced individual (Greenberg & Mettke-Hofmann, 2001; Visalberghi, Valente, & Fragaszy, 1998) while it

can also enhance orientation and navigation performance (Balcomb, 1977; Chernetsov, Berthold, & Querner, 2004; Couzin, Krause, Franks, & Levin, 2005; Hamilton, 1967; Moore, 1990; Simons, 2004). Therefore, we should expect that the use of social information is elevated in inexperienced migrants.

Prediction 8: Variability in stopover conditions. Ecological conditions (e.g., resource availability, competitor density, risk of mortality, habitat heterogeneity, weather or proportion of novel food types or predators) vary along a migratory route as a function of time and space, both on the local and global scale. As a high degree of variability is associated with increased uncertainty of stopover success, migrants should value a more complete assessment of stopover conditions and rapid information updates, both of which should favor the use of social information.

Conclusions

Studying the ecology of information use within the context of migration provides insight into the rules of decision making under multiple simultaneous constraints (i.e., time, energy, information and predation). Social context and the importance of social information in decision making during different stages of migration have been largely overlooked despite their significant role in influencing annual schedules and aiding navigation and resource acquisition (Hamilton, 1962, 1967; Helm et al., 2006; Wallraff, 1978).

High concentrations of migrants at stopovers are often considered as competitors that reduce fitness in a density-dependent manner (Fretwell & Lucas, 1970; Moore et al., 1995). However, residents and other migrants, both conspecifics and heterospecific competitors, can also be an important source of information that reduces risks and

uncertainty, as it speeds up the process of resource assessment and fuel deposition rate (Németh & Moore, 2007; Valone, 2007). Thus, we may start to think about stopover sites as additional sources of information where temporarily associating with others can have important and long lasting benefits. Moreover, as conditions at stopover sites seem to change in unpredictable ways over the continental scale due to global climate change (Bairlein & Hüppop, 2004), rapid information transfer by social learning can aid adjustments to the changing global environment (Helm et al., 2006). Therefore, we encourage theoreticians to incorporate information use into models of optimal migration strategies and field researchers to test the assumptions and predictions of social and asocial learning during migration.

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CHAPTER III

SEASONAL VARIATION IN CREB IMMUNOREACTIVITY IN THE

HIPPOCAMPAL FORMATION OF FIRST YEAR MIGRATORY SONGBIRDS

Abstract

Given the largely unfamiliar and unpredictable conditions experienced along migratory routes, natural selection should favor cognitive processes that reduce en route risks and uncertainties in migratory birds. These cognitive processes, however, are poorly understood. We used two intercontinental nocturnal migrants, the long-distance migrant Veery (*Catharus fuscescens*) and the shorter distance migrant Wood Thrush (*Hylocichla mustelina*), to assess the levels of spatial learning during the first year of songbird migrants, a critical period in constructing their navigational map. To estimate long-term memory formation, we measured immunoreactivity to cAMP response element binding protein (CREB) in hippocampal samples collected at autumn and spring stopover sites and at a breeding site. CREB-responsive transcription in the hippocampus is thought to play a central role in long-term memory formation. CREB expression overall was lower in the long-distance migrant and showed seasonal low levels during autumn (first) migration whereas high levels during the breeding season. Our findings suggest that young migratory birds may store relatively little spatial information until their global navigational map is fully developed and gain the ability to compensate for displacement. We discuss the adaptive value of spatial memory in short- and long-distance migrants, which may be influenced by differential time and energetic constraints.

Introduction

By integrating global and local cues with stored (genetically coded and learnt) information, migrants successfully travel across continents and arrive to their breeding and wintering quarters with high accuracy (Berthold, 2001). While we have extensive knowledge about the navigational cues used by a migrant to find the appropriate direction (Åkesson & Hedenström, 2007) we are far from understanding how important *en route* learning is in meeting the challenges of long-distance migration (Moore, Gauthreaux, Kerlinger, & Simons, 1995).

The adaptive advantage of learning is apparent with more informed individuals being better able to cope with environmental challenges (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005). In theory, natural selection should favor individuals with the ability to learn and remember spatial and olfactory cues along their route as well as habitat characteristics at stopover sites (Mettke-Hofmann & Gwinner, 2003), minimizing unpredictability during passage and ultimately, saving valuable time and energy by refueling at high quality stopover sites. However, increased learning and memory formation would require larger and more complex neural substrate, the maintenance and development of which would increase the energy and time costs of migration (Johnston, 1982; Winkler, Leisler, & Bernroider, 2004). Moreover, continuous compensation for wind drift and displacement in order to revisit learned, familiar stopover sites along the migratory route, would further increase the energy cost of migration (Alerstam, 1979; Catry et al., 2004). Thus, it remains to be determined how much migratory birds invest in spatial memory during migration relative to the breeding season when the benefits of long-term memory is more apparent (Godard, 1991).

In this study, we addressed the importance of spatial learning during a migratory songbird's first year, a critical period for migrants in constructing their navigational map (Perdeck, 1958; Thorup et al., 2007). We investigated long-term memory formation as a function of season (fall: first migration to the wintering ground, spring: return migration to the natal area and the first breeding season) in two migratory thrush species (*Turdinae*) that differ in migration distance (see below). To assess long-term memory formation, we measured immunoreactivity to cAMP response element binding protein (CREB) from hippocampal samples. CREB-responsive transcription in the hippocampus plays a central role in long-term memory formation in several species from *Drosophila* (Goda, 1995) to mice (Yin & Tully, 1996), therefore we expect that the levels of CREB immunoreactivity positively correlate with the extent of long-term memory formation in thrushes.

We test the following predictions: (a) If the development of the global navigation system of a songbird migrant is based on experience, that is, juvenile migrants first have to reach and spend time in the wintering area before gaining the ability to home to that location (Thorup et al., 2007), then *en route* CREB immunoreactivity and consequently long-term spatial memory formation should be at the lowest level during fall migration. (b) The highest level of CREB immunoreactivity should be found during the breeding season when selection should favor long-term knowledge of the local landscape and breeding territory.

Material and Methods

Study Species

We chose two ecologically similar Nearctic-Neotropical migratory thrush species that differ in migration distance to test our predictions. The Veery (*Catharus fuscescen*)

(Bevier, Poole, & Moskoff, 2005), a typical long-distance migrant, on average migrates

more than twice as far between its breeding and wintering grounds than the Wood Thrush

(*Hylocichla mustelina*) (Roth, Johnson, & Underwood, 1996), a shorter distance but still

intercontinental migrant.

Wood thrush (n_{total}=18) and veery specimens (n_{total}=15) were collected [federal

permit # 21221 (FRM) and IACUC protocol 217-003] during three periods within the

annual cycle: fall migration/stopover along the northern coast of the Gulf of Mexico in

Fort Morgan, AL in 2005-2006, spring migration/stopover along the northern Gulf coast

in Johnson Bayou, LA in 2005-2006, and in the breeding season in northeastern

Pennsylvania in Lackawanna County in 2006. Neither thrush species breed at the fall and

spring stopover sites (Bevier et al., 2005; Roth et al., 1996). Birds were captured

passively using mist-nets, age determined by plumage characteristics (Pyle, 1997) and

study subjects were euthanized via CO_2. The carcasses were kept frozen at -20°C until

hippocampal tissue was collected and Western blot analysis was performed. The

remaining organs and tissues of the carcasses are being used for several ongoing research

studies (Németh et al., unpubl. data; Owen et al., unpubl. data).

Western Blot

Standard Western blotting analysis was performed as described previously

(Tchantchou, Xu, Wu, Christen, & Luo, 2007). Briefly, hippocampal samples were

homogenized in the lysis buffer containing: 50 mM Hepes, pH 7.5, 6 mM $MgCl_2$, 1 mM

EDTA, 75 mM sucrose, 2.5 mM benzamidine, 1 mM dithiothreitol and 1% Triton X-100.

Equal amounts of protein (20µg) were resolved on a 12% SDS–PAGE, then transferred

to polyvinylidene difluoride membranes and blocked with 5% non-fat dry milk. This was

followed by overnight incubation at 4°C with different primary antibodies, which included antibody against phosphorylated CREB (pCREB, 1:1000) or CREB (Santa Cruz, Inc., Santa Cruz, CA; 1:500). The blots were then incubated with horseradish peroxidase-conjugated secondary antibodies (Santa Cruz Inc., Santa Cruz, CA; 1:5000). Immunoreactivities were detected by an enhanced chemilunescence kit (Amersham Biosciences, Piscataway, NJ). The immunoreactive bands from Western blots were scanned and the mean density was obtained with AlphaEase FC software (Alpha Innotech, San Leandro, CA).

Statistical Analyses

We conducted a two-way ANOVA in two steps. First, we tested for interaction between the factors (species and season); then, as we did not find significant interaction, we tested for significant main effects with the interaction term removed from the two-way ANOVA model. We used Tukey HSD *post-hoc* pairwise comparisons to test for statistically significant differences in CREB immunoreactivity between seasons. Statistical significance level was set at $\alpha = 0.05$. All data analyses were done by SPSS 15.0 (SPSS Inc., Chicago, IL, USA).

Results

CREB protein expression in the hippocampus differed in the two thrush species and varied seasonally. The two-way ANOVA indicated no interaction between season and species ($F_{2,27} = 0.548$, $p = 0.585$, $\eta^2 = 0.039$) but showed significant main effects for both season ($F_{2,27} = 3.345$, $p = 0.049$, $\eta^2 = 0.187$) and species ($F_{1,27} = 29.651$, $p < 0.001$, $\eta^2 = 0.506$) (Figure 1). Tukey HSD procedure revealed that CREB protein expression was significantly higher during the breeding season than during fall migration ($p = $

0.039). There was no significant difference between CREB expression in thrushes from the breeding season and from spring migration ($p = 0.426$) neither between thrushes from spring migration and from fall migration ($p = 0.394$).

Discussion

Our study suggests that the extent of long-term memory formation may vary with season in two migratory thrush species. Long-term memory formation was at the lowest level during the first migratory trip when the bird had no prior experience with their wintering area. Whereas, memory formation was highest during the breeding season when the benefits of being informed about the risks and resources of the breeding territory and the surrounding landscape would likely favor higher investment in long-term memory. While we did not sample thrushes on the wintering grounds, we would expect selection pressures similar to the breeding season to play a role in shaping long-term memory formation during the wintering phase.

These findings are consistent with the notion that land-mark based navigation and consequently the hippocampus have relatively little importance during global navigation in long-distance migrants (Bingman & Cheng, 2005). Bingman and Cheng (2005) proposed that migrants might be guided by multiple navigational mechanisms working at different scales. For example, a low resolution global geomagnetic grid could be the basis of navigation over large stretches of unfamiliar areas whereas when the migrant approaches the goal area (wintering or breeding region) an olfactory map of atmospheric odors might provide better resolution during homing. Finally, on an even smaller scale, a landmark-based map could guide the migrant over the familiar landscape to her breeding home range. Thus, the hippocampus should have a serious role in fine tuning navigation

as the migrant is approaching goal areas (Bingman & Cheng, 2005). Indeed, migratory experience seem to increase the size and/or neuron density of the hippocampus (Cristol et al., 2003; Healy, Gwinner, & Krebs, 1996; Pravosudov, Kitaysky, & Omanska, 2006).

The role of memory is particularly interesting during the first migration when the navigational map of hatch year migrants are not fully developed. Our results are in line with Perdeck's hypothesis that migrants have to experience and spend time in their wintering grounds before gaining the ability to home after wind displacement (Chernetsov, Kishkinev, & Mouritsen, 2008; Mouritsen & Larsen, 1998; Perdeck, 1958; Thorup et al., 2007). If so, a juvenile migrant may invest little in long-term memory formation before reaching the wintering ground and navigates using only genetically programmed directional and distance information (Berthold, 2003). Once the wintering ground is reached, the new home range (or territory) will serve as a future spatial reference point. Learning landmark- or map-based cues during the first migration, when inexperienced, often displaced young birds end up in low quality stopover sites, thus would carry little benefits for future migrations.

