

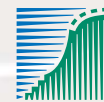
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Waterbirds around the world

A global overview of the conservation,
management and research of the
world's waterbird flyways

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Cross-cutting research on a flyway scale - beyond monitoring

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ABSTRACT

Research on the population ecology of migratory birds is facilitated by a holistic or “cross-cutting” approach that synthesizes information gathered across the entire flyway, throughout the annual cycle and utilizing different research disciplines. Radio-tracking Western Sandpipers *Calidris mauri* from non-breeding to breeding grounds documented migration timing and usage of stopover sites. Data collected throughout the non-breeding range showed that females migrated farther south than males, and that juveniles were over-represented towards the extremes. Collaboration documented a latitudinal “life-history divide”: northerly juveniles migrate and attempt to breed, while southerly juveniles overwinter at non-breeding sites. As predicted by life history theory, southerly birds appear to have higher annual survival rates than migrants. Comparing daily survival rates during breeding, non-breeding and annual periods permits the calculation of survival rates during migratory periods. Integrated studies of behavioral ecology, demography and physiology allowed interpretation of an apparent local population decline in migrating Western Sandpipers. Dramatically decreased usage of a small stopover site occurred despite abundant food resources, and appeared to be caused by a behavioral change in response to increasing falcon populations, rather than a decrease in numbers of migrants. The combination of approaches allowed testing alternative hypotheses as likely causes for the change in site usage.

INTRODUCTION

Understanding population regulation is a key issue in the study of migratory birds, but it acquires special urgency in species that suffer from decreasing population numbers. In shorebirds (family Scolopacidae), population declines are widespread: more than half of all shorebird populations world-wide are thought to be declining (International Wader Study Group 2003, Stroud *et al.* 2004, 2006), and within North America, this estimate is as high as 80% (Morrison *et al.* 2001).

A long-term research program organized by the Centre for Wildlife Ecology (CWE) at Simon Fraser University, Canada, is using a cross-seasonal and cross-disciplinary approach to study population ecology and, ultimately, population regulation of a migratory shorebird (Nebel & Lank 2003). This holistic approach is based on the synergy gained from synthesizing information sampled across the entire flyway, throughout the annual cycle, and utilizing different research disciplines, creating opportunities for conservation work (Harrington *et al.* 2002).

The Western Sandpiper *Calidris mauri* was chosen as a model species, being the most abundant shorebird on the American Pacific coast. Western Sandpipers breed in western Alaska and eastern Siberia, and overwinter along the American

Pacific coast between southern Canada and Peru, and, in smaller numbers, along the Atlantic coast and in the Caribbean (Wilson 1994, Nebel *et al.* 2002). Over 90% of captured birds may be confidently assigned a sex based on bill lengths (Page & Fearis 1971).

The CWE fostered research on diverse aspects of the species’ biology by organizing a loose association of researchers working throughout the species’ range to collaborate and exchange information (see Acknowledgements). Members consulted with government wildlife managers and non-governmental agency scientists, recruited academics in complimentary fields to work with the species, steered post-doctorate, graduate and undergraduate students towards particular projects, and provided seed funding for researchers elsewhere, particularly in Latin America. The group created a sense of common purpose during annual workshops, which attracted additional participants to the network, and through an electronic list-server.

CUTTING ACROSS THE FLYWAY

A series of radio-tracking studies of migrant Western Sandpipers conducted over five seasons between 1995 and 2004 during northward migrations from Mexico and California to Alaska capitalized on this network. Collaborators produced detailed information on the movements and stopovers of individual shorebirds with respect to age, sex, time of year, weather conditions, staging site, and year (Iverson *et al.* 1996, Butler *et al.* 1997, Bishop & Warnock 1998, Warnock & Bishop 1998, Butler *et al.* 2002). These studies strengthened the evidence that 80-90% of the Western Sandpiper population use the Copper River Delta, Alaska, towards the end of their northward migration. The length of stay estimated for that site from radio-tracking data was integrated with census data to improve estimates of the species’ total population size (Bishop *et al.* 2000). Further analysis of the wealth of data generated by this work will help test individually-based models of migratory strategy, which may be used to predict the population consequences of migratory habitat change.

As a second example, we improved the resolution of a pattern of sexual segregation of Western Sandpipers during the non-breeding season by combining information from 13 different sites, and discovered a novel pattern with respect to age (Nebel *et al.* 2002). Females migrate farther south than males, creating a latitudinal cline between sex ratio and Great Circle distance from the breeding grounds (Fig. 1). The local proportions of juveniles fit a significant U-shape with respect to migration distance (Fig. 2), which interacts with the sexual segregation such that juvenile males are substantially over-represented in samples from the northern end of the distribu-

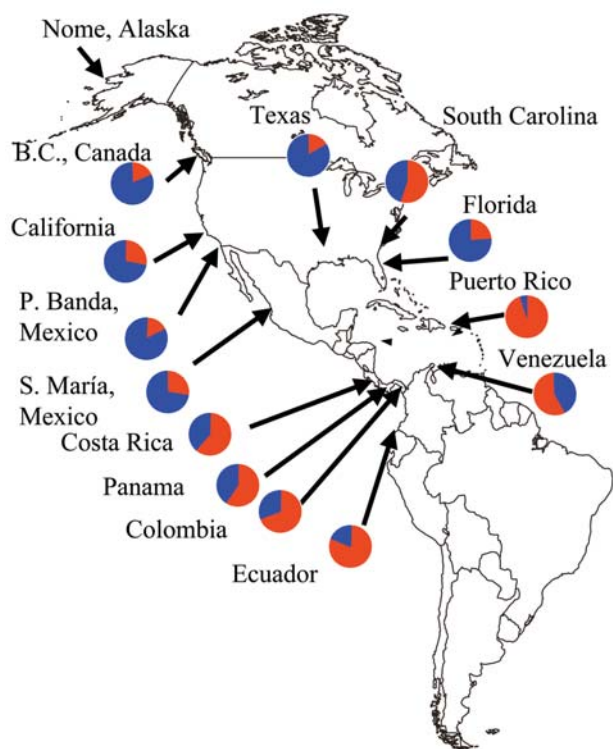


Fig. 1. The proportion of female (red) and male (blue) Western Sandpipers *Calidris mauri* on the non-breeding grounds.

