

Cross-seasonal and cross-disciplinary studies of migratory shorebirds

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Many scientific questions and conservation challenges regarding migratory shorebirds will be best and most efficiently addressed by combining information from different disciplines and the entire annual cycle. We present examples that integrate physiological, behavioural, and population data collected on breeding grounds, on migration, and on non-breeding grounds, focusing on work with Western Sandpipers. We suggest ways to apply this approach generally to address scientific and conservation questions in other shorebirds species in the future.

INTRODUCTION

Twenty-one years ago, J.P. Myers (1981a) published “Cross-seasonal Interactions in the Evolution of Sandpiper Social Systems”. The paper considered aspects of the entire annual cycle to explain phenomena often conceptualised as driven within one seasonal dimension. Concurrently, Rudi Drent and co-workers at the University of Groningen emphasised the potential value of studying the foraging, migration and breeding success of individually marked geese of known age, gender, social status and body condition. The Western Sandpiper Research Network adopted and expanded these cross-seasonal and cross-disciplinary approaches when it originated within the Centre for Wildlife Ecology at Simon Fraser University, Vancouver, British Columbia, Canada, 10 years ago, building on earlier work by the Canadian Wildlife Service (Butler *et al.* 1987). The network now includes behavioural and population ecologists, physiologists, and wildlife managers. This breadth has allowed us to combine information from different disciplines gathered on the breeding grounds, at migratory stopover sites, and on wintering areas, to increase our understanding of, and maintain appropriate conditions on the landscape for, migratory shorebirds. We present here examples of the utility of this approach for addressing novel and crucial questions, and believe it has substantial potential for future research and conservation work (Harrington *et al.* 2002).

We assert that an attempt to understand individual strategies and population dynamics will benefit from viewing the birds as predators, prey, and as competitors. A central concept for most of the Western Sandpiper researchers is that habitat choices, particularly on migration and during the winter, will reflect “state-dependent tradeoffs” between foraging efficiency and safety from predators (Ydenberg *et al.* 2002). Under “state”, we here include morphological sex differences, age-specific attributes and experience, body size and mass, and diverse aspects of physiological condition. Under “habitat choice”, we consider not only choice of local foraging sites such as mudflat, beach, or farmland, but also choice on the scale of wintering latitude. Two companion essays in this volume emphasise work by members of our network on sandpiper options for feeding (Elner & Seaman) and preventing

being fed on (Butler, Ydenberg & Lank). The ideas in both essays arise from and address information gathered throughout the species’ range and annual cycle, and both utilise cross-disciplinary approaches in their discussions.

Western Sandpiper *Calidris mauri*

The Western Sandpiper Research Network chose to focus on the most common species of shorebird on the American Pacific Coast because of the practical advantage of doing so for developing novel techniques and testing ideas with potential general applicability, including species of greater direct conservation concern. Western Sandpipers are relatively easy to capture in mist-nets, to sex, and age (Prater *et al.* 1977). They breed in a relatively compact area of western Alaska and the eastern edge of Siberia, and spend the non-breeding season spread along the Pacific coast from southern Canada to Peru, and to a lesser extent, along the east coast of the Americas (Wilson 1994, Nebel *et al.* 2002). Colleagues and collaborators have been working at three Alaskan breeding ground sites (Nome: Sandercock 1997, 1998, Neville 2002; Kanayaraq: Ruthrauff 2002; Cape Espenberg: Schamel & Tracy unpubl. data); a large and a small migratory stopover site near Vancouver B.C. (the large Fraser River Delta and the small isolated Sidney Island: Butler *et al.* 1987, Lissimore *et al.* 1999, Ydenberg *et al.* 2002) and, a larger set of stopover sites in southern British Columbia and Washington state (Seaman & Williams, Pomeroy, unpubl. data); and five overwintering sites spanning the species’ range (San Francisco Bay: see Warnock & Takekawa 1995; Punta Banda, near Ensenada, in northwestern Mexico: Buenorostro *et al.* 1999, Fernández *et al.* 2001, 2003; Bahia Santa Maria, on the central-west coast of Mexico; Chitré, on the Pacific coast of Panama: O’Hara 2002, O’Hara *et al.* 2002; and La Libertad, in Ecuador: Harrington & Haase 1988). Radio-tracking studies have provided direct information on cross-seasonal movements, primarily on northward migration from California to Alaska (Iverson *et al.* 1996, Warnock & Bishop 1998, Bishop & Warnock 1998), but also on southward migration (Butler *et al.* 1996). Such widespread geographical coverage and cooperation enables us to address questions in several fields in ways never previously possible.



