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Source: The Auk, 131(2) : 186-194

Published By: American Ornithological Society

URL: https://doi.org/10.1642/AUK-13-195.1

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The Auk
Ornithological Advances
www.aou.org

Volume 131, 2014, pp. 186–194
DOI: 10.1642/AUK-13-195.1

REVIEW

Information acquisition during migration: A social perspective

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Received December 16, 2013; Accepted January 3, 2014; Published March 19, 2014

ABSTRACT

Information can enhance fitness, and the ways in which organisms acquire and use information are of heightened interest in ecological studies today. Migratory birds, as long-distance travelers of the globe, depend on rapid access to accurate information and thus provide particularly interesting study subjects for cognitive ecology. Yet, questions regarding how migratory birds collect information and make decisions en route remain to be answered. Here, we review the current status of this field of study and focus our attention on social learning (broadly defined as the use of inadvertently produced social information) as an important cognitive mechanism that can operate across taxonomic boundaries. We argue that social learning is critical to accelerate resource acquisition while reducing risks and uncertainties during migration. We put forward eight testable predictions in relation to when increased use of social information might be expected. Finally, we argue that migrant communities at stopover sites may serve as additional sources of information where transient associations with others may have important and long-lasting benefits.

Keywords: stopover, social information, social learning, bird migration

Adquisición de información durante la migración: Una perspectiva social

RESUMEN

La información puede mejorar la aptitud, y las formas en que los organismos adquieren y usan información son de gran interés en los estudios ecológicos actuales. Las aves migratorias, al ser viajeras de largas distancias en el mundo, dependen del acceso rápido a información precisa. Por lo tanto, son sujetos de estudio interesantes para la ecología cognitiva. Sin embargo, preguntas sobre cómo las aves migratorias recolectan información y toman decisiones en sus rutas aún no han sido respondidas. Revisamos el estado actual de este campo y enfocamos nuestra atención en el aprendizaje social (definido ampliamente como el uso de información social producida involuntariamente) como un mecanismo cognitivo importante que puede operar cruzando los límites taxonómicos. Argumentamos que el aprendizaje social es crítico para acelerar la adquisición de recursos al tiempo que reduce los riesgos e incertidumbres durante la migración. Establecemos ocho predicciones comprobables en relación con el momento en el que se espera ver un aumento del uso de la información social. Finalmente, argumentamos que las comunidades migratorias en los sitios de parada podrían servir como fuentes adicionales de información, en donde las asociaciones temporales con otras aves podrían tener beneficios importantes y de larga duración.

Palabras clave: sitios de parada migratoria, información social, aprendizaje social, migración de las aves

Migration is a life-history strategy that evolved to facilitate the exploitation of seasonally abundant but distant resources (Dingle 1996). The cost that migrants pay to gain access to these resources can be measured in time, energy, and mortality (Alerstam et al. 2003). Indeed, most mortality may occur during the migration phase of the annual cycle (Sillett and Holmes 2002, Klaassen et al. 2014), suggesting that migration can be a significant limiting factor (Newton 2006). This may not be surprising in light of the many challenges that migrants face en route. Aside from navigating across vast continents and coping with adverse weather conditions, migrants must meet the high energy demands of long-distance travel under unpredictable conditions (Moore et al. 1995, 2005). This means that a migrant's fitness is dependent upon the timely and safe acquisition of resources at often 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 considered to be adequate information under the simultaneous constraints of time minimization and energy requirements?

The information that migratory birds use to make decisions about resources and sources of stress during stopover and the manner in which they do so are poorly understood (e.g., Moore and Aborn 2000). The develop-

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ment of the ecology of information use (Giraldeau 1997, Dall et al. 2005) and the recent advancement in our understanding of the role of social interactions in information acquisition (Giraldeau et al. 2002, Danchin et al. 2004, Laland 2004, Galef and Laland 2005, Kendal et al. 2005, Bonnie and Earley 2007, Seppänen et al. 2007, Valone 2007, Hoppitt and Laland 2008, Guttal and Couzin 2010, Schmidt et al. 2010, Rieucau and Giraldeau 2011, Avarguès-Weber et al. 2013, Mueller et al. 2013) 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 (Dukas 1998). After landfall, migrants can sample resources directly through their personal experience (asocial learning), or can acquire information indirectly by observing the location and behavior of others (social learning; Moore and Aborn 2000, Németh and Moore 2007). Asocial learning (sensu Laland 2004) allows migrants to gather accurate, up-to-date information, although the sampling process requires significant investment of time and energy and may lead to delayed refueling and increased exposure to predators. Social learning (sensu Laland 2004), on the other hand, may provide a shortcut to information acquisition by relying on readily available information obtained vicariously through other migrants, while the observer may stay in the relative safety of a foraging flock or in cover (Németh and Moore 2007, Nocera et al. 2008). By using social information, a migrant searching for profitable resources after landing may be able to 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 as asocial, direct sampling about the location and quality of food resources, type(s) of novel food sources and the appropriate foraging technique(s) to access them, and the location of predator(s) and current levels of predation risk at a site (Galef and Giraldeau 2001, Galef and Laland 2005).