We also observed interspecific differences in overall investment in memory formation. This difference may be due to different selective pressures associated with short and long-distance migration (Alerstam & Lindström, 1990). Short distance migrants are, by definition, closer to the goal areas during migration, travel slower (Ellegren, 1993) and spend more time at stopover sites (Rabøl & Petersen, 1973). For example, the wood thrush takes, in average, a day longer stopover after a trans-Gulf flight at our coastal study site in Louisiana than the Veery (Wang & Moore, 1997). This more relaxed schedule may provide more opportunity to select favorable weather conditions to revisit

familiar high quality stopover sites. Long-distance migrants, on the other hand, are faced

with increased time and energetic demands, which may leave less room for energetically

expensive adaptations such as elevated long-term memory formation and compensation

against wind displacement to follow a learnt route.
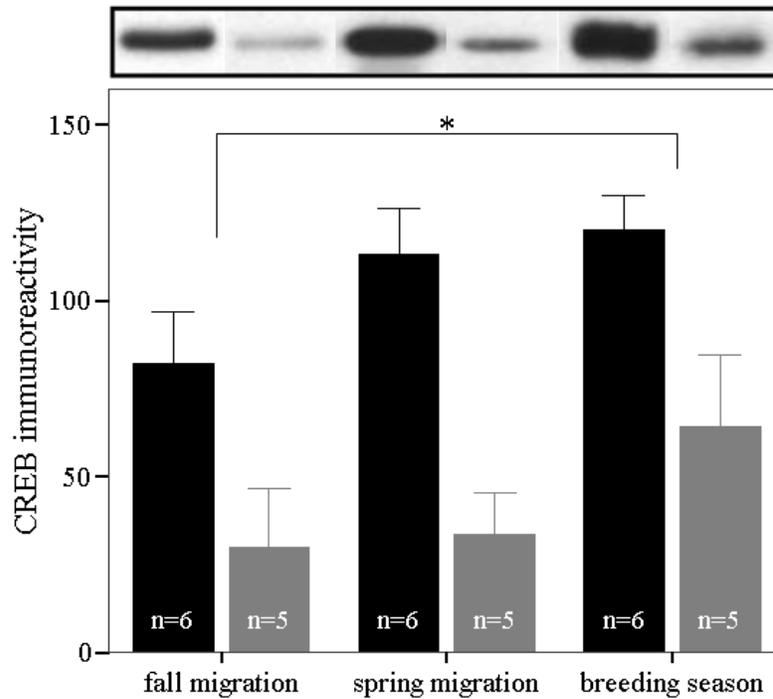
Figure 3.1. Representative Western blot and quantitative analysis of CREB protein expression in hippocampal samples collected in different phases of the annual cycle [■ Wood Thrush, ■ Veery]. Mean CREB immunoreactivity was determined from scanned immunoreactive bands by using AlphaEase FC software. Bars indicate Mean ± 1 SE.

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CHAPTER IV

SOCIALITY AND INFORMATION ACQUISITION DURING STOPOVER

Abstract

The better informed an individual, the better able to meet the demands of a variable environment. When a migratory bird stops over during passage, she must adjust to unfamiliar surroundings, satisfy nutritional demands, compete with other migrants and resident birds for limited resources, avoid predation, balance conflicting demands between predator avoidance and food acquisition, and often cope with unfavorable weather. A successful migration depends on solving these and other problems, the solutions to which are measured in units of time and condition. Migrants that gather reliable information about unfamiliar habitats in a timely fashion increase the likelihood of a successful migration. For example, a migrant may estimate food availability or predator pressure faster and more accurately by combining personal information gathered while sampling with social information obtained while observing the behavior of other migrants. In this paper, we present data from a field investigation of the use of social information by migrants. Focal sampling of free ranging and radio-tagged Nearctic-Neotropical passerine migrants in coastal habitat following flight across the Gulf of Mexico suggests that migrants respond to a lack of information by foraging in temporary feeding assemblages. This preference for flock foraging declines over the course of the stopover period in insectivorous migrants, but persists in omnivorous birds, which suggests that the value for social information depends in part on a migrant's foraging ecology. We argue that social foraging enables migrants to assess more fully unfamiliar

environments during stopover, thereby reducing risks associated with lack of prior information.

Introduction

Although many migratory birds are capable of making spectacular, non-stop flights over ecological barriers, few actually engage in nonstop flights between points of origin and destination, rather they stopover periodically and often before resuming migratory flights. Indeed, the cumulative amount of time spent at stopover sites far exceeds time spent in flight and determines the total duration of migration (Alerstam, 1993). When a migrant stops over, she finds herself in unfamiliar surroundings (Moore, Kerlinger, & Simons, 1990; Petit, 2000) at a time when energy demands are likely to be high (Loria & Moore, 1990), often faced with the need to acquire food in a short period of time, while balancing conflicting demands between predator avoidance and food acquisition (Cimprich, Woodrey, & Moore, 2005; Lindström, 1990; Moore, 1994), competition with other migrants and resident birds for limited resources (Hutto, 1985; Moore & Yong, 1991), not to mention the need to make accurate orientation decisions (Able, 1972). How well migrants "offset" the costs of migration depends on how well they solve the problems that arise during passage. Solution of *en route* problems determines the success of a migration, while a successful migration is ultimately measured in units of time and condition during passage and upon arrival at the destination (see Sandberg & Moore, 1996; Smith & Moore, 2003).

When trying to understand how migrants solve problems that arise *en route*, it is important to recognize that migration occurs over a broad geographic, yet a relatively short temporal scale, which necessarily limits time and information available to migrants

to evaluate different sites. Given the time, energy and information constraints at stopover sites, migratory birds are expected to employ efficient cognitive strategies to compensate for the lack of prior information about stopover sites when making decisions in response to novel habitat features and food types. Cognitive processes (e.g. exploration and learning) are likely to contribute to the successful completion of migration by increasing the chance of a rapid assessment of resources and predation risk (Cimprich et al., 2005). When settling in a habitat with unpredictable spatial distribution of optimal resources, the initial exploration or "discrimination phase" (Ward, 1987) may carry costs in the form of time away from foraging while increasing the risk of predation, an especially serious problem for a fat-depleted, energetically stressed migrant. A foraging migrant, however, may supplement personal sample information (i.e., *private information* gained on its own) with socially acquired cues provided inadvertently by other foraging individuals (*inadvertent social information*) (Danchin, Giraldeau, Valone, & Wagner, 2004; Nocera & Ratcliffe, 2010; Nocera, Taylor, & Ratcliffe, 2008; Valone & Templeton, 2002). The combination of private information with social information obtained from observing the location and successful or unsuccessful sampling activities of others improves the speed and accuracy with which an individual assesses habitat quality (Rafacz & Templeton, 2003; Smith, Benkman, & Coffey, 1999; Templeton & Giraldeau, 1996; Valone, 1989). Thus social learning enables the individual to more completely assess an unfamiliar environment (Galef & Giraldeau, 2001; Galef & Laland, 2005; Hoppitt & Laland, 2008; Kendal, Coolen, van Bergen, & Laland, 2005; Valone, 1989, 2007), which may be particularly important for migrants under time, energetic and information constraints (see Chapter II).

Theory predicts that the use of social information may depend on the predictability of the environment (Boyd & Richerson, 1985, 1988). For example, if the location of food is predictably associated with contextual cues in one environment, European starlings (*Sturnus vulgaris*) are less likely to rely on social information than in another environment where these cues are unpredictable (Rafacz & Templeton, 2003). Furthermore, there is an evolutionary trade-off between using accurate but costly private information and easily accessible but potentially less reliable socially acquired information (Galef & Laland, 2005; Kendal, Coolen, & Laland, 2009). Boyd and Richerson's evolutionary model (1988) predicts that individuals should use social learning when individual learning is difficult or costly (e.g. learning to avoid a predator by private sampling). Empirical evidence suggests that starlings, for example, use information obtained by observing other individuals' foraging success to determine whether to remain in or leave a foraging patch only when information about patch quality was difficult to acquire by personal sampling (Templeton & Giraldeau, 1996). Moreover, increased reliance on social information within a group can result in an informational cascade in which the socially acquired information overrides personal information (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Giraldeau, Valone, & Templeton, 2002). As a consequence, individuals may copy decisions blindly with the potential of transmitting erroneous information (e.g. false alarm flights).

Clearly, migration represents an ecological setting when social information may provide unique benefits to individuals who forage in flocks and gain access to supplementary information that ultimately reduces uncertainty and time associated with risk and resource assessment (Moore & Aborn, 2000; Nocera & Ratcliffe, 2010; Nocera

et al., 2008). In this study, we tested the hypothesis that migrating birds use inadvertent social information to reduce time and risks associated with environmental assessment after arrival at stopover sites (*Information Constraint Hypothesis*). In order to obtain social information, migrants have to join social assemblages temporarily, thus the duration or frequency of flock participation should be indicative of social information use. We used the time a migrant spent in a flock as a surrogate measure of social information use to test the following three predictions derived from the Information Constraint Hypothesis:

1. Migrants should exhibit high flocking propensity after arrival.

2. Flocking propensity should decline over time as birds gain more information and the costs of obtaining social information (e.g. competition from flock members and non-optimal foraging and/or movement rate to maintain flock membership (Hutto, 1988) gradually outweigh the value of social information.

3. Social information use should be condition dependent, that is, migrants in better arrival condition may afford to take the time away from refueling to gain reliable private information, therefore should value social information less than migrants in poor arrival condition.

We tested these predictions at a spring stopover site located in southwest Louisiana along the northern coast of the Gulf of Mexico. Spring migrants usually arrive at our study site in the afternoon hours following a trans-gulf flight (Gauthreaux, 1971) allowing us to compare social behavior soon after arrival, when migrants lack information about the stopover site, with behavior the next morning when the migrant has had a chance to explore and collect information. We conducted transect surveys to assess

the proportion of migrants participating in flocks under these two conditions. In addition to the surveys, we collected foraging behavior from several Parulid warblers in solitary and social settings to assess the costs and benefits of social foraging, and whether there is a cost associated with the acquisition of social information. Finally, a more controlled component of the study involved radio-tracking male Hooded Warblers (*Wilsonia citrina*) (Evans Ogden & Stutchbury, 1994) from the time of arrival till departure to monitor their social, spatial and foraging behavior and gain a better understanding of the migrants' response to the changing value of social information.

Methods

Study Site and Mist-Netting

The study was conducted at a long-term banding station (29°45'N, 93°37'W) situated within a coastal forested wetland site near Johnson Bayou, in southwestern coastal Louisiana (for detailed habitat description see Barrow, Chen, Hamilton, Ouchley, & Spengler, 2000). Birds were captured daily between 7:00 - 16:00 CST using 26-30 mist nets (12 x 2.6 m with 30 mm mesh) from the last week of March through the first week of May, 2004-2007. Nets were checked every 30 minutes. We identified species, sex and age by using plumage characteristics (Pyle, 1997), and measured unflattened wing length (to the nearest 0.5 mm) and body mass (to the nearest 0.1 g) of all captured individuals. We quantified fat stores by scoring visible subcutaneous fat deposits on the furcular and abdominal region using a 6 point ordinal scale (according to Helms & Drury, 1960). Breast muscle mass was estimated using the 4-point ordinal scale of Bairlein (1995). Mist-netting provided male Hooded Warblers for the radio-telemetry component of this study.

Transect Surveys

We conducted transect (650m x 50m) surveys daily during the spring banding seasons of 2004 and 2005, once in each afternoon (n = 58; at 15:30 CST) and again the next mornings (n = 58; at 7:00 CST). The survey transect was flagged at every 25 m along the center line and on both sides to aid distance estimation and spatial coordination. We walked the center line slowly (approximately 500 m/hour) and recorded the spatial position of each bird detected by sight or sound on a grid map. In addition, the social status of each migrant encountered was classified as solitary or flocking, where an individual was flocking if it was foraging within 15 m to another migrant, and they were moving in the same general direction. We calculated the proportions of migrants that were in flocks for each survey and compared the mean proportion for the afternoon with that of the morning surveys with a paired t-test. We analyzed our survey data separately for insectivorous and omnivorous migrants to test for the effect of resource distribution on social behavior.

Radio-telemetry

The "pulse-like" pattern by which migratory songbirds arrive at stopover habitats along the northern coast of Gulf of Mexico (Kuenzi, Moore, & Simons, 1991; Moore & Kerlinger, 1987; Moore et al., 1990) allow us to infer arrival time for the captured Hooded Warblers. Male Hooded Warblers were fitted with a radio transmitter (Holohil® LB-2, 0.5 g) and tracked until departure in the spring of 2006 and 2007. Daily tracking started at 7:00 CST and ended minimum at 17:00 CST but lasted often until sunset. We assessed the target bird's social status (i.e., solitary or flocking) and recorded its location in every 15 minutes by marking its positions on a grid map referenced to a flagged grid

system (with 25 x 25 m grid cells) at the study site. The grid maps were georeferenced for data analyses. The spatial coordinates of birds that moved out of the study site were recorded by using a GPS unit. Because most Hooded Warblers stopover for only a few days at our study site (median stopover length of Hooded Warblers staying beyond the day of capture was 3 days in 2001-2005; Németh and Moore, unpubl. data) and we expected to see a change in the migrant's familiarity with local conditions over a few days, as well as, to minimize extra effort spent on outlier birds, target birds were followed for a maximum of four days. Any bird that stayed longer than four days was located once a day to obtain information on exact stopover length. When the transmitter signal was not detectable in the morning, the observer drove around the study site in an approximately one km radius and checked signal reception repeatedly to make sure that the bird did not relocate to a woodlot nearby between two tracking periods. If no signal was detected we considered the bird departed for migration. Although, the lack of signal detection may also be due to transmitter failure, the likelihood of that occurring over night as opposed to a nocturnal migratory flight is relatively small. We made every effort to visually relocate the tagged individuals in every 15 minutes and assess their social status without disturbing the bird. However, when this was not possible due to thick vegetation, location was estimated by biangulation and social status assessed based on the presence or absence of other migrants within 15 m radius of the estimated location of the tagged bird. We calculated the following parameters: (a) proportion of time spent in a flock on each day, (b) condition index for each individual by dividing its arrival mass with its wing chord, and (c) linear distance between the two furthest locations the bird was observed during the course of each day.