LIFE HISTORY DIFFERENCES IN NON-BREEDING DISTRIBUTIONS

Our widespread geographic coverage uncovered two significant and surprising pieces of natural history. It was previously recognised that male Western Sandpipers wintered farther north than females (Harrington & Hasse 1988), but with extensive collaboration we have produced a more detailed picture of this cline, and discovered that the latitudinal pattern differs between age classes in an unexpected way (Nebel *et al.* 2002). We have also discovered an intriguing life-history difference. In their first spring of life, birds wintering in Panama, and presumably farther south, remain resident on the non-breeding grounds, whereas those wintering in central Mexico, and presumably farther north, migrate north (O'Hara *et al.* 2002, Fernández *et al.* 2003, see Summers *et al.* 1995 for Old World examples). Somewhere between these areas, there is a "life history divide". Finally, within each sex, Western Sandpipers are larger in body size, and particularly in wing length, farther south (O'Hara 2002).

What accounts for these patterns? Are the sex, age, and size differences related to state-dependent feeding/safety tradeoffs due to the bill dimorphism and latitudinal gradients in the availability of different food types (Elnor & Seaman, this volume) and/or latitudinal differential risk of predation (Clark & Butler 1999, Butler *et al.*, this volume)? Do breeding ground considerations favour northward non-breeding sites for males (Myers 1981b)? A novel hypothesis emerging from our group is that a higher amount of primary feather wear selects against northward migration by first-year birds wintering farther south. Some shorebird species have evolved a partial or even complete wing moult during their first winter (Prater 1981), but we have no evidence that this occurs in Western Sandpipers. Thus primaries grown after hatching must support three migratory flights prior to replacement, while adults moult primaries after two migratory flights. This means that by the end of their second summer, the primaries of juveniles are extremely worn, potentially resulting in inefficient flight and/or increased vulnerability to predation (O'Hara *et al.* 2002, Nebel *et al.* 2002, Yen *et al.*, MS). There are at least two factors that could lead to increased feather damage at more southern latitudes: the longer migration distance and the higher UV intensity (Yen *et al.* MS). Higher feather wear at southern latitudes would affect the primaries of juveniles more than those of adults, as the former have experienced substantially more wear. Feather wear might therefore be a significant factor when choosing a non-breeding latitude. An extensive network allows collection of feather samples needed to test this hypothesis. More importantly, to what extent are such patterns general (e.g. Shepherd *et al.* 2001), but currently unrecognised in other species, and what ecological and/or historical factors might be tested in comparative studies of the strength of size and sexual clines in non-breeding distributions?

TIMING OF MIGRATION AND MOULT

As with many other small calidrids, adults migrate north prior to first-year birds. Males travel more rapidly than females at the end of spring migration (Warnock & Bishop 1998), but remain longer on the breeding grounds. Sandercock *et al.* (1999) measured seasonal trends in fecundity that could provide benefits for birds breeding earlier. He also showed that mate fidelity rates of Western Sandpipers are lower than

those of the later-arriving Semipalmated Sandpipers (*C. pusilla*) (Sandercock *et al.* 2000). These results are consistent with the idea that cross-seasonal interactions exist between migration distance, and arrival times on the breeding grounds, resulting in potential advantages of a sex or species spending the non-breeding season closer to the breeding grounds (Myers 1981a,b).

One difficulty with arguments relating migration distance and timing of arrival has been identifying the costs of starting northward or southward a few days earlier to make up for a longer migration distance. Interestingly, although females leave breeding territories a week or more prior to males (Neville 2002, Ruthrauff 2002), there is a much smaller difference in southward migration timing at temperate latitudes (Niehaus *et al.* unpubl. data). This suggests that different factors drive brood abandonment and migration timing decisions. Our thoughts about the timing of migrations of shorebirds and predators (Lank *et al.* in press, see Butler *et al.*, this volume) have led us to new hypotheses involving costs and benefits that determine southward migration and moult timing. Those individuals overwintering in Panama, both yearlings and adults, complete primary moult 3–4 weeks earlier than adults that are returning from the breeding grounds. Moulting earlier, which we argue is advantageous to do prior to the arrival of migratory falcons, may partially compensate residents for the loss of a breeding opportunity (O'Hara *et al.* 2002; Watts pers. comm.). This argument assumes that birds or classes of birds with higher wing-loading, whether due to extra fuelling for migratory flight, more worn wings, or allometric differences between the sexes, are at greater risk of predation (Burns & Ydenberg 2002). This may be tested in part by inferring the relative fatness of birds taken by predators, based on extrapolation of fat in wings discarded by avian predators (Guglielmo & Burns 2001), and comparison of sex ratios of carcasses, as determined by molecular sexing (Nebel & Cloutier unpubl. data), versus those present in local populations. We look forward to future studies employing these techniques.

MEASURING INDIVIDUAL STATE AND PERFORMANCE

An emphasis on state-dependent decision-making by individuals or classes of individuals requires appropriate measures of state. Elnor & Seaman (2003) consider how morphological variation can affect our estimates of "state". Physiologists are measuring aspects of condition and performance that are not possible or practical to assess from behavioural observations, and relating these measurements to ecological conditions. One of the most exciting integrations of these measurements thus far is using circulating levels of triglycerides to measure fuelling rate (see below). In general, the physiological ecology group has focused on individual and class-specific differences in organ allocation throughout the annual cycle, on circulating levels of other metabolites of potential ecological interest and on digestive enzymes.