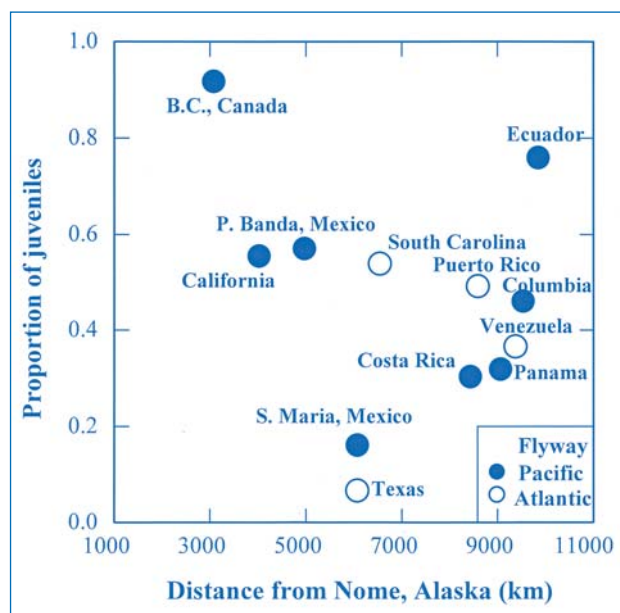


Fig. 2. Age ratios of Western Sandpipers *Calidris mauri* captured at 12 non-breeding locations. The local proportions of juveniles caught at each site vs. migration distance described a U-shaped pattern ($F_{1,22}=5.08$, $P<0.005$; after Nebel *et al.* 2002, reproduced with permission from *The Auk*).

tion, and juvenile females over-represented in samples from the southern end.

The distributions of sex and age classes also interact with a latitudinal difference in life history strategy (Fernández *et al.* 2004, O'Hara *et al.* 2005). Juveniles at non-breeding sites in Mexico predominantly migrate north and attempt to breed as

one-year-olds, while juveniles in Panama do not migrate, and instead "oversummer" on the non-breeding grounds. We infer that juveniles adopt one of two life history strategies, with shorter-distance migrants opting to attempt migration and breeding at a younger age, and longer-distance migrants maximizing first year survival at the expense of an earlier potential breeding opportunity.

This difference in strategies could map onto biological population differentiation, but none is currently recognized, and disproportionate representation of the sexes at different non-breeding areas makes this seem an unlikely situation. Alternatively, we may have documented two tactics of a conditional strategy (*sensu* Gross 1996), in which case the choice of tactics depends on an environmental cue, such as hatch date, and/or on developmental characteristics, such as body size. In this situation, migration distance itself might follow from a life-history decision based on condition made in Alaska prior to migration, or the opposite might occur, namely that the life history difference might follow from factors determining migration distance (O'Hara *et al.* 2002, O'Hara *et al.* 2005).

If lifetime reproductive success of individuals migrating south to different latitudes is similar, annual survival rates should be higher among oversummering juveniles than among juveniles migrating north in their first year, in order to offset the earlier age of first reproduction of migrants. Western Sandpiper researchers throughout the range and annual cycle have used mark-recapture studies to estimate ϕ , the rate of local survival, which provides a minimum estimate of true annual survival rate (Table 1), and return rates, which will approach ϕ if detection rates are high. Estimates of survival rates obtained at breeding and non-breeding grounds show some general agreement, assuming similar levels of permanent emigration. As predicted, local annual survival is lower in Mexico than Panama. As mark-recapture studies proliferate, comparisons among local survival rates derived from different situations and/or populations may refine our views of local habitat suitability and other aspects of population structure.

CUTTING ACROSS THE ANNUAL CYCLE

Population managers recognize that partitioning the timing of annual mortality across seasons and locations improves their ability to target conservation action. Studies based on band recovery data can rarely address this question directly. The development and widespread availability of capture-recapture analysis tools (Lebreton *et al.* 1992, White & Burnham 1999) enabled researchers at different sites and seasons to collaborate to obtain the necessary information. The best examples are studies of individually marked geese, which carry conspicuous markers that facilitate re-sightings. For some populations, lower daily survival rates occurred during migration than in winter or summer (Owen & Black 1991, Clausen *et al.* 2001), perhaps due to hunting (Ward *et al.* 1997). Other studies found lower survival rates during breeding seasons (including migratory flights) (Madsen *et al.* 2002), concluded that breeding, wintering and even migration seasons had similar rates of natural mortality (Gauthier *et al.* 2001), or that seasonal patterns differed by sex (Schmutz & Ely 1999). Each study suggests specific management actions, and the ecological reasons for the diversity of situations contribute towards our general understanding of population regulation.

The use of mark-recapture information was taken a step further by combining information derived from different

Table 1. Annual local survival rates for Western Sandpipers *Calidris mauri* studied at breeding