Foraging Observations

Foraging behavior data were collected on both unmarked warblers and radio-tagged Hooded Warblers in 2004-2007. We systematically traversed the study site once a day in the morning hours to look for individuals of four focal species: Hooded Warbler, Tennessee Warbler (*Vermivora peregrine*), Black-and-white Warbler (*Mniotilta varia*) and Worm-eating Warbler (*Helmitheros vermivorus*). These species were selected because of their relative abundance at the site during spring migration and because they vary in the degree of foraging specializations and flocking propensity within wood-warblers (*Parulidae*) during the non-breeding season (Morse, 1989). When a focal individual was encountered, the observer recorded the sequence of foraging maneuvers, according to the terminology set by Remsen and Robinson (1990), the type of substrates used by the bird, the distance moved between each maneuvers and the estimated height (in 0.5 m units) the behavior was observed. Only sequences of foraging maneuvers longer than 20 seconds were used for analysis (Robinson & Holmes, 1982). If a second individual of the same species and sex (when identifiable) was encountered on the same transect, only birds that were at least 100 m apart were observed to ensure the independency of the observation. If multiple foraging sequences were recorded for an individual, the sequences were pooled and a mean value was considered as an independent unit for the analysis. We calculated the following parameters for solitary and social conditions separately: (a) foraging rate: the number of foraging maneuvers exhibited per minute; and (b) movement rate: distance moved per minute. Mean foraging and movement rates under the two conditions were compared using t-tests. Statistical

analyses were performed using SPSS 15.0 (SPSS Inc., 2006) and all tests were two-tailed unless specified otherwise.

Results

Significantly more migratory birds (mean ± SD = 69.18 % ± 24.73) participated in flocks at our study site following a trans-gulf flight than one would expect it only by chance (one sample t-test, $t_{(57)}$ = 5.907, $P < 0.001$). This high flocking propensity in migrants declined significantly by the next morning (one-tailed paired t-test, $t_{(57)}$ = -1.810, $P = 0.037$). However, foraging ecology seems to influence this change in social behavior. We found that insectivores were more likely to flock soon after arrival than the next morning ($t_{(57)}$ = -2.326, $P = 0.024$, Figure 4.1A), whereas omnivores showed no difference over time ($t_{(55)}$ = -0.279, $P = 0.781$, Figure 4.1B).

In radio-tracked Hooded Warblers, the amount of time spent in flocks declined by the latter part of the stopover period (paired t-test; $t_{(9)}$ = 2.322, $P = 0.045$; Figure 4.2). This shift in sociality was accompanied by a significant reduction in linear space explored by the migrant (paired t-test; $t_{(9)}$ = 2.545, $P = 0.031$; Figure 4.3). However, there was only a weak, non-significant, negative correlation between arrival energetic condition and time spent in flocks on the first day of stopover (Pearson's r = -0.299, N = 15, $P = 0.279$, Figure 4.4). Finally, the age of the migrant did not significantly influence its affinity to flocks (ANCOVA with condition index as a covariate; $F_{(12)}$ = 3.289, P = 0.095).
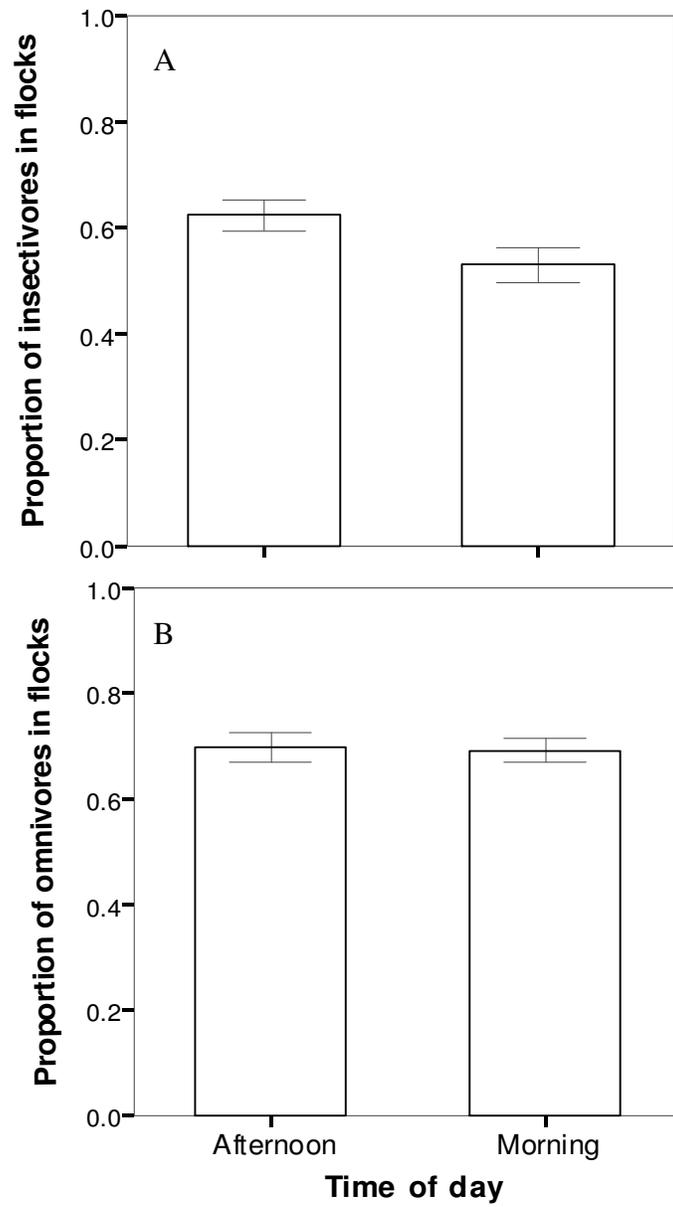
Figure 4.1. Proportion of insectivorous (A) and omnivorous (B) migrants found flocking on the afternoon of arrival and the next morning. Error bars represent Mean ± 1 SE
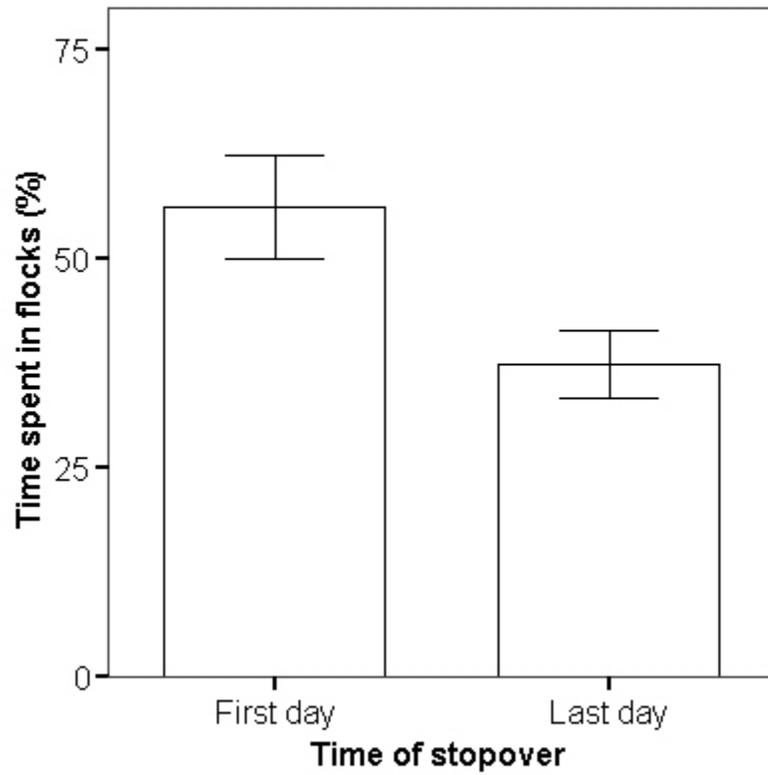
Figure 4.2. Percent of time spent in flocks by radio-tracked Hooded Warblers (*N* = 10) on the first and last day of stopover. Error bars represent Mean ± 1 SE
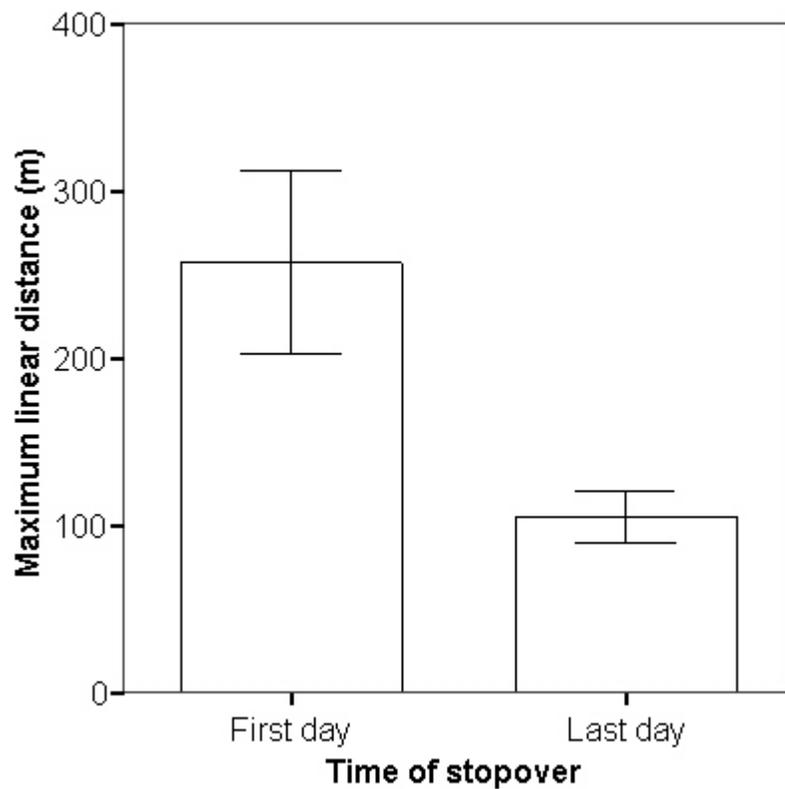
Figure 4.3. Linear distance between the two furthest points radio-tracked Hooded Warblers ($N = 10$) were observed on the first and last day of stopover. Error bars represent Mean ± 1 SE
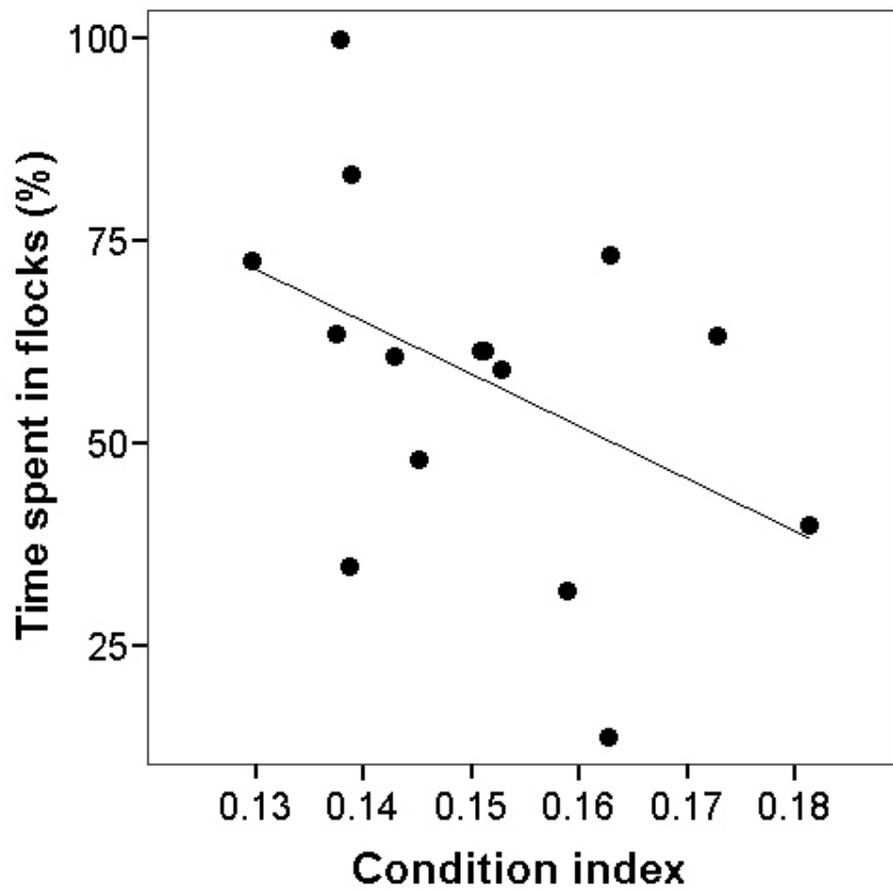
Figure 4.4. Percent of time spent in flocks by radio-tracked Hooded Warblers (*N* = 15) on the first day of stopover in relation to arrival energetic condition.

