Lingering Consequences: How Important are Carry-over Effects in Arctic-breeding Shorebirds?

by Willow English

INTRODUCTION

Conservation biology is the study of biodiversity loss and the ways in which this loss can be reversed. As the unprecedented and accelerating rate of global biodiversity loss threatens ecosystems as well as human economies (IPBES, 2019), conservation biology is more important than ever. While conservationists might try to recover populations by managing habitats or competition with invasive species, for example, the ultimate mechanism through which populations decline or increase is through variation in survival and reproduction rates. These demographic rates and the factors that affect them, therefore play a fundamental role in conservation biology. Understanding the demography of migratory species presents an additional challenge, as individuals change their geographic location, behaviour, and physiology seasonally (e.g., Rushing et al., 2017).

Technological limitations have, until very recently, prevented us from following small-bodied migratory species from one location to another and documenting individual variation in demographic rates over time. Instead, population-level studies at different locations along the migratory pathways have been carried out and linked post hoc. Studies carried out in this way can overlook the existence of individual level carry-over effects, and their impacts on demographic rates. In ecology, the term “carry-over effects” refers to previous experiences affecting an organism’s abilities in a subsequent temporal stage (O’Connor et al., 2014). The importance of such carry-over effects has been increasingly revealed as technological innovations have provided methods to follow individuals of smaller migratory species throughout the entire year (Harrison et al., 2010).

One of the first studies to highlight the importance of carry-over effects in a small-bodied migratory bird was conducted by Marra et al. (1998) on American Redstarts (*Setophaga ruticilla*). Through the analysis of stable isotopes, they found a difference in arrival dates to the breeding grounds that could be traced back to the quality of a bird’s wintering habitat. These timing differences translated into substantial differences in reproductive output: males from high quality winter habitats produced, on average, 25% more fledglings than males from low quality habitats; and females from high quality habitats produced 66% more fledglings (Norris et al., 2004). Thus, a complete understanding of reproductive variation during the breeding season would be impossible without considering the effects of circumstances during the non-breeding season. This body of work not only showed that carry-over effects were present, but that they could have major effects on demographic rates. The conservation implications are substantial, as this study suggests that ongoing habitat destruction and degradation in the neotropics may not only affect migratory birds’ over-wintering survival, but also their subsequent reproductive output.

Further study of carry-over effects has been facilitated by advances in tracking technology, the analysis of stable isotopes and feather corticosterone, and other methods that provide information about previous conditions that can be linked to present capabilities (Harrison et al., 2010). As carry-over effects have been studied in an increasing number of species, it has become increasingly clear that their importance varies widely across systems. Much remains to be learned about the factors that determine the importance of carry-over effects for a particular species. Some studies have found carry-over effects to be present and strong, while others have failed to identify them or found them to be context-dependent (Bourgeon et al. 2014; Fayet et al. 2016; Bogdanova et al. 2017). More study, especially large-scale, multi-species comparisons using consistent methodology, is needed before we can begin to predict the influence of carry-over effects has on a particular species or population. Given the potential conservation implications, these studies could greatly alter our approach for conserving migratory species.

Shorebirds (Charadriiformes) are an ideal group of species for studying carry-over effects. As long-distance migrants who rely on ephemeral resources and whose reproductive success is highly affected by the timing of nesting, theory predicts that they should be susceptible to strong carry-over effects (Fig. 1). Delays in the timing of migration that result in sub-optimal access to resources could cause a cascade of further delays with consequences such as reduced survival and impaired breeding.

Shorebirds are also a group of major conservation concern that would benefit from an increased understanding of the factors underlying their demographic rates (Harrison et al., 2010; Barshep et al., 2013; Méndez et al., 2018). Comparisons across shorebird species should also be informative, as the large number of closely related species differing in traits like body size or migration distance provide an effective means to test which factors affect the presence and extent of carry-over effects among species.

However, few studies have so far tested for the presence of carry-over effects in shorebirds. Gill et al. (2001) found that Icelandic Bar-tailed Godwits (*Limosa limosa islandica*) at low-quality wintering sites subsequently had lower breeding success than individuals from high-quality sites; this effect appeared to be mediated by differences in the

FIG. 1. Photograph of Willow English holding a Black-bellied Plover. Black-bellied Plovers show high variation in the latitude at which they winter, making them a good species to test whether traits like migration distance carry-over to affect breeding characteristics.

timing of breeding. However, studies testing for temporal carry-over effects in New Zealand Bar-tailed Godwits (*Limosa limosa baueri*) and Hudsonian Godwits (*Limosa haemastica*) suggested that timing delays in one season had little effect on timing in subsequent seasons (Conklin & Battley, 2012; Senner et al., 2014). Why does the importance of carry-over effects appear to differ between closely related species, or even different populations of the same species? This is currently unknown, but may be related to different methodologies among studies or different selective pressures between species and populations.