Juveniles making their first southward migration have a higher index of muscle damage than adults, as assessed from metabolites in blood samples (Guglielmo *et al.* 2001), and lower levels of fatty acid binding protein levels, which is an intracellular protein crucial to the utilisation of stored fat reserves by muscle during endurance flight (Guglielmo *et al.* 1998, Guglielmo *et al.* 2002a). These findings may provide a measure of the extent to which young birds undertake



longer migratory flights than adults or are less effective when flying similar routes. In contrast, prior to departure from the breeding grounds in Alaska, and during stopovers on southward migration, juveniles have substantially longer and heavier small intestines than adults, or than later in life (Stein 2002, Guglielmo & Williams 2003). These data potentially contradict the observations of reductions in gut size during migration reported in other species (Piersma & Gill 1998, Weber & Hedenström 2001). In addition, we have documented significant age-related and seasonal variation in digestive enzyme activities in migrating Western Sandpipers (Stein 2002). Age-related differences in digestive function and seasonal differences in diet composition might be associated with different age-dependent migration strategies in future studies.

ASSESSING HABITAT QUALITY THROUGH PHYSIOLOGY AND DEMOGRAPHY

Shorebird researchers commonly attempt to assess habitat patch quality directly from physical and prey-related parameters, such as mud samples. We have also done so (e.g. Shepherd & Lank, MS), but have also taken alternative approaches. Working with overwintering Dunlin *C. alpina pacifica*, Evans Ogden (2002) determined the relative contributions of marine versus terrestrial food sources based on stable isotope ratios in blood, and compared these with time budget data on habitat utilization, as derived from radio-tracking studies of the same population (Shepherd 2001; Shepherd *et al.*, this volume). At a smaller scale, we are testing the utility of infrared photography of mudflat surfaces to assess patch primary productivity (Pomeroy & Butler, pers. comm.). At a fine scale, for diet choice, we have also attempted to assess diet composition by comparing samples from sites where birds have and have not been feeding (Sutherland *et al.* 2000, Wolf 2001).

A novel approach appears useful when fattening rates are important, as at migration stopover sites or prior to departure from wintering areas. Levels of triglycerides in circulating blood provide an index of birds' fattening rates (Williams *et al.* 1999, Ydenberg *et al.* 2002, Guglielmo *et al.* 2002b). At the landscape level, preliminary data suggest that there is (a) significant inter-site variation in this index of fattening rate, especially during northward migration, (b) intra-site consistency in rates across seasons and years, and (c) a positive relationship between total macrofaunal prey abundance and rates, as expected (Seaman & Williams, unpubl. data). This direct assessment of the birds' condition sidesteps complications regarding measuring prey abundance versus its availability to shorebirds (Backwell *et al.* 1998). In the end, analysing blood rather than mud may provide a more efficient and effective tool for ranking the utility of sites for migrants. "Landscape Physiology" (Williams, pers. comm.) may help us make decisions about shorebird conservation.

An entirely different approach to assessing relative habitat quality is rates of local philopatry and/or residence time, as determined by mark-recapture studies. Within seasons, we have shown, for example, that length of stays have declined over the past 17 years at a small site, despite abundant food (Ydenberg *et al.* 2002, Butler *et al.*, this volume), and we argue that the resurgence of Peregrine falcon populations during the 1990s decreased habitat suitability for sandpipers. On a longer time scale, we can estimate within-season and annual "apparent survivorships" from several breeding and

wintering sites (e.g. Sillett & Holmes 2002). Since non-return to an area indicates either permanent emigration or death, we suggest that comparing values among sites based on local or "apparent survivorships" allows the birds themselves to indicate relative habitat suitabilities (Fernández *et al.* 2003, Lank *et al.* MSb).

INDIVIDUAL-BASED MODELLING OF POPULATION CONSEQUENCES

Many components of behaviour, physiology, and demography were integrated in a state-dependent dynamic programming model of northward migration strategies (Clark & Butler 1999). We hope in coming years to expand this model to provide a tool for exploring additional behavioural decisions throughout the annual cycle, and to move from modelling individual decisions to predicting population consequences based on those decisions. Eventually we hope to include the bird's year-round distributions, which would allow our models to be used as a predictive management tool.

CONCLUSION

We recognise that allocation of resources to the extensive and intensive study of a single species is not an approach everyone might take. We believe, however, that developing fundamental understandings of how this species operates throughout its annual cycle, at physiological, individual, and population levels, will prove useful when we are forced to make decisions about species where critical information cannot be obtained. Species differ in specific aspects of their lives; nonetheless, we hope that generalities emerging from our research will be of value to all shorebirds, to other long distance migrant species, and those who appreciate them.

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