Foraging observations revealed that Hooded Warblers had higher foraging success and a more rapid movement pattern when foraging alone than when foraging in flocks (Table 4.1). Similarly, solitary foraging resulted in higher movement rate in Black-and-white Warblers and higher foraging success in Tennessee Warblers. We were not able to collect foraging data from a large enough sample of Worm-eating Warblers, thus we excluded this species from the analyses.

Discussion

When migrants stopover during passage, they often find themselves locally concentrated and facing heightened energy demand (Moore, Gauthreaux, Kerlinger, & Simons, 1995). To the extent they are unfamiliar with the area within which they stopover, which is probably true of most migrants (Catry et al., 2004) and certainly true of naïve, birds-of-the-year, exploration immediately after arrival might serve to gather reliable information about resources and sources of stress (Aborn & Moore, 1997; Moore & Aborn, 2000). Our study demonstrated that the frequency of flocking is relatively high in the early phase of stopover and declines later; as would be expected if the value of social information decreased over time as the migrant is continuously gathering information while facing the constant costs of social foraging (e.g. competition or non-optimal movement patterns) (Greenberg, 2000; Hutto, 1988; Krebs & Inman, 1992). This pattern is consistent with the predictions of our Information Constraint Hypothesis, which proposes that migrating birds use inadvertent social information to reduce time and risks associated with environmental assessment after arrival at stopover sites.

Table 4.1. Comparison of Foraging and Movement Rates of Three Parulid Warblers during Spring Stopover According to Social Status (i.e. Solitary or Social Foragers).

Species	Measure	Status	N	Mean (± SD)	t	df	P
Hooded Warbler	Foraging rate (# attacks/min)	Solitary	108	2.68 (± 2.11)	3.165	114.717	0.002
		Flocking	45	1.73 (± 1.50)			
	Movement rate (distance/min)	Solitary	108	9.43 (± 5.95)	4.421	149	< 0.001
		Flocking	43	4.86 (± 5.11)			
Black-and-white Warbler	Foraging rate	Solitary	38	3.03 (± 3.03)	0.280	82	0.780
		Flocking	46	2.84 (± 3.14)			
	Movement rate	Solitary	38	7.38 (± 3.95)	2.396	82	0.019
		Flocking	46	5.33 (± 3.88)			
Tennessee Warbler	Foraging rate	Solitary	22	9.97 (± 6.44)	2.328	29.044	0.027
		Flocking	47	6.49 (± 4.05)			
	Movement rate	Solitary	22	4.61 (± 1.98)	0.009	67	0.993
		Flocking	47	4.60 (± 4.77)			

Use of information is not the only factor likely to influence social behavior during stopover. Resource distribution (Brown, 1964; Grant, 1993) and foraging ecology (Greenberg & Salewski, 2005) are known to play a significant role in the organization of non-breeding social behavior. For example, omnivorous migrants (e.g., tanagers, vireos, thrushes and buntings), which utilize patchily distributed abundant resources such as fruits and seeds as well as more dispersed arthropod prey, might differ from strictly insectivorous migrants (e.g., wood warblers and flycatchers) in their use of information during stopover. Theoretical models (Clark & Mangel, 1986) predict that animals foraging on patchily distributed, concentrated resources (such as omnivorous migrants) will reduce variation in food intake rate over time by foraging in groups and sharing information. If so, omnivorous migrants might stay in flocks during most of the stopover period. In addition, the concentrated, superabundant nature of some of the food sources omnivorous migrants exploit during stopover may lead to the formation of temporary foraging assemblages simply due to the inability of any migrant to monopolize such resources (Grant, 1993; Rappole, 1995). Either way, social information continues to be important during the course of stopover and our survey results support this notion. Insectivorous migrants, however, would not necessarily benefit from flock membership by virtue of their foraging ecology because their prey is distributed in a more predictable, homogenous fashion, hence the value of social information for insectivorous migrants may decline after a certain period of time, which pattern was demonstrated by our survey and radio-telemetry results. It is worth noting that our survey results are more robust than first appears because it could be argued that migrants should exhibit higher flocking propensity in the morning than in the afternoon because foraging activity is usually

highest in the early morning hours. The value of information available through flock participation soon after arrival would appear to be strong enough to override any time of day effect on social behavior.

Observing other migrants' behavior may be particularly valuable source of information for energetically constrained individuals. Individuals who cannot afford to lose foraging time or to risk safety while sampling on their own may be more willing to trade off the reliability of information gained on their own for quicker access to information gained by foraging in a flock. However, we did not find evidence to our prediction that the arrival energetic condition of the migrant should negatively correlate with its use of social information soon after arrival. It is possible that the net benefits of the easily accessible but less reliable inadvertent social information is high enough during the early phase of stopover that migrants rely heavily on this type of information regardless of energetic condition or age.

To gain access to social information, individuals need to join flocks more or less temporarily, which migratory birds do often during the non-breeding season (Morse, 1989; Rappole, 1995). Maintaining flock membership, however, may impose a cost on species that are required to move through areas or forage with a speed that is inappropriate for their optimal foraging strategy (Buskirk, 1976; Hutto, 1988). Moreover, with the size of the flock fluctuating over time, its collective speed may change as well (Gradwohl & Greenberg, 1980; Morse, 1970; but see Powell, 1980), requiring further behavioral adjustments from joining migrants. Foraging data collected in our study revealed that foraging success and movement rate may differ between birds participating in flocks and foraging solitarily. The usually solitary and in the non-breeding season

often territorial Hooded Warbler showed both higher foraging success and faster

movement pattern when foraging alone, suggesting a significant cost associated with

social foraging in this species. The more social Black-and-white Warbler exhibited higher

movement rate when foraging solitarily, whereas the Tennessee Warbler exhibited higher

foraging success under the same condition. Although these two species are often seen in

mixed-species flocks during migration (Morse, 1989; Rappole, 1995; personal obs.), they

too might pay the costs of flock membership. Migratory wood-warblers (Parulinae) have

been shown to exhibit a larger repertoire of foraging maneuvers during migration than

during other phases of their annual cycle (Martin & Karr, 1990), thus in theory, they

should have the capacity to compensate for the costs of flocking. Further studies are

needed to clarify the costs of obtaining social information during migration and whether

foraging specialists benefit from heterospecific social information the same way as

generalists do (Seppänen, Forsman, Mönkkönen, & Thomson, 2007).

If migrants can monitor and assess the success of the foraging maneuvers used by

nearby members of the same or ecologically similar species (Krebs, 1973; Palameta &

Lefebvre, 1985; Sasvári, 1979), then social learning of the location of profitable food

patches as well as copying the successful foraging maneuvers may play a role in

diversifying an individual's feeding repertoire, thereby increasing rate of fuel deposition

and shortening duration of stopover. Moreover, novel stopover sites may be associated

with novel, heretofore unrecognized food types, which may require feeding techniques

not found in the individual's foraging repertoire. A new feeding technique is easier to

acquire in a flock through the diverse experience of others than 'invent' one by trial and

error (Liker & Bokony, 2009). The acquisition of novel foraging techniques via social

learning may be especially beneficial to young, inexperienced individuals completing their first migratory journey.

In conclusion, our survey results in concert with the telemetry data are consistent with the argument that social foraging enables migratory birds to assess more fully unfamiliar environments upon stopover, thereby reducing the risk associated with lack of information. The observed temporal changes in social behavior suggest that migrating birds compensate for the lack of prior information about the stopover sites when making decisions in response to novel habitat features and food types but the costs of obtaining social information may outweigh its value over time.

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CHAPTER V

THE EFFECT OF SOCIAL FACILITATION ON NEOPHOBIA

IN A MIGRATORY BIRD

Introduction

Social foraging is a frequently favored behavior by birds as it improves feeding efficiency and reduces predation risk (reviewed in Greenberg, 2000; Krause & Ruxton, 2002; Morse, 1970, 1977; Powell, 1985; Sridhar, Beauchamp, & Shanker, 2009). The social setting provides opportunities for a foraging individual to gain a more complete knowledge of the immediate environment (i.e., location and abundance of resources and predators, safety of novel food items, etc) or speed up the learning process through information inadvertently produced by other foraging individuals (i.e. *inadvertent social information*) (Danchin, Giraldeau, Valone, & Wagner, 2004; Galef & Giraldeau, 2001; Galef & Laland, 2005; Kendal, Coolen, van Bergen, & Laland, 2005; Valone, 1989, 2007). Therefore, social learning may be particularly important for animals living in seasonally fluctuating environments where they frequently encounter unfamiliar habitats, rapidly changing ecological conditions and novel food items.

Upon encountering a novel place, object or food item, individuals usually exhibit two types of behavioral responses: (a) fear and aversion (i.e. neophobia), and/or (b) curiosity and attraction (i.e. neophilia) towards novelty (Corey, 1978). While neophilia and the tendency to explore novelty facilitate information acquisition in an unfamiliar environment, neophobia generally hinders this process of familiarization and must be overcome by the individual before acquiring a new food item or learning a new foraging behavior (Greenberg, 2003). Although neophobia appears to be widespread across a wide

range of vertebrate taxa (Corey, 1978), certain ecological factors, developmental stages

and life history characteristics seem to be good predictors of high degrees of neophobia

(Greenberg, 1990a; Greenberg & Mettke-Hofmann, 2001; Mettke-Hofmann, Winkler, &

Leisler, 2002). For example, when compared with the resident Sardinian Warbler (*Sylvia

melanocephala*), the migratory Garden Warbler (*Sylvia borin*) showed increased object

neophobia (Mettke-Hofmann, Rowe, Hayden, & Canoine, 2006). Furthermore, ecological

plasticity and foraging specialization was also associated with higher feeding (i.e. object)

neophobia in migratory *Dendroica* warblers (Greenberg, 1983, 1984) as well as in

Melospiza sparrows (Greenberg, 1990b).

Migration, as a life history trait, predisposes animals to frequent exposures to

novel habitat types, risks and food items. However, successful migration requires the

deposition of large fuel stores in a timely manner while avoiding predators at unfamiliar

stopover sites (Alerstam, 1993; Catry et al., 2004; Moore, Gauthreaux, Kerlinger, &

Simons, 1995), which is challenging if the migration trait is associated with elevated

neophobia. Besides relaxing spatial neophobia during migration (migrant-neophobia

hypothesis; Mettke-Hofmann & Greenberg, 2005; Mettke-Hofmann, Lorentzen, Schlicht,

Schneider, & Werner, 2009), migrants may join flocks to take advantage of social

information and reduce feeding neophobia. Conspecific social environment may facilitate

the approach of novel microhabitats, objects or food items (Coleman & Mellgren, 1994;

Galef, 1993; Galef & Giraldeau, 2001; Soma & Hasegawa, 2004; Visalberghi, Valente, &

Fragaszy, 1998), whereas heterospecific cues might be less important (Greenberg, 1987).

Reduced neophobia can be achieved as a consequence of the approach behavior of more

experienced or simply inherently less neophobic, bolder individuals (Greenberg &

Mettke-Hofmann, 2001; van Oers, Drent, de Goede, & van Noordwijk, 2004), which can ultimately lead to faster problem solving and the transmission of behavioral innovations (Greenberg, 2003; Liker & Bokony, 2009). On the other hand, social learning can act as a conservative force as well, inhibiting or delaying the approach of novel objects (Galef, 2003; van Oers, Klunder, & Drent, 2005).

Indeed, most migratory birds show increased flocking propensity during the non-breeding season, particularly during migration (Morse, 1970, 1989; Rappole, 1995). As flocks may act as a source of information during migration (Moore & Aborn, 2000; Németh & Moore, 2007; Nocera, Taylor, & Ratcliffe, 2008; Chapters II, IV and V), one would expect that (a) individual migrants reduce their feeding neophobia in a social setting and that (b) the neophobic response of the entire flock converges upon that of the least neophobic individual (Greenberg & Mettke-Hofmann, 2001). We tested these predictions by presenting captive Indigo Buntings (*Passerina cyanea*) with a series of novel objects next to their feeding dishes under both solitary and flocking conditions and measured the intensity of their neophobic response as a latency to approach and feed from the feeder.