Their life history traits make shorebirds good candidates for the study of carry-over effects, but it is their conservation status that makes understanding the consequences of carry-over effects in this group so crucial. Shorebirds are among the most rapidly declining groups of birds around the globe, especially species that are long-distance migrants (Andres et al., 2012; Rosenberg et al., 2019; Smith et al., 2020). Migratory birds rely on habitat and resources along their entire migratory routes and are vulnerable to changes anywhere across their entire range (Piersma and Lindström, 2004; Martin et al., 2007; Bairlein, 2016; Szabo et al., 2016). The extreme distances and locations covered by shorebirds make the identification of factors contributing to declines more challenging. The factors driving declines are diverse and likely differ in importance among species. Habitat loss, for example through development of coastal sites, loss of wetlands, and water diversion to agriculture, is thought to be a major factor, as is habitat degradation through increased anthropogenic disturbance (Stillman et al., 2007; Fernández and Lank, 2008; Studds et al., 2017). Climate change is also likely affecting shorebirds in myriad ways—the abundance and timing of invertebrates and predators is changing rapidly in the Arctic, while wind patterns encountered during shorebirds' migrations are changing, rising sea levels are likely to affect coastal areas, and extreme weather events such as hurricanes and floods are increasing throughout the year (Lindström and Agrell, 1999; Galbraith et al., 2002; Stillman et al., 2007; Senner et al., 2015). Some conservation concerns are more localized, such as the effects of sport hunting of shorebirds in the Caribbean and market hunting in areas of South America (Watts and Turrin, 2016). Other concerns, such as atmospheric deposition of contaminants such as mercury and other heavy metals, are more widespread (Hargreaves et al., 2010; Perkins et al., 2016).

As funding for conservation measures is limited, factors causing declines must not only be identified, but prioritized so that available funds can be used efficiently. If carry-over effects are not considered, conservation actions may be misdirected in space and time because the true causes of declines are not recognized. For example, endangered Red Knots (*Calidris canutus rufa*) migrating through Delaware Bay showed low summer adult survival and low recruitment rates, which led many to believe that conditions in the Arctic were negatively affecting this species (Niles et al., 2005; Fig. 2). However, further investigation found that the weight at which adults were leaving Delaware Bay on their northward migration was related to over-summer survival, and that birds were leaving at lower weights than in previous years, likely owing to reduced food abundance from overharvest of horseshoe crabs (Baker et al., 2004; McGowan et al., 2011). Without knowledge of carry-over effects, events occurring during migration might not have been considered as contributors to summer demographic rates. The study of carry-over effects is vital for understanding the underlying causes of effects that may be seen months later and thousands of kilometres away, thereby helping to focus in on issues that need to be addressed.

The field of carry-over effects is relatively young, as only recently has technology made following individual birds over time possible. Most studies of carry-over effects focus on single species, and in the case of shorebirds, have been limited to large-bodied species able to carry tracking devices. In order to understand how traits such as migration distance, migration strategy, mating system, and body size influence carry-over effects, multi-species studies using consistent methodology are needed. Shorebirds are ideal for this type of comparison, as these traits vary between closely related species that otherwise have similar life histories, reducing confounding factors.

RESEARCH APPROACH

The first component of my research focuses on the timing of migration and breeding. I have organized an international collaborative project, aggregating geolocator and satellite tracking data from almost 500 individuals of eight species of Arctic-breeding shorebirds: American Golden-Plover (*Pluvialis dominica*) n = 45; Black-bellied

FIG. 2. Red Knots at the East Bay (Qaqsauqtuuq) Migratory Bird Sanctuary on Southampton Island, Nunavut, Canada. The rufa subspecies of Red Knot breeds in the Canadian Arctic and winters as far south as Tierra de Fuego in South America. This species has undergone major declines in recent years linked to factors like the loss of food resources at stopover sites, especially Delaware Bay, and climate change.

Plover (*P. squatarola*) n = 34; Hudsonian Godwit (*Limosa haemastica*) n = 62 Ruddy Turnstone (*Arenaria interpres*) n = 35; Red Knot (*Calidris canutus*) n = 99; Dunlin (*C. alpina*) n = 138; Semipalmated Sandpiper (*C. pusilla*) n = 40, and Whimbrel (*Numenius phaeopus*), n = 43. This is the largest shorebird tracking data set ever assembled. Geolocators take frequent light level readings and contain an internal clock; together, the light and time data can be used to estimate day length and timing, which can then be used to estimate latitude and longitude (Phillips et al., 2004). However, as light levels can be affected by many other factors, considerable processing is needed to obtain location estimates, and locations are imprecise (Lisovski et al., 2012; Rakhimberdiev et al., 2016). To ensure consistency between studies, I re-analysed the tracks using FLightR (Rakhimberdiev et al., 2017). The output of this program is a list of locations at which the bird spent more than 48 hours, the duration of the stopover period, and a measure of uncertainty around the location estimate (Fig. 3). I further processed the output by merging locations estimated to be < 250 km apart and smoothed the tracks by eliminating sudden backtracks. As geolocators use differences in light levels to estimate location, locations above the Arctic circle are not available, as this area experiences 24-hour light while the birds are present. Satellite tracking data are much more precise, but locations are only transmitted when there is sufficient power generated from the solar panel. I processed the satellite data to be comparable with the geolocator data by grouping periods where the birds moved < 250 km in 48 hours or more, and excluding tracks with long gaps in location estimates during which the birds moved substantial distances, as movement dates could not be obtained from these data.

