Wader Study 127(3): xxx–xxx
doi:10.18194/ws.00210

In this series, coordinated by Thomas Mondain-Monval (Lancaster University, UK, *t.mondain-monval@lancaster.ac.uk*), invited authors discuss themes in wader/shorebird biology, ecology or conservation that arise from publications other than *Wader Study*.

What strategy to choose? Migration distance and body condition as modulators of migration and stopover behaviors in Arctic-breeding waders

Bird migration strategies have evolved to maximize fitness, allowing birds to adapt to and survive the climatic and environmental variations that occur in seasonal environments[1]. For long-distance migrants, the energetic cost of flight, the timing of migration, mortality cost, competition, orientation and navigation are among the many factors affecting variation in the extent and patterns of migration[2].

Within migratory birds, waders vary widely in both migration behavior and distance. Behavioral adaptations allow individuals to respond to variable conditions during the journey (e.g. rainfall, wind), but there are also many differences in migratory behavior between species, even those which are closely related[3]. Therefore, a central question in wader ecology has been to understand which factors, both ecological and evolutionary, influence migration patterns. The investigations that have been carried out so far suggest that many factors affect the costs and benefits of migration and movement decisions, including food availability, wind patterns, predation risk, habitat use, and also parasites and pathogen infection[3–7].

Recently published work by Anderson and colleagues[8] suggests that the migration strategies of small Nearctic waders are linked to migration distance, and that departure from stopover sites and flight behaviors are moderated by body condition. These findings match previously observed patterns of a time-minimizing migration strategy in long-distance migrants[9]. Optimal migration theory predicts that animals make minimization trade-offs between energy and time when migrating. It is believed that the minimization of energy costs and predation risk might mold adaptive behaviors, such as when and at which fuel load to leave a stopover site. The time-minimization strategy predicts that natural selection favors traits that maximize the overall migration speed. Hence, survival could be maximized by reducing the overall duration of migration (speed maximization) and exposure to risks[10].

Under these assumptions, Anderson *et al.*[8] present empirical evidence showing that adult long-distance Nearctic migrant waders use a time-minimizing strategy during southbound migration. To do this, they captured juveniles and adults of six Arctic-breeding waders with variable migration distances at James Bay, Ontario, Canada, during peak southward migration. Each bird was aged as juvenile or adult, mass and wing length were measured, and subcutaneous fat score was recorded. They used these capture data to calculate relative fuel loads (ratio of fat mass to lean mass), and population-level rates of mass change, which were used to estimate departure mass. Before birds were released, they were also fitted with nanotags, which were used to provide high temporal resolution estimates of length of stay, departure timing, and flight speeds. This allowed them to evaluate the influence of weather conditions (wind and precipitation) on the timing of departure and to determine whether birds stopped elsewhere in North America after leaving James Bay.

They found that adult long-distance migrants had longer stopovers in James Bay and higher relative fuel loads than those migrating shorter distances. They also appeared to migrate with faster air and ground speeds and had a

[1]Bell, C.P. 2000. Process in the evolution of bird migration and pattern in avian ecogeography. *Journal of Avian Biology* 31: 258–265.
[2]Alerstam, T., A. Hedenström & S. Åkesson. 2003. Long-distance migration: evolution and determinants. *Oikos* 103: 247–260.
[3]Piersma, T. 2007. Using the power of comparison to explain habitat use and migration strategies of shorebirds worldwide. *Journal of Ornithology* 148: S45–S59.
[4]Schneider, D.C. & B.A. Harrington. 1981. Timing of shorebird migration in relation to prey depletion. *Auk* 98: 801–811.
[5]Butler, R.W., T.D. Williams, N. Warnock & M.A. Bishop. 1997. Wind assistance: a requirement for migration of shorebirds? *Auk* 114: 456–466.
[6]Clark, N.J., S.M. Clegg & M. Klaassen. 2016. Migration strategy and pathogen risk: non-breeding distribution drives malaria prevalence in migratory waders. *Oikos* 125: 1358–1368.
[7]Conklin, J.R., N.R. Senner, P.F. Battley & T. Piersma. 2017. Extreme migration and the individual quality spectrum. *Journal of Avian Biology* 48: 19–36.
[8]Anderson, A.M., S. Duijns, P.A. Smith, C. Friis & E. Nol. 2019. Migration distance and body condition influence shorebird migration strategies and stopover decisions during southbound migration. *Frontiers in Ecology & Evolution* 7: 251.
[9]Nilsson, C., J. Bäckman & T. Alerstam. 2014. Seasonal modulation of flight speed among nocturnal passerine migrants: differences between short-and long-distance migrants. *Behavioural Ecology & Sociobiology* 68: 1799–1807.
[10]Hedenström, A. 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. *Philosophical Transactions of the Royal Society B* 363: 287–299.

lower probability of stopping elsewhere in North America on their southbound migration than the species that migrate shorter distances, although this was largely driven by the high flight speeds of adult White-rumped Sandpipers *Calidris fuscicollis*. This suggests that there may be less flexibility in migratory strategies for long-distance migrants than short-distance migrants, potentially making them more susceptible to climate change. Interestingly, this work also provides further evidence that some individuals may attempt non-stop transoceanic flights to the Caribbean or South America.

The study also revealed differences between age groups, with the relationship between migration strategy and migration distance not as clear for juveniles as it was for adults. For juveniles there was no definitive association between departure fuel loads and migration distance; instead they only found that those with higher fuel loads at capture had shorter stopover durations. The influence of weather conditions on departure timing was also age-dependent. Adults were less likely to depart during wet weather whereas juveniles departed irrespective of weather conditions. The authors consider this could be a result of either inexperience or time constraints, as juveniles tend to arrive in James Bay later than adults. However, all of the wader species studied were wind-selective at departure regardless of migration distance. Although this suggests an energy-minimization strategy, the authors point out that it could also reduce overall migration time through faster flight speeds.

Body condition adjustments are often studied under controlled experimental conditions. The work by Anderson *et al.* provides much-needed field-based research on migratory waders confronted with departure decisions. From their results, it seems probable that departure for migration is triggered by some minimum fuel load and further influenced by local weather and geographical factors, particularly in adults. Documentation of such adjustments in the wild provides information on the extent to which behavioral and body adjustments increase fitness. These kinds of studies can help us to predict how birds will react to climate change, whether they depart sooner from wintering sites or whether migration speed is affected by changes in stopover conditions along the migration route.

This study is also important because it provides some of the first fine temporal scale migration tracks of White-rumped Sandpipers, Least Sandpipers *Calidris minutilla*, and Semipalmated Plovers *Charadrius semipalmatus* outside of their stopover or breeding sites.

Tracking technologies, such as satellite transmitters, are increasingly facilitating the execution of field studies, which will help researchers to understand the biological adaptations required by migratory waders all along their routes. While these techniques have recently advanced, there is much to learn about the migratory routes of many Nearctic waders. Flyway studies should be a priority, particularly when conservation and management actions are needed along the entire flyway. Studying the diversity of migration patterns will help to identify the relative importance of different selective factors, such as the physiological, behavioral, immunological and navigational adaptations that are involved with migration. For animals living in seasonal environments, understanding the timing of their migration behaviors in relation to ecological conditions is crucial for their conservation.

Sofía Capasso

Centro de Estudios Parasitológicos y de Vectores (UNLP-CONICET), Argentina

Sandpipers stopping at James Bay on southbound migration (photo: Christian Friis).