Methods

Subjects and Housing

We captured 30 hatch-year Indigo Buntings (16 females and 14 males) between 19 September and 27 October 2005 at the Bon Secour NWR near Fort Morgan, AL (federal permit #21221, IACUC protocol # 06030101). All birds were transported to the University of Southern Mississippi Animal Care and Research Facility in Hattiesburg, MS, and placed in cages (35cm x 45cm x 51cm). Each cage housed two birds in the first

month then birds were moved to individual home cages and remained there until the test. The buntings were maintained on millet seeds enriched with Vionate ® vitamins and minerals. The birds also received boiled egg food mixed with wheat germ oil and chopped alfalfa sprout and mustard leaves.

Birds were kept under natural photoperiod (13L:11D) occurring in October in Hattiesburg, MS. As the season progressed, we gradually decreased the length of daylight to correspond with natural photoperiod experienced at the birds' tropical wintering ground. Thus, by the end of November, the photoperiod was 12L:12D (lights on 7:00 – 19:00 CST). The birds stayed on this photoperiod throughout the experiment.

Experimental Design

Twenty four individuals (12 females and 12 males) were randomly selected for the neophobia experiment. The experiment had a within-subject, repeated measures two-way ANOVA design; that is, each bird experienced all levels of both factors. The two factors were social condition (with two levels: solitary and flocking) and treatment (with two levels: control and novel objects present). Each bird experienced three novel objects in flocking condition and three other novel objects when solitary. The novel objects were all similar in size (8-9 cm diameter) to avoid extreme novelty responses (Heinrich, Marzluff, & Adams, 1995) but differed in shape and color to prevent habituation to a certain characteristic (Soma and Hasegawa, 2004). The following six objects were used: blue paper mache apple ("Blue apple"), white Styrofoam ring ("White ring"), flat wooden jack-o-lantern ("Pumpkinhead"), yellow feathery egg-shaped plastic chicken ("Easter chicken"), plastic flower with purple, green, and yellow petals ("Mardi Gras flower"), and a glittery pink plastic heart ("Pink heart"). All objects were fixed on the top of

wooden skewers and were placed in the middle of the feeder. The feeder consisted of a platform (5 cm thick and 20 cm wide Styrofoam disk) and four 8 cm diameter clay food dishes attached to it. In total, each bird participated in twelve 30-minute trials (6 with novel objects at the feeder and 6 without the novel objects present). Social condition (flock of three birds or solitary condition) and the order of novel object presentation were alternated and balanced throughout the series of trials to control for habituation.

Four days before the start of the experiment, the birds were moved into a separate test room, and into slightly larger flight cages (70 cm x 50 cm x 40 cm) to acclimate. The night before each trial, the feeders were removed from the flight cages and were only returned when the experiment started; an hour after the lights came up in the morning. Depending on the treatment assigned to the actual trial, the feeder either had a novel object attached to the middle or not. Four cages (one holding a flock of three birds and three holding solitary birds) were recorded simultaneously by a camcorder. Video recording started as the experimenter left the room. Each day two sets of four cages, a total of 12 birds were filmed at once with two camcorders. The 24 birds were tested in two phases, which spanned from January 29, 2006 till March 06, 2006. Each cage was visually isolated from the others. Sex ratio was balanced across flocks, that is, half of the flocks consisted of two males and one female while the other half had two females and one male bird.

Data Analysis

We measured the following variables from the video recordings: (a) latency to approach the feeder within one body length; (b) latency to feed and (c) the order of feeding within the flock or if solitary within the three solitary birds tested at the same

time. If a bird failed to approach or feed at the feeder during the 30-min trial, the latency

was assumed to be 1800 sec. The birds experienced a different set of novel objects when

flocking than in solitary condition, however, certain objects may evoke stronger reactions

than others and could bias our results. Thus we tested for object effect with a one-way

ANOVA and simultaneous Tukey HSD post-hoc tests with object type as a factor and

latency to feed as a dependent variable. The object "Blue apple" caused extremely high

($p < 0.001$) latencies (Figure 5.1). Because birds that experienced this object under

solitary condition experienced the "Pink heart" under social condition, and vice versa;

and because this latter object also evoked stronger neophobic response than the others,

we excluded both of these objects from further analyses. Latency values were pooled

across trials and mean values were used for each individual. After testing that the

assumptions of parametric tests were met, we used two-way repeated measures ANOVA-

s to examine the effects of social condition and the presence of novel objects on approach

and feeding latencies, as well as test for interaction effects. Furthermore, we employed

two-way ANOVAS-s to find out whether the feeding latencies of flock members

converge upon the least neophobic member's response, and whether those latencies differ

between birds of the same feeding order but different social condition. All tests were two-

tailed and were performed using SPSS 15.0 (SPSS Inc., 2006).
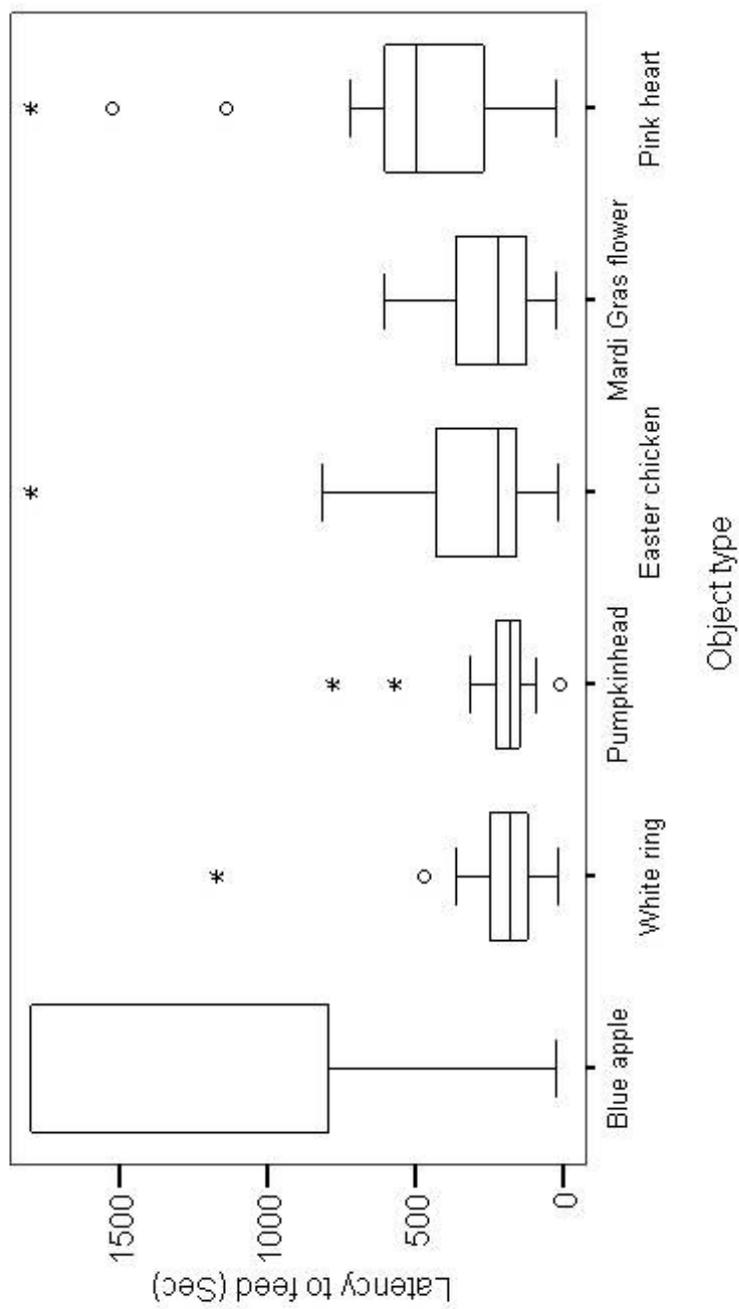
Figure 5.1. Boxplot of neophobic reactions to different types of novel objects. Boxes represent first and third quartile, line shows median and whiskers represent minimum and maximum. ○ and * depict outliers and extreme data points, respectively.

Results

Indigo Buntings reduced their hesitation to approach and feed at the feeder when

they were in flocks, regardless whether there was a novel object attached to the feeder or

not (latency to approach and feed, social condition main effects: $F_{1, 23} = 10.222$, $p =$

0.004; $F_{1, 23} = 8.723$, $p = 0.007$, respectively). In the same time, birds responded to the

presence of a novel object with delayed approach and feeding behavior (latency to

approach and feed, treatment main effects: $F_{1, 23} = 9.850$, $p = 0.005$; $F_{1, 23} = 11.076$, $p =$

0.003, respectively). We found no significant interaction between the factors social

condition and treatment in either the latency to approach or the latency to feed dependent

variables ($F_{1, 23} = 0.43$, $p = 0.837$; $F_{1, 23} = 0.16$, $p = 0.900$, respectively) (Figure 5.2).

To find out the mechanism behind the reduced neophobia in flocks, we compared

feeding latencies in treatment groups between birds based on their order of feeding in a

flock or among the three solitary birds tested in the same time. That is, we compared the

mean latency of the first bird to feed in the social condition with that of the first bird in

the solitary condition of the corresponding group. The same planned post hoc

comparisons were made for the second and third bird as well. Because birds may fall into

different order categories when presented with different novel objects, we could not pool

and average the latency data across trials. Therefore, we conducted two tests separately.

Each test uses one feeding latency data point per bird for both flocking and solitary

conditions given as response to two different novel objects. When feeding latencies

analyzed according to order of feeding in the presence of a novel object under flocking

and solitary conditions, there is an order effect (two-way ANOVA for objects

"Pumpkinhead" and "Easter chicken": $F_{2, 42} = 6.739$, $p = 0.003$ [Figure 5.3a.]; "White