Most of the tracking devices I used were deployed on the breeding grounds and have associated breeding data. Searchers found the nests and determined the estimated initiation date by floating the eggs or back counting in the case of incomplete clutches (Liebezeit et al., 2007). When the tracking devices were deployed, the birds were caught on the nest and morphometric measurements such as mass and bill, leg, and wing length were taken. In some species, it was also possible to determine sex and age. Nests were then monitored through the breeding season to determine whether the bird successfully produced chicks. The majority of tracks used in the study were from geolocators, which must be recovered to obtain the data. Tags were recovered by finding breeding birds in subsequent years and re-catching them on the nests; for these birds, breeding data

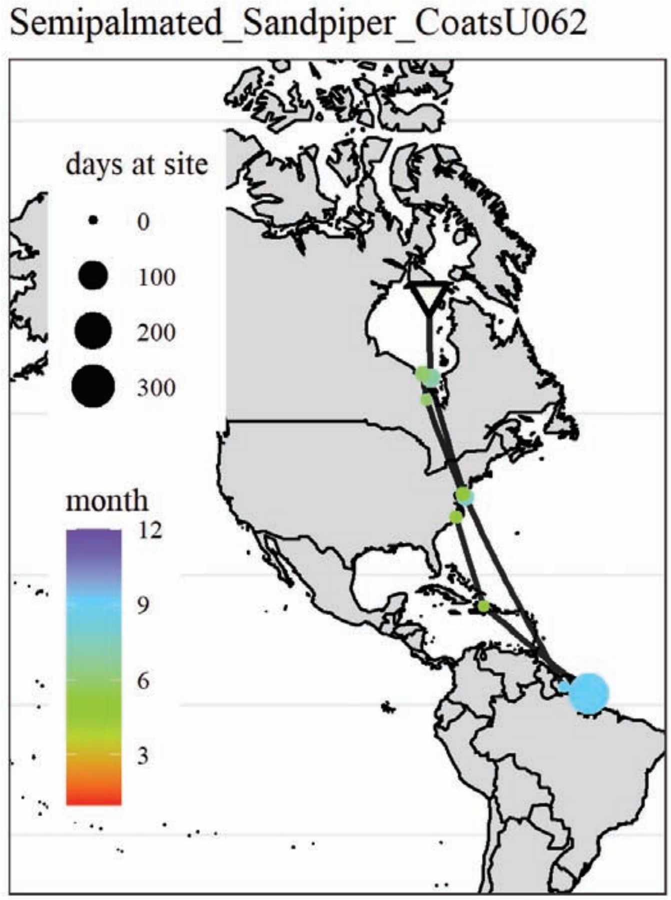

FIG. 3. Geolocator-derived yearly movement patterns of a Semipalmated Sandpiper breeding on Coats Island, Nunavut, Canada. The size of the points increases with the duration of time spent at that location, and the colour of the point indicates the month during which the bird arrived at that location.

are also available for the tag recovery year. In some cases, geolocators were deployed at migratory stopover sites or on the wintering grounds. For these individuals, although the breeding location of the bird was unknown, it was possible to estimate nest initiation date using the geolocator's light data, as the geolocator is covered by the bird's feathers during incubation, and the pattern of light to dark during incubation is distinctive.

In general, Arctic-breeding shorebirds who nest early relative to their breeding population have better reproductive success, possibly due to seasonal changes in predation pressure (Weiser et al., 2018; McGuire et al., 2020). In some cases, early nests are subject to higher levels of depredation, suggesting that synchronous nesting may be more advantageous; however, nests lost early in the season are more likely to be replaced (Meltofte et al., 2007; Smith et al., 2010). However, while we know that local conditions such as snow melt affect the timing of nest initiation, the influence of prior events such as migration timing is largely unknown (Smith et al., 2010). I will be using the tracking dataset to determine whether nest initiation date is more affected by breeding site conditions, or conditions prior to arrival that have caused birds to start their migrations later or spend longer on migration. If the latter has a greater effect, it would suggest that the timing of breeding, and perhaps nest success, are limited by conditions prior to arrival, instead of local conditions in the Arctic.