Although social learning may be viewed as a cognitive mechanism that facilitates the rapid assessment of risks and resources, social information is potentially less reliable than privately asocially acquired information, largely because of its second-hand nature (Giraldeau et al. 2002). The cost of relying on socially obtained information when making decisions during stopover may outweigh the 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 ecological conditions (e.g., competitor density, food availability and abundance, predation risk, inhospitable weather events) vary widely in space and/or time (Boyd and Richerson 1988). 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, likely provide less useful information about resources and foraging techniques than conspecifics (Seppänen et al. 2007). On the other hand, seasonal changes in behavior such as foraging and diet plasticity can reduce this ecological distance among heterospecifics (Martin and Karr 1990) and consequently may 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), for example by joining and following a foraging flock, may become costly if it results in increased competition and/or forces the migrant into a suboptimal 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, where the migrant's preference will likely depend on the interplay between its internal state and the external ecological context.

To better understand information use by migrants during 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 easily accessible but potentially less reliable social information over costly but more accurate personal sampling information. Their models predict that individuals will rely more heavily on social information (1) when personal sampling information will be too costly to obtain ("copy when asocial learning is costly" social learning strategy; Laland 2004), or (2) 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 to leave a foraging patch when information about patch quality is difficult to acquire by personal sampling, thus using social information in a manner consistent with the "copy when asocial learning is costly" strategy (Templeton and 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 environments where these cues are unpredictable, lending importance to the "copy when uncertain" strategy (Rafacz and Templeton 2003).

Although R. Boyd and P. Richerson developed their models with humans in mind, the assumptions and predictions of their models have been applied to other organisms and were used to create a theoretical foundation

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TABLE 1. Summary of predictions of social information (SI) use by migrants in different ecological contexts.

Ecological factor	Prediction
1. Endogenous control	Stricter endogenous program will allow less reliance on SI.
2. Migration distance/speed	The value of SI will correlate with migration distance/speed.
3. Ecological flexibility	Specialists will prefer conspecific SI, while generalists will also value heterospecific SI.
4. Energetic condition and requirements	Lower reserves and higher energy demand will promote the use of SI.
5. Age and experience	Younger and less experienced individuals will derive more benefit from SI.
6. Personality	More social, slower-exploring, and shyer individuals will place more value on SI.
7. Unfamiliarity	The value of SI will decrease over time as the individual gains more familiarity.
8. Environmental variability	Moderately variable environmental conditions will promote the use of SI.

for social learning studies (e.g., Giraldeau 1997, Laland 2004, Galef and Laland 2005, Kendal et al. 2005). Here, we use their models to propose a predictive framework to study information use when migratory birds stop over during passage. Many ecological factors increase not only the cost of asocial learning but also the uncertainty attached to the value of that learned information, which ultimately increases the cost of decisionmaking. Therefore, we combine these two conditions under a single, "costly information" hypothesis, and advance eight testable predictions about ecological factors that may promote social information use during migration (Table 1).

Hypothesis and Predictions

Costly information hypothesis. Migration is associated with a set of ecological conditions under which social information should be favored when available. Migrating birds are under time and energetic constraints (Alerstam and Lindström 1990, Alerstam and Hedenström 1998), so any factor that causes a delay in refueling and departure from a stopover, including increased risk of predation (Cimprich and Moore 1999, Cimprich et al. 2005), inclement weather (Newton 2007), unfamiliar habitat (Németh and Moore 2007), and sleep loss (Fuchs et al. 2006, 2009, Németh 2009) can be viewed as increasing the cost of information acquisition and should promote social information use in migrants.