ring" and "Mardi Gras flower": $F_{2, 48} = 5.973$, $p = 0.005$ [Figure 5.3b]) but no significant effect of social condition (two-way ANOVA for objects "Pumpkinhead" and "Easter chicken": $F_{1, 42} = 1.598$, $p = 0.213$; "White ring" and "Mardi Gras flower": $F_{1, 42} = 2.469$, $p = 0.124$) neither a significant interaction between order and social condition ("Pumpkinhead" and "Easter chicken": $F_{2, 42} = 2.59$, $p = 0.87$; "White ring" and "Mardi Gras flower": $F_{2, 42} = 2.339$, $p = 0.109$). That is, there is only a non-significant tendency in flocking birds to follow the response of the least neophobic individual in the group and consequently reduce the average feeding latency of the flock.
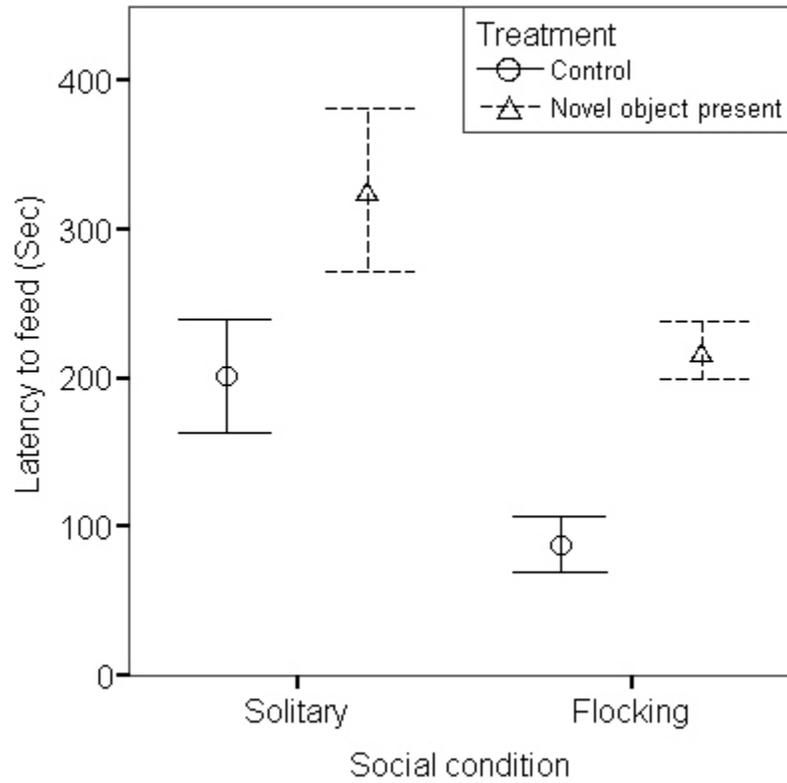
Figure 5.2. Mean feeding latency under solitary and flocking conditions in control and treatment trials. Error bars represent Mean ± 1 SE.
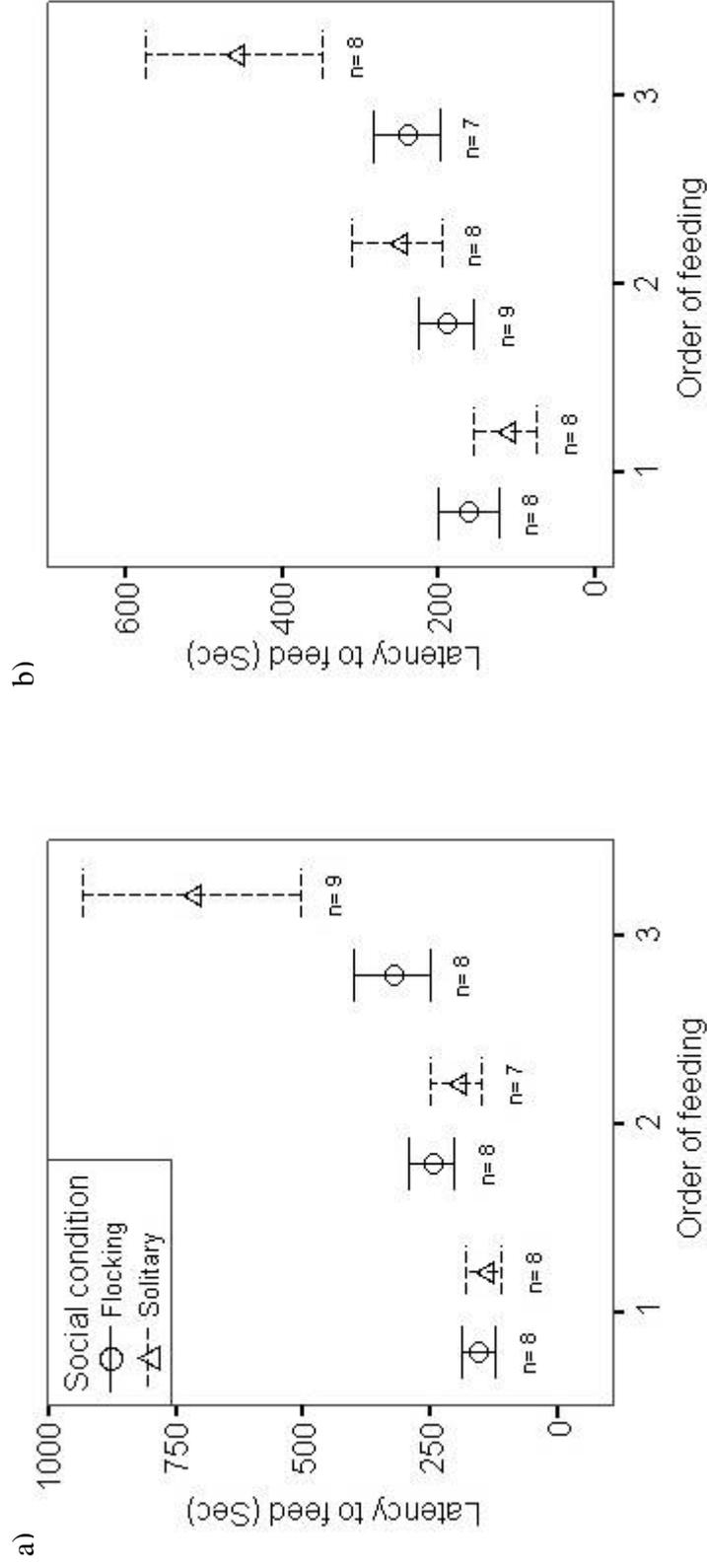
Figure 5.3. The effects of feeding order and social condition on feeding latency in treatment trials. (a) Novel objects: "Pumpkinhead" and "Easter chicken"; (b) Novel objects: "White ring" and "Mardi Gras flower".

Discussion

Our study demonstrated that Indigo Buntings reduce object neophobia in a social setting. Although our study was conducted under a photoperiod that mimicked the wintering (stationary non-breeding) season, we would expect to find this effect during the migratory period as well. Our findings are consistent with other studies showing mitigating effects of social facilitation on feeding neophobia in resident, highly social birds (Coleman & Mellgren, 1994; Soma & Hasegawa, 2004; Tolman, 1964) as well as in social mammals (Forkman, 1991; Visalberghi et al., 1998). In contrast to the findings of a previous study conducted on the effect of mixed species flocking on feeding neophobia in migratory *Dendroica* warblers (Greenberg, 1987), our study suggests that participating in monospecific flocks could be advantageous when individuals encounter unfamiliar habitat or foraging conditions. Similarly, when Eastern Kingbirds (*Tyrannus tyrannus*) were presented with novel objects next to their familiar food cups, the presence of other kingbirds in adjacent cages facing the same problem lowered the kingbirds average feeding neophobia compared to kingbirds presented with the same objects in visually isolated cages (Mabey unpubl. data).

Interestingly, in Indigo Buntings, flocking reduced the latency to approach and feed at a familiar feeder as well and not only at the one with a novel object in the middle. This shorter hesitation to attend a familiar feeder in flocking condition could be due to less than optimal time spent with acclimation to the test cage and feeder or, alternatively, it could indicate an inherently strong neophobia in the species. Although, the Indigo Bunting seems to be social and often joins monospecific flocks during the non-breeding season (Payne, 2006), it is unlikely that it has a stronger novelty response in a solitary,

familiar setting than the highly social Zebra Finch (*Taeniopygia guttata*) or Budgerigars (*Melopsittacus undulates*), both of which showed no difference in feeding latencies when tested alone and in flocks without novel objects present (Coleman & Mellgren, 1994; Soma & Hasegawa, 2004).

In contrast to other studies suggesting that the feeding latencies of flock members converge upon the least neophobic member's novelty response (Coleman & Mellgren, 1994; Greenberg & Mettke-Hofmann, 2001; Soma & Hasegawa, 2004), we only found a non-significant tendency for this pattern. It is important to note that the first two birds to feed in flocks and in solitary condition did not differ in their neophobic response and the non-significant tendency for longer latency to feed was observed only in the third bird in the solitary condition. Larger flock sizes and larger sample sizes may reveal whether the reduced average novelty response in flocks is due to following response and lowered latency to feed in highly neophobic members of the flock. If so, highly neophobic individuals would benefit from joining foraging flocks, especially when stopping over at unfamiliar stopover sites. On the other hand, the costs of flock participation (e.g., competition and non-optimal movement and foraging pattern) may outweigh the benefits for individuals with less neophobic and bolder personality.

The degree of neophobia animals exhibit in unfamiliar situations have a significant negative effect on their problem solving ability (Seferta, Guay, Marzinotto, & Lefebvre, 2001; Webster & Lefebvre, 2001). Thus lowering the emotional response to novelty would not only speed up the familiarization process with novel features of the immediate environment but would facilitate learning new behaviors, innovation or simply recognizing new food items (Greenberg, 2003), any of which could be important when an

individual is under time and energetic stress. We argue that migration represents an

ecological context, in which social foraging provides a suite of important benefits, and

one being reduced neophobia.

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CHAPTER VI

SEASONAL VARIATION IN SOCIAL LEARNING PERFORMANCE IN A

MIGRATORY SONGBIRD: IS THERE A COGNITIVE DEFICIT

ASSOCIATED WITH MIGRATION?

Abstract

Seasonal behaviors are organized around the annual cycle to meet the demands of the fluctuating environment while optimizing fitness. A number of these behaviors can be observed in seasonally breeding birds and some, such as migration, require exceptional energetic investment. However, very little is known about the cognitive consequences of seasonal changes in behavior. In this study, we examined whether migratory condition is associated with a change in cognitive performance relative to non-migratory, wintering condition in an intercontinental migratory songbird, the Indigo Bunting (*Passerina cyanea*). Specifically, we tested whether migratory condition, induced via increased photoperiod, affected the birds' performance on a social learning test. We presented naïve observer buntings with a novel feeder that had to be manipulated to gain access to the seeds inside. The correct feeding technique was presented by a trained demonstrator in a separate section of the observer's cage. While buntings in migratory and non-migratory condition showed no difference in the latency to approach the novel feeder, migratory buntings were slower and less successful in extracting seeds from the novel feeder. In addition, migratory buntings had significantly higher baseline plasma corticosterone levels but hormone titers did not predict performance on the social learning test. Although the function and causal mechanism of this compromised cognitive performance is unclear, we suggest that the high energetic demand and, as a consequence, fuel

deposition associated with migration may indirectly influence the migrant's ability to learn a new foraging technique via social cues. In a heightened motivational state, birds in migratory condition may narrow their attention to the food while ignoring contextual cues; ultimately, resulting in poor social learning performance. However, the slower tendency to learn from others may be compensated by the increased amount of time migrants spend in flocks during migration.

Introduction

Seasonal variation in the availability and predictability of resources in an organism's environment creates a dynamic ecological landscape in which an organism must produce the adequate physiological and behavioral strategies to maximize its fitness. For example, a typical migratory bird that breeds in the temperate forests of the northern hemisphere will have to time and synchronize a number of seasonal behaviors, including molt, migration and breeding, some of which are energetically expensive, so that its offspring are raised at the time of the highest resource abundance (Lack, 1968).

Although little is known about the seasonal variation in cognitive function, given the distinct periods during the annual cycle when high, long term premium is placed on the ability to perceive, store or retrieve large amounts of information (e.g. during territory acquisition, nest site selection, song learning or production, food hoarding and retrieving), the physiological and behavioral periodicity is likely accompanied by seasonal variation in cognitive demand. Indeed, seasonal plasticity of neural structures and variation in correlated behaviors have been clearly demonstrated in the song control system of songbirds (Nottebohm, 1981; Nottebohm, Nottebohm, & Crane, 1986; Tramontin & Brenowitz, 2000) and proposed in the hippocampal formation of food

hoarding (Barnea & Nottebohm, 1994; Clayton & Cristol, 1996; Shettleworth, Hampton, & Westwood, 1995; Smulders, Sasson, & Devoogd, 1995; Smulders, Shiflett, Sperling, & DeVoogd, 2000) and brood parasitic birds (Clayton, Reboreda, & Kacelnik, 1997).

Photoperiod is the major initial *zeitgeber* that birds use to organize seasonal behaviors within the annual cycle (Dawson, King, Bentley, & Ball, 2001), and synchronize their circannual rhythm with the temporal structure of the environment (Gwinner, 1989). Seasonally breeding birds, including migratory birds, experience distinct physiological phases in which the sensitivity to photoperiod, particularly to long days changes throughout the annual cycle (Nicholls, Goldsmith, & Dawson, 1988). Birds become photosensitive during the short days of late winter. This process enables them to respond to the longer days of spring and turn on the production of gonadotropic hormones that induces gonadal growth and prepares them for breeding (Nicholls et al., 1988). In many migratory birds, the beginning of the spring gonadal cycle is synchronized with the onset of spring migration and migratory restlessness (i.e. *Zugunruhe*), an important characteristic of migratory behavior that can be observed in captive birds (Berthold, 2001; Gwinner, 1989).

Migration, as one of the energetically most expensive seasonal behaviors (Berthold, 2001; Blem, 1980), requires the rapid deposition of fat stores and muscle mass that fuel and enable long-distance migratory flights. During this energetically demanding phase of the annual cycle, migrants must negotiate the competing demands of rapid resource acquisition and predator avoidance under stronger time pressure than experienced in any other season (Moore, Gauthreaux, Kerlinger, & Simons, 1995). As evidenced by the seasonal shifts in habitat (Petit, 2000) and diet selection (Moore &

Simm, 1985; Parrish, 1997), digestive physiology (Biebach, 1998; McWilliams &

Karasov, 2001), sleep budget (Fuchs, Haney, Jechura, Moore, & Bingman, 2006; Fuchs,

Maury, Moore, & Bingman, 2009; Rattenborg et al., 2004), and foraging (Martin & Karr,

1990; Parrish, 2000) and risk taking behaviors (Metcalfe & Furness, 1984; Moore, 1994),

migratory life style is associated with a suite of seasonally plastic phenotypic traits that

together facilitate long-distance migration (Dingle, 2006; Piersma, Perez-Tris, Mouritsen,

Bauchinger, & Bairlein, 2005). Similarly, given the largely unfamiliar nature of stopover

sites and increased unpredictability of *en route* conditions, rapid information acquisition

and decision-making are expected to be favored by natural selection (Mettke-Hofmann &

Greenberg, 2005; Németh & Moore, 2007).

The purpose of this study was to test whether migratory condition, induced by

photo-stimulation, is associated with a change in cognitive performance in a migratory

songbird, the Indigo Bunting (*Passerina cyanea*). Specifically, (a) we compared the

performance of long day (16L:8D) photostimulated birds in migratory disposition on a

social learning task with that of shorter day (12L:12D) photosensitive birds in non-

migratory condition. The birds were asked to extract food from a novel feeder in the

presence of a trained demonstrator providing for the task. As birds exhibit seasonal

variation in exploratory behavior (Mettke-Hofmann, 2000, 2007), one may expect that

migration is a period when the fear of novel objects and locations (i.e. neophobia;

Greenberg, 1990) is relaxed to facilitate the timely acquisition of resources (Mettke-

Hofmann & Greenberg, 2005). Because the sooner individuals overcome their neophobia

the sooner they can gain access to novel resources, (b) we also compared the neophobic

reaction exhibited in response to the novel feeder between the two groups of birds.