Long-distance migrants, especially those who depend on ephemeral resources, have tight schedules into which they must fit breeding, pre-migration fueling, migration and stopovers, moult, and other activities. If birds are delayed at any point during their annual cycle, they may suffer from sub-optimal access to resources, and this could cause further delays. I will use the tracking dataset to determine whether delays are accumulating in any of the species in this study, and if so, whether there is any relationship between the extent to which delays accumulate and a species' traits such as total migration distance, the average length of each migration leg, and body size. For example, species that have longer migrations must spend longer periods preparing for migration and flying, and therefore may be even more time-constrained and lacking in capacity to make up for delays.

Shorebirds are thought to time their breeding so that their chicks hatch when insect food is most abundant (Saalfeld et al., 2019). The date of peak insect emergence appears to be changing more quickly than the date of nest initiation, leading to concerns about a mismatch between insect emergence and shorebird hatch. The seeming inability of shorebirds to track the timing of insect abundance may be related to the variable rates of climate warming across shorebirds' large geographic ranges. The Arctic is warming much faster than the temperate regions shorebirds rely on for stopover sites on their migrations (IPCC, 2021). If stopover sites are not becoming available early enough, shorebirds may be blocked from earlier arrival to the Arctic. I will use the tracking data and global weather information to determine whether the stopover areas used by northward migrating shorebirds in North America are used by shorebirds as soon as they're available, and whether this has changed over time. I will also be comparing the routes of early- and late-migrating individuals to see if there are differences in route selection that may be related to stopover availability. If shorebirds are unable to advance the timing of their breeding in the Arctic because of slower warming in temperate zones, they may be unable to adapt to the rapidly changing conditions in the Arctic.

Not all shorebirds are suitable for current tracking methods, so the second part of my project uses intrinsic physiological measures instead of technology to link a bird's prior experiences to its current condition (Fig. 4). Elevated levels of stress hormones can have negative effects on an organism's health, including through immune function (Butler et al., 2010; Gao et al., 2017). In birds, a "snapshot" of past stress hormone levels can be found in feathers, as hormones are incorporated into the feathers during growth and remain static after growth stops (Bortolotti et al., 2008). I can thus use feathers collected in the summer to link a bird's current breeding condition to its winter stress levels when the feathers were grown.

FIG. 4. Photograph of a Red Phalarope moulting into winter plumage and feathers taken for corticosterone analysis. Red Phalaropes are understudied in the non-breeding season, as they winter on the open ocean, and current tracking devices are not appropriate for this species. Using feather corticosterone levels to assess winter stress allows us to test for carry-over effects in individuals caught during the summer breeding period.

I have assembled feather samples and breeding data from 545 individuals of ten species of shorebirds: American Golden-Plover (*Pluvialis dominica*), n = 69; Black-bellied Plover (*Pluvialis squatarola*), n = 38; Long-billed Dowitcher (*Limnodromus scolopaceus*), n = 61; Red Phalarope (*Phalaropus fulicarius*), n = 66; Red-necked Phalarope (*P. lobatus*), n = 72; Ruddy Turnstone (*Arenaria interpres*), n = 74; Pectoral Sandpiper (*Calidris melanotos*), n = 60; Semipalmated Sandpiper (*C. pusilla*) n = 30; Western Sandpiper (*C. mauri*) n = 60; White-rumped Sandpiper (*C. fuscicollis*) n = 15 collected at three sites across the North American Arctic. I will use these feathers to test whether stress on the wintering grounds could be related to the reproductive success of birds in the Arctic, by comparing their winter feather corticosterone levels to their reproductive characteristics, such as the date of nest initiation, breeding success, and in females, egg size. If there is a relationship between winter stress and breeding metrics, it would suggest that carry-over effects are present and must be considered when designing conservation actions.

SIGNIFICANCE

The importance of carry-over effects is becoming increasingly apparent as new technology allows us to follow birds across their whole annual cycles, but much remains to be learned. My PhD study will provide information on carry-over effects in an array of species that are known to be declining, which could provide information helpful to their conservation. My study of feather corticosterone will contribute not only information about carry-over effects, but to our understanding of this novel technique that may prove to be very important for the study of carry-over effects. With its extensive sample size and broad array of species, my study will provide an opportunity not only to asses carry-over effects in specific shorebird species, but also to better understand how carry-over effects relate to other life history traits. This knowledge will help us to predict the species for which carry-over effects are likely to be important, and to better understand the diversity of mechanisms through which carry-over effects operate. Given the current declines seen in shorebirds and other avian species, the ability to recognize causal factors of conservation problems, even if they occur in a different time and place from the observed effects, will be vital to making effective management decisions and using conservation dollars efficiently.

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