However, during migration ecological conditions can change very rapidly and often in unpredictable ways, resulting in an ever-shifting ecological context within which migrants must make appropriate decisions to meet the energetic demands of long-distance travel. Migrants often arrive at stopover sites with little or no information about local conditions, and start refueling only after an initial familiarization period (Moore et al. 1990, Moore and Aborn 2000). During the transition from arrival to refueling and then to departure, the relative value of social versus personal information continuously changes (Németh and Moore 2007). Even if a migrant obtains reliable, personal sampling information about the distribution and quality of food resources at an unfamiliar stopover site, as the ecological context at a stopover site changes the once-accurate information becomes erroneous and outdated, leaving the migrant uncertain about the success of its decisions. Several factors can modify the costs of decisionmaking for migrating birds and here we focus on eight of them (Table 1).

Prediction 1: Endogenous control. A migrant's annual schedule is shaped by the interplay between its endogenous program and proximate factors such as photoperiod, weather, food supply, and social interactions (Gwinner 1996, Berthold 2001, Gwinner and Helm 2003, Helm et al. 2006). Depending on the rigidity of the endogenous program, social information may play a significant role in determining the timing of migration, as well as facilitating navigation and habitat selection (Hamilton 1967, Terrill 1987, Chernetsov et al. 2004, Helm et al. 2006, Mueller et al. 2013). For example, in long-distance nocturnal migrants a strict endogenous program may leave less room for the use of social information after the initial exploratory period than in diurnal, short-distance, irruptive, and partial migrants, which may use social cues to find and track resources and to maintain cohesive flocks during migration, possibly to reduce predation risk and to benefit from the navigational experience of conspecifics (Dolnik and Blyumental 1967, Rabøl and Noer 1973, Chernetsov et al. 2004, Cornelius et al. 2010, Newton 2012, Mueller et al. 2013).

Prediction 2: Migration distance and speed. Migration distance likely has a 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 and Lindström 1990, Alerstam 2003), thus we could expect that incentive for timely refueling would increase tolerance of risk and use of potentially less accurate social information (Metcalfe and Furness 1984, Moore 1994, Cimprich et al. 2005). Consistent with this prediction is the finding that long-distance migrants tend to travel in larger groups than shorter-distance migrants (Beauchamp 2011). Because migration speed seems to increase with migration distance (Ellegren 1993, Alerstam 2003), speed may be a good predictor of social information use: The faster the migration (either at the species,

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population, or individual level), the higher the likelihood that a migrant will use social information when available to reduce time and risks associated with environmental assessment after landing. Migrants that are delayed in their departure from breeding sites also exhibit faster traveling speed (Ellegren 1993) and may attempt to 'catch up' and reduce their lag behind their conspecifics traveling to the same general destination (Fransson 1995, Drent et al. 2003). This increased time constraint should also promote the use of social information.

Prediction 3: Ecological flexibility—habitat, diet and foraging behavior. The likelihood that a migrant will be able to find suitable stopover sites during passage is largely determined by the migrant's ecological tolerance of different habitat types and the availability of the preferred habitat type across the landscape (Moore et al. 1995, Buler et al. 2007). For example, Palearctic *Acrocephalus* warblers 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. For these species, the value of revisiting or finding high-quality stopover sites is likely high, and the incentive to learn and remember the location of previously used high-quality reed beds or to use social information (e.g., conspecific vocal cues) during habitat selection to locate such habitats should also be high. The relatively high stopover site fidelity rate (Cantos and Telleria 1994) and the high responsiveness to conspecific vocal cues (Mukhin et al. 2008) in some of these species relative to habitat generalists support this prediction.

Diet and the distribution of food resources determine foraging strategies and consequently the cues and information that foragers use to locate resources (Moore and Aborn 2000). Despite the important roles of foraging and diet plasticity during passage (Graber and Graber 1983, Loria and Moore 1990, Martin and Karr 1990, Parrish 2000, Wang and Moore 2005), omnivorous migrants use patchily distributed, locally abundant resources such as fruits, nectar, and seeds, whereas strictly insectivorous migrants feed only on insect prey, which is often more evenly distributed (Chernetsov 2012). These 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 this food should promote social foraging and the long-term use of social information in omnivores (Greenberg and Salewski 2005). On the other hand, the likelihood of finding evenly distributed food may not increase substantially if one foraging insectivorous migrant joins another, but competition may. Consequently, uniformly distributed arthropod prey promotes restricted space use and, potentially, the defense of temporary territories (Bibby and Green 1980, Chernetsov 2012). Consistent with this notion, insectivorous migrants were found to decrease their propensity to forage in flocks the day after they arrived at a stopover site, while omnivorous migrants were just as likely to be found in flocks then as when they first arrived (Németh and Moore 2007). Making this distinction is useful when one would like to understand the source and the value of information used by refueling migrants.