Finally, corticosterone, a major glucocorticoid hormone in birds, has important regulatory roles in preparing a migrant physiologically for the energetic demands of migration by increasing food intake (Lõhmus, Sundstrom, & Moore, 2006), facilitating fat deposition (Holberton, 1999) and mobilizing resources in relation to migratory flights (Landys, Wingfield, & Ramenofsky, 2004; Lõhmus, Sandberg, Holberton, & Moore, 2003; Ramenofsky, Savard, & Greenwood, 1999; Ramenofsky & Wingfield, 2007). However, very little is known about the effects of seasonally up-regulated plasma corticosterone on the cognitive performance of migrants. Although chronic stress and chronically elevated levels of glucocorticoids are assumed to be associated with impaired learning and memory functions (Bowman, Beck, & Luine, 2003; Hodgson et al., 2007; McEwen, 2000; Sapolsky, 1996), in food caching Mountain Chickadees (*Poecile gambeli*), long-term moderate elevations of corticosterone enhances spatial memory (Pravosudov, 2003). We (c) examined the relationship between baseline levels of plasma corticosterone and cognitive performance in both photostimulated birds in migratory condition and photosensitive non-migratory birds.

Methods

Subjects and Housing

We used 37 hatch-year Indigo Buntings (23 females and 14 males) as experimental subjects. They were captured between 13-21 October 2006 at two coastal banding sites during autumn migration: at the Bon Secour NWR near Fort Morgan, AL and at the Grand Bay NERR, near Moss Point, MS (federal permit #21221, IACUC protocol # 06030101). All birds were transported to the University of Southern Mississippi Animal Care and Research Facility in Hattiesburg, MS, and placed in cages

(75cm x 45cm x 45cm)**.** Each cage housed two birds separated with a wire mesh divider. The buntings were maintained on millet seeds enriched with Vionate ® vitamins and minerals. The birds also received boiled egg food mixed with wheat germ oil and chopped alfalfa sprout and mustard leaves.

Birds were kept under natural photoperiod (13L:11D) occurring in October in Hattiesburg, MS. As the season progressed, we gradually decreased the length of daylight to correspond with natural photoperiod experienced at the birds' tropical wintering ground. Thus, by November 15th, the photoperiod was 12L:12D. On the 15th of December, 5 birds were randomly selected to be trained as demonstrators (3 females and 2 males). The rest of the birds were randomly assigned to one of two groups, either to a long daylight group (i.e. spring migratory group, LD hereafter) or to a short daylight group (i.e. wintering group, SD hereafter). Birds in the LD group experienced increasing length of daylight starting on the 11th of January with photo-stimulation continuing for eight days with 30 minutes longer daylight period each day. By the 19th of January, birds in the LD group were under a 16L: 8D photoperiod. Meanwhile, birds in the SD group stayed on a 12L:12D photoperiod characteristic of the tropical wintering season.

Experimental Design

The social learning task was designed to test how quickly a naïve migrant (observer) can gain access to familiar food items presented in a novel feeder while the solution was accessible via an informed conspecific (demonstrator) foraging nearby. The novel feeder (Figure 6.1) consisted of six transparent plastic tubes (each 5 cm long, 0.6 cm wide) glued to wooden bar, which could be easily attached to the cage wire with rubber harnesses. Each plastic tube contained approximately 20 millet seeds and was

closed with a cotton ball at the bottom end. The feeder was positioned above the food cup so if the bird removes the cotton ball the seeds would fall into the cup.

During demonstrator training, the birds were allowed to explore the novel feeder and learn by trial and error for three continuous hours a day while having an unobstructed view of the other demonstrators to speed up the training process. The demonstrators were visually isolated from the rest of the birds. Each training session was preceded with a three hours of food deprivation to increase motivation. The birds had to empty all six tubes of a feeder within five minutes of its presentation to qualify for the demonstrator role. The training started on the 3rd of January and within four days all five individuals satisfied this criterion. To maintain their performance, demonstrators continued to receive food in this feeder twice a day, each time after a three hour long food deprivation period. This schedule corresponded with the experimental schedule thus they were well habituated to perform this task with high efficiency.
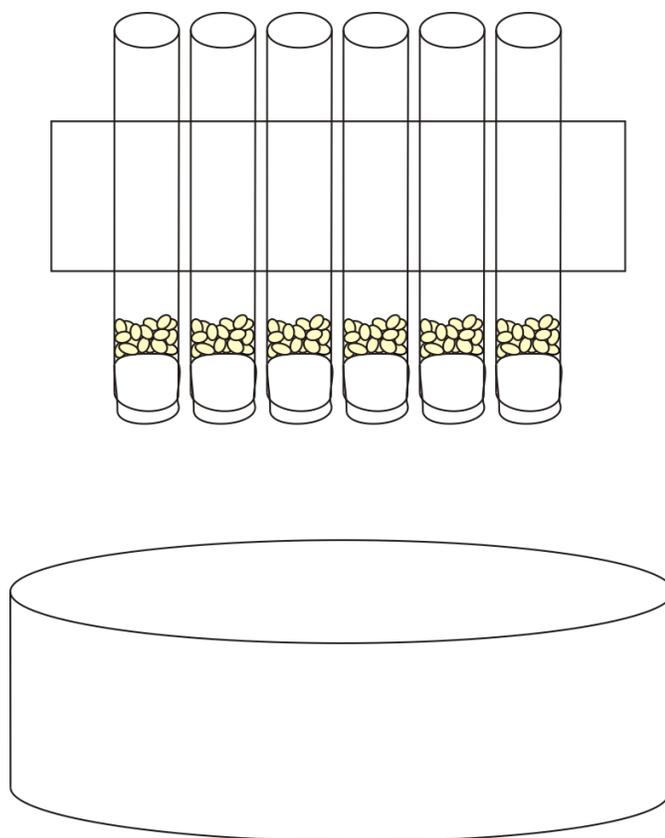
Figure 6.1. Schematic representation of the novel feeder.

The experiment consisted of four trials spanning over two consecutive days (a morning and an afternoon trial on each day). The day before the first trial, we put one of the demonstrators in the other, separated half of the observer's home cage. During the first two trials, the demonstrator was providing the solution to extract food from the novel feeder while the observer had access to its own feeder. The distance between the two feeders was 20 cm. On the next day (during the third and fourth trials), only the observer was presented with the feeder while the demonstrator had free access to its regular open food cup. Three-hour long food deprivation period preceded the morning trial and a two-hour long one the afternoon trial. Each trial lasted for 30 minutes. Birds had access to

food for three hours prior to the morning food deprivation period, for a half an hour before the onset of the afternoon food deprivation period, and for the rest of the day after the afternoon trial (i.e., 2.5 and 6.5 hours in the SD and LD groups, respectively).

We assessed night-time migratory restlessness (i.e. *Zugunruhe*) in both the SD and LD groups by using an infrared camera system (SVAT Clearvu Q1404, SVAT Electronics). We monitored migratory restlessness for two hours each night starting 80 min after the lights went out to focus on the time of peak migratory activity, which occurs in the first half of the night in this species (Emlen, 1967). We counted the number of hops and flights the birds exhibited in 2-minute blocks and classified a block active if the number was at least 2. Based on the proportion of active blocks within the 2-hour sample period, we assigned birds to "migratory" and "non-migratory" categories. We considered a bird being in "migratory" condition at the time of the cognitive test if it exhibited high level of migratory restlessness consistently over two nights leading up to the test and during the two nights of the test. That is, if the mean percentage of active blocks within the 2-hour sample periods across the four days was at least 80% the bird was assigned to the "migratory" group, whereas a bird with less than 10% of mean night-time activity was considered "non-migratory". Birds that exhibited inconsistent or moderate levels of night-time activity were excluded from the analyses.

All trials were videotaped and the following variables were measured: (a) observer latency to approach the novel feeder (i.e. perch on the food cup), (b) demonstrator latency to feed (trials 1 and 2 only), (c) observer latency to feed and (d) the number of feeder tubes emptied by the observer during the trial.

Hormonal Assay

Blood was drawn to measure baseline plasma corticosterone within a week of the social learning tests. Each individual was sampled only once, at 14:30 CST, and each sample (75 µl) was taken within 3 minutes of entering the room (Romero & Reed, 2005). We measured the plasma levels of corticosterone using a competitive enzyme immunoassay (ELISA; Assay Designs Inc., Ann Arbor, MI). Samples were diluted 35X in assay buffer and mixed with an equal volume of steroid displacement reagent (1:1000 concentration). All samples were assayed on the same 96-well plate. Six 5-fold serial dilution of 20,000 pg/ml concentration of corticosterone was added to the plate in triplicate. The plate had negative and positive controls and was read using a microplate reader and optical density of 405nm. The intra-assay coefficient of variation was 0.11.

Results

Eight individuals were assigned to the non-migratory group whereas six birds were in migratory condition at the time of the test as a result of the photostimulation. We used a two-way between-subjects repeated measures ANOVA to evaluate the effects of season on cognitive performance. The dependent variable was observer latency to feed corrected for demonstrator performance (i.e. demonstrator latency to feed). The within-subjects factor was trial with four levels and the between-subjects factor was condition with two levels (migratory and non-migratory). The trial main effect and the trial x condition interaction effect were tested using the multivariate criterion of Wilks' lambda (Λ) due to the violation of the sphericity assumption (Mauchly's $W = 0.096$, $df = 5$, $p < 0.001$). The trial main effect was significant ($\Lambda = 0.180$, $F_{(3, 10)} = 15.146$, $p < 0.001$), whereas the trial x condition interaction effect was not ($\Lambda = 0.523$, $F_{(3, 10)} = 3.035$, $p =$

0.080). The between-subjects univariate test for the condition main effect showed a significantly longer latency to extract food from the novel feeder in migratory condition ($F_{(1, 12)}$ = 10.221, p = 0.008, Figure 6.2).

We assessed the effect of season on cognitive performance using another dependent variable as well, the number of tubes emptied by the observer within a trial. Because the data did not meet the normality assumption, we conducted four pairwise comparisons between the two conditions using Mann-Whitney U tests. Our tests showed that birds in migratory condition opened significantly lower number of tubes in the first (U = 8.500, p = 0.033) and the second trials (U = 9.000, p = 0.024) but did not differ significantly in the third (U = 14.500, p = 0.122) and fourth (U = 21.000, p = 0.386) trials (Figure 6.3).
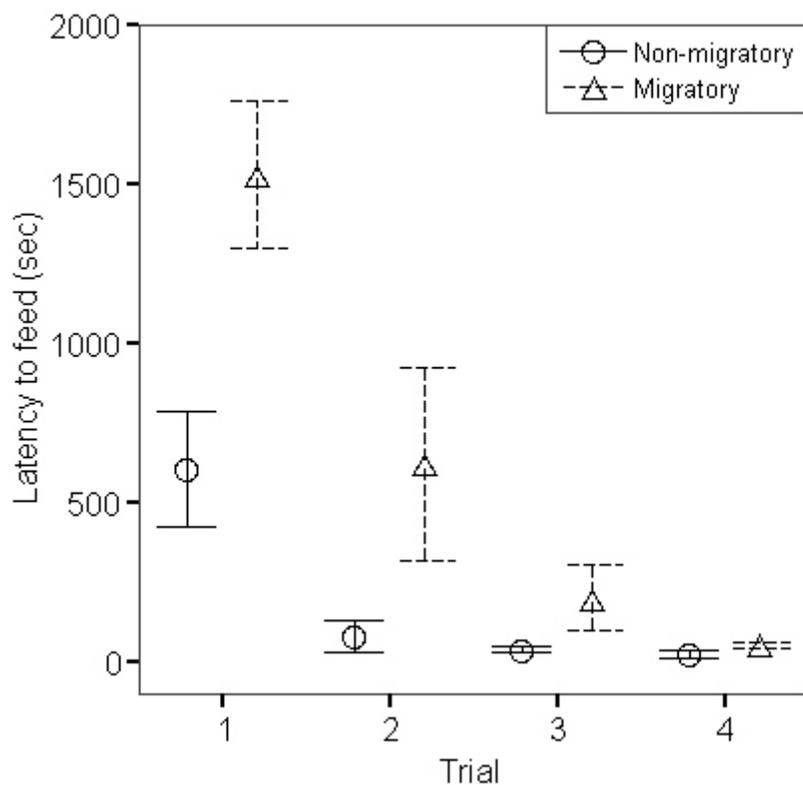
Figure 6.2. Latency to extract food from a novel feeder in migratory (N = 6) and non-migratory (N = 8) condition. In trials 1 and 2, a trained demonstrator provided the proper foraging behavior, while in trials 3 and 4, only the observers were presented with the feeder. Error bars represent Mean ± 1 SE.
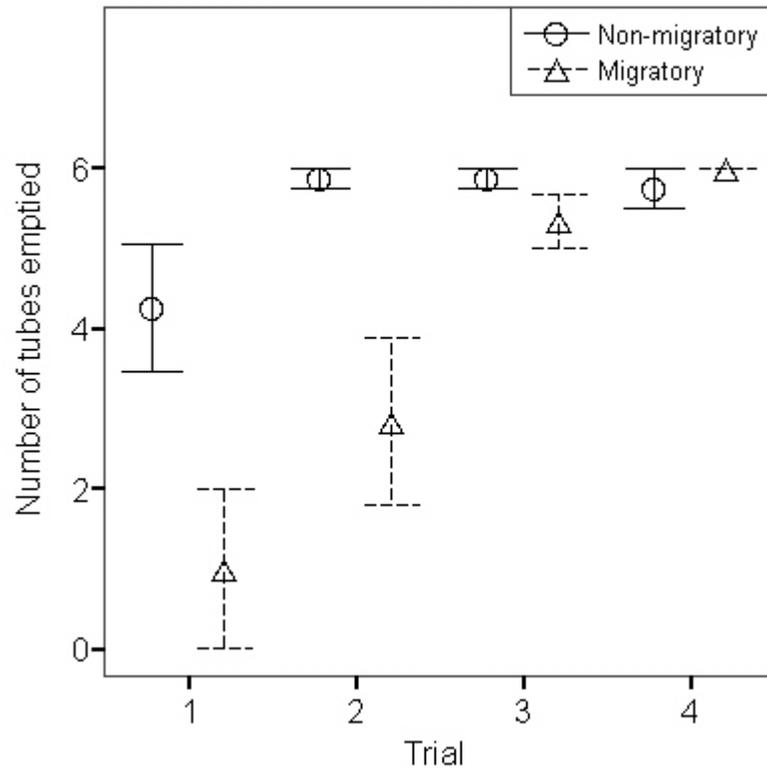
Figure 6.3. Number of feeder tubes emptied by observer buntings in migratory (N = 6) and non-migratory (N = 8) condition. Error bars represent Mean ± 1 SE.