Prediction 4: Energetic condition and requirements. The amount of energy reserves that a bird has should influence its social foraging tactic in relation to its flock members; that is, whether to actively search for food (producer tactic) or to utilize others' findings (scrounger tactic; Barta and Giraldeau 2000). Lean House Sparrows (*Passer domesticus*) have been shown to prefer scrounging, which provides less variable feeding rates (Lendvai et al. 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 over private information after landing to reduce the energetic costs and time of exploration. Lean migrants show increased motivation to maximize food acquisition: they invest more in competitive interactions (Moore et al. 2003), diversify their foraging behavior (Loria and Moore 1990, Wang and Moore 2005), and resume foraging sooner after exposure to a predator (Cimprich and 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 et al. 2004, Németh and Moore 2007).

However, some migratory flights require more energy than others. Migrants preparing to cross ecological barriers such as deserts, mountain ranges, and large bodies of water increase the amount of fat deposited as these flights are often longer and riskier than 'normal' migratory flights over more hospitable terrain (Sandberg and Moore 1996, Smolinsky et al. 2013). The need to meet this elevated energetic demand should further increase the incentive to favor social information when sampling the environment.

Prediction 5: Age and experience. A successful migration is dependent upon how well a migrant can cope with en route challenges (Alerstam and 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 (Woodrey 2000, Moore et al. 2003). Young, inexperienced individuals are often socially subordinate to adults and use suboptimal, often riskier, foraging sites due to inexperience or interference competition (Ekman and Askenmo 1984, Woodrey 1995). This competitive disadvantage during fat deposition can result in higher mortality, longer stopovers

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due to lower fat deposition rates, and suboptimal departure fuel loads, which may be especially critical at sites near ecological barriers where migrants may concentrate (Alerstam 1978, Moore et al. 1995) and where departing migrants face long-distance, non-stop flights. Furthermore, young, inexperienced migrants are more likely to make orientation errors than adult birds (Moore 1984, Sandberg et al. 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 be dependent on experience, and flock members may be important sources of information in this context. In general, social learning hastens the familiarization process with novel situations (Galef and Giraldeau 2001), often by reducing neophobia in the inexperienced individual (Visalberghi et al. 1998, Greenberg and Mettke-Hofmann 2001), but also by enhancing orientation and navigation performance (Hamilton 1967, Balcomb 1977, Moore 1990, Chernetsov et al. 2004, Simons 2004, Couzin et al. 2005). Therefore, we should expect that the use of social information is elevated in inexperienced migrants.

Prediction 6: Personality. Individuals often show consistent behavioral differences in their response to the environment: they differ in where and how they forage, where they build their nests, and how they respond to the presence of predators and novel situations. That is, they exhibit personality traits (Réale et al. 2007, Carere and Maestripieri 2013). Therefore, the way in which individuals collect and use information may vary according to the personality or behavior type of the individual (Carere and Locurto 2011). Certain personality types are more likely to rely on social information than others (Marchetti and Drent 2000, Nomakuchi et al. 2009). For example, in an experimental foraging context, bolder Barnacle Geese (*Branta leucopsis*) used social information less frequently than shy geese (Kurvers et al. 2010). On the other hand, fast-exploring Great Tits (*Parus major*), which are also bolder, copied the feeding site choices of a demonstrator more often than slower-exploring, and shyer, conspecifics (Marchetti and Drent 2000). In general, however, bolder, more aggressive, and fast-exploring individuals tend to be less sociable and are often the first to disperse and colonize new habitats (Cote and Clobert 2007, Duckworth and Badyaev 2007, Cote et al. 2010). Bolder individuals are also more likely to migrate in a partially migrant population (e.g., Chapman et al. 2011).

Although they have been rarely studied in this respect, migratory birds do show personality traits (Battley 2006, Marchetti and Zehtindjiev 2009). Because there is still very little known about the ecological consequences of personality traits in the context of migration, our prediction is derived from the numerous studies conducted in other contexts (see above). We predict that individuals along the shy–bold personality continuum will differ in their use of social information. If bolder individuals are faster explorers, more aggressive, and less social, the cost of maintaining flock membership in order to continuously supplement personal sampling information with social information may be higher than the added benefit provided by social information. In contrast, slow-exploring, shy individuals should benefit more from rapid assessment of unfamiliar stopover habitat facilitated by the use of social information.

Prediction 7: Unfamiliarity. Novel environments increase the costs of collecting information (Dukas 1998). In a previous study (Németh and Moore 2007), we tested whether migrants relied more heavily on social information soon after arriving at a novel stopover site to compensate for the lack of prior information. We called this the Information Constraint Hypothesis. We predicted that social information use would vary temporarily, i.e. decline over time as migrants familiarized themselves with the stopover site. Consistent with this prediction: (1) migrants were more likely to be found in flocks upon arrival at our study site along the northern coast of the Gulf of Mexico than the following morning; and (2) individually radio-tracked Hooded Warblers (*Setophaga citrina*) exhibited a higher propensity to join flocks on the day of arrival than on the day of departure (Németh and Moore 2007).

Prediction 8: Environmental variability. Ecological conditions (e.g., resource availability, competitor density, risk of mortality, habitat heterogeneity, weather, proportion of novel habitat, food types, and predators) vary along a migratory route as a function of time and space, both on the local and global scale. As higher degree of evironmental variability is associated with increased uncertainty of refueling 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. However, similarly to conditions that favor phenotypic plasticity (Piersma and van Gils 2011), only moderately variable environments should promote social information use because in highly variable environments the costs associated with copying, potentially outdated information increase (Boyd and Richerson 1985, 1988).

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). The social context and the importance of social information in decisionmaking during different stages of migration have been largely overlooked, despite their significant roles in influencing annual schedules and aiding navigation and resource

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acquisition (Hamilton 1962, 1967, Wallraff 1978, Helm et al. 2006, Guttal and Couzin 2010, Mueller et al. 2013).

High concentrations of migrants at stopover sites are often considered to increase individual competition that reduces fitness in a density-dependent manner (Fretwell and Lucas 1970, Moore et al. 1995). However, residents and other migrants, both conspecifics and heterospecifics, can also be important sources of information that reduce risks and uncertainty and speed up the process of resource assessment and, ultimately, fat deposition rate (Németh and Moore 2007, Seppänen et al. 2007, Valone 2007). Moreover, as conditions at stopover sites are likely to change in unpredictable ways over a continental scale due to global climate change, habitat degradation, and urbanization (Bairlein and Hüppop 2004), rapid information transfer by social learning could quicken and improve migrants' responses to the changing global environment (Helm et al. 2006). Thus, we could start to think about migrant communities at stopover sites as additional sources of information where transient associations with others could have important and long-lasting benefits. Migrants from different geographical regions and habitat types offer a diverse pool of experience, behavioral repertoires, and decisions (sensu Giraldeau 1984) that can translate into beneficial information in a social foraging context in novel ecological settings. 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.

Tests of our proposed predictions under natural conditions may often require longitudinal data collection from marked individuals. With the miniaturization of tracking devices, more affordable technology, and automated remote data collection methods, technological and computational advances now allow researchers to test the importance of en route social learning in novel ways, potentially along entire migratory journeys (Nagy et al. 2010, Bridge et al. 2011, Mueller et al. 2013). It may be particularly rewarding to explore the effects of individual state (e.g., age, experience, and energetic condition) on social interactions and information use among individuals by using tags that communicate with each other and record proximity to other tagged individuals. These modern tags could indicate the emergence of collective behaviors as well as distinguish information producers from scroungers by identifying leaders in social groups (Guttal and Couzin 2010, Flack et al. 2012, Liedvogel et al. 2013). A similarly exciting way to test some of these predictions could be to manipulate the perceived landscape of social information available to an individual, for example by broadcasting conspecific or heterospecific vocal cues associated with different ecological contexts (Mukhin et al. 2008, Nocera et al. 2008, Nocera and Ratcliffe 2010).

Finally, we offer a conservation-related footnote: If social learning at stopover sites improves the likelihood of successful migration, and the amount of useful information inadvertently presented by migrants correlates with the abundance and diversity of the migrant community, then conservation practitioners should look for ways to harness and maximize the effect of this cognitive mechanism. This can be achieved by, and presents another line of argument for, increasing the size and quality of protected stopover sites (Mehlman et al. 2005) and prioritizing conservation effort for the sites comprising a variety of habitat types.

ACKNOWLEDGMENTS

Thanks to C. Mettke-Hofmann, J. J. Nocera, and three anonymous referees for comments that improved an earlier version of this manuscript. These ideas were developed while our research on migratory birds during stopover was supported by the National Science Foundation (IOB 0078189, DEB 05544754).

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