Migratory condition did not have an effect on the birds' latency to approach a novel feeder (two-way between-subjects repeated measures ANOVA; trial main effect was significant, $\Lambda = 0.166$, $F_{(3, 10)} = 16.748$, $p < 0.001$, but neither the trial x condition interaction effect $\Lambda = 0.927$, $F_{(3, 10)} = 0.264$, $p = 0.850$, nor the condition main effect $F_{(1, 12)} = 1.814$, $p = 0.203$ was significant, Figure 6.4).
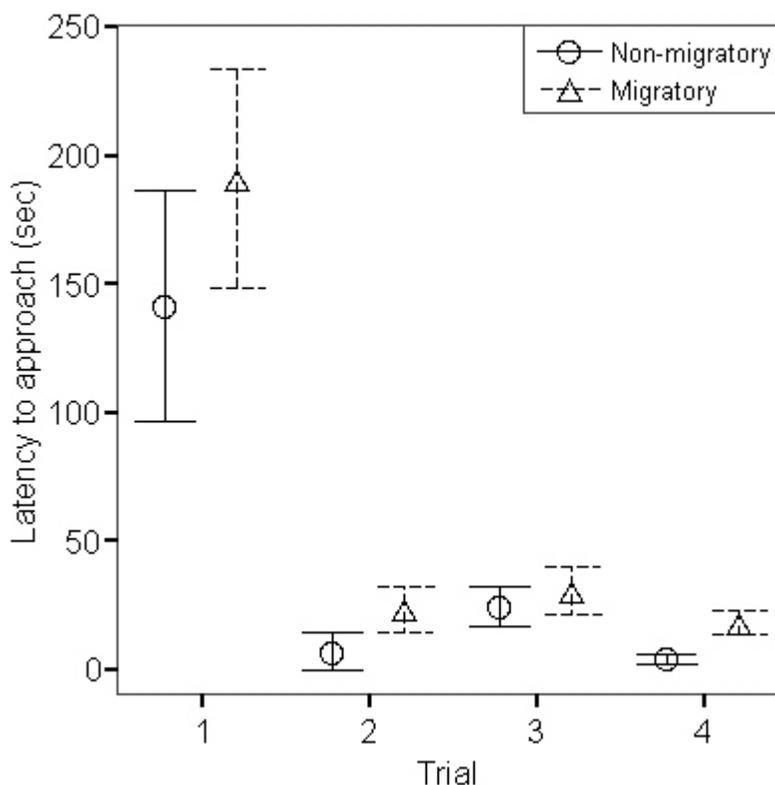
Figure 6.4. Neophobia towards the novel feeder in migratory (N = 6) and non-migratory (N = 8) Indigo Buntings. Error bars represent Mean ± 1 SE.

Finally, mean baseline plasma corticosterone level was significantly higher in the migratory than in the non-migratory group (t-test; t = 3.726, df = 12, p = 0.003, Figure 6.5), however it did not seem to influence social learning performance in the first trial when controlling for migratory condition (ANCOVA with latency to feed in the first trial as a dependent variable, condition as a fixed factor and corticosterone as a covariate; $F_{(1, 11)}$ = 0.496, p = 0.496). Neither did it influence the number of tubes emptied in the first trial ($F_{(1, 11)}$ = 0.569, p = 0.467) or the latency to approach the novel feeder in the first trial ($F_{(1, 11)}$ = 1.004, p = 0.338).
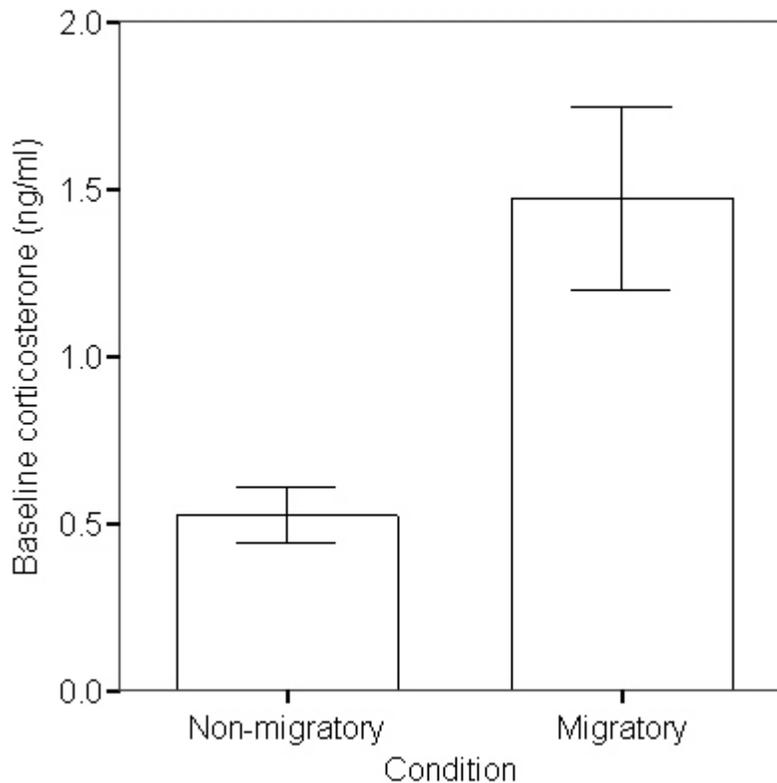
Figure 6.5. Baseline levels of plasma corticosterone in migratory (N = 6) and non-migratory (N = 8) Indigo Buntings. Error bars represent Mean ± 1 SE.

Discussion

Our study demonstrated that migratory condition is associated with a reduced performance on a social learning test in captive Indigo Buntings. Contrary to our expectations, birds exhibiting high levels of migratory restlessness were slower in recognizing the correct way to extract food from a novel feeder (i.e. learning a new foraging behavior) and gained access to lower amounts of food than their conspecifics in non-migratory condition.

Migratory birds are faced with significant time and energetic demands during their journeys between the breeding and wintering grounds (Alerstam, 1993; Alerstam & Lindström, 1990). These demands can act as selective forces to shape their physiology and behavior (Dingle, 2006; Piersma et al., 2005). Furthermore, given the largely unpredictable *en route* conditions, unfamiliar stopover sites and the fitness payoff associated with timely refueling, one would expect that selection favors an up-regulated cognitive system during migration. However, the development and running costs of the brain are energetically very expensive, 8 to 10 times as high, per unit mass, as those of skeletal muscle (Aiello & Wheeler, 1995; Isler & van Schaik, 2006, 2009). Thus *en route* cognition may be limited by energetic demand because energy is allocated primarily to the exercise organs (e.g. heart, lungs and flight muscles) rather than to the brain – not unlike the plasticity observed in digestive organs (Biebach, 1998; Piersma, 1998).

Alternatively, reduced social learning performance may be a byproduct of increased motivation to feed as part of the endogenously programmed hyperphagia (Berthold, 2001). Indigo Buntings in our study did not show reduced neophobia in migratory condition and exhibited similar motivation to attend to the novel feeder as the non-migratory individuals. It is noteworthy, however, that in our test a trained demonstrator was feeding from the novel feeder without hesitation, which likely lowered the observer's fear toward the novel feeder. Social facilitation is known to reduce observer neophobia (Coleman & Mellgren, 1994; Soma & Hasegawa, 2004), thus could have masked any difference that might have existed in a non-social setting. Hyperphagia is mediated by increased levels of corticosterone (Lõhmus et al., 2006; Meier & Farner,

1964; Ramenofsky, 1990). Although Indigo Buntings in migratory disposition had significantly higher titers of baseline plasma corticosterone, these titers did not predict social learning performance. As elevated levels of corticosterone leads to higher motivation to feed, which often affects performance on cognitive tests (Healy, Bacon, Haggis, Harris, & Kelley, 2009; Macphail, 1982), it is conceivable that birds in migratory condition narrow their attention on the food in the feeder and rely less on contextual (e.g. social) cues, which in turn would lead to errors and poor performance on a social learning test (Easterbrook, 1959; Mendl, 1999). This type of shift in attention and in the value of contextual information has been observed in studies that compared time allocated to anti-predatory behavior in birds in migratory and non-migratory condition (Metcalfe & Furness, 1984; Moore, 1994). These studies concluded that optimal behavior shifts to risk-prone behavior in migratory condition because the cost of reduced rate of fuel deposition outweighs the risk of predation (Metcalfe & Furness, 1984; Moore, 1994).

These seasonal physiological and behavioral changes allow a migrant to complete a series of long-distance flights in a relatively short period of time at the cost of relatively slower cognitive response to environmental fluctuations. However, this interference may not be significant enough to compromise fitness or there is a compensatory mechanism in place that provides accessible and relatively reliable information in a timely fashion to assess risks and resources after landing at an unfamiliar site. Social learning provides a mechanism that reduces time and risks associated with environmental assessment by reducing the time and energy costs of private sampling and ultimately facilitating problem solving, innovation and the rapid acquisition of information under novel circumstances (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Danchin,

Giraldeau, Valone, & Wagner, 2004; Hoppitt & Laland, 2008; Kendal, Coolen, van Bergen, & Laland, 2005; Seppänen, Forsman, Mönkkönen, & Thomson, 2007; Valone, 1989). In the same time, individuals who rely heavily on social information may pay the cost of erroneous or outdated information (Giraldeau, Valone, & Templeton, 2002). Migrants can obtain relatively reliable information in a short period of time by simply spending time in foraging assemblages and watching and copying the decisions of successful individuals, which might also be the cheapest way to reduce risks and uncertainties at a novel stopover site (Németh & Moore, 2007; Nocera, Taylor, & Ratcliffe, 2008; Valone, 1989, 2007). This mechanism of information acquisition is facilitated by a seasonal increase in preference for flocking (Moore, 1990; Morse, 1989) as well as a temporary peak in flocking propensity upon landing at stopover (Moore & Aborn, 2000; Németh & Moore, 2007), and may be adaptively beneficial by aiding rapid and safe refueling and ultimately timely arrival to the breeding or wintering grounds.

More studies are needed to answer fundamental questions about the cognitive demands of migration and the adaptations in place to meet them (Mettke-Hofmann & Greenberg 2005). Although one cannot generalize from a single type of cognitive test, our results suggest that migration may not only be a period of extreme energetic demand (Berthold, 2001; Blem, 1980), increased risk of mortality (Newton, 2006, 2007; Sillett & Holmes, 2002) and reduced immune function (Owen & Moore, 2006, 2008) but a period of compromised cognitive ability as well. Questions about the functional significance and the underlying causal mechanism of this cognitive deficit remain to be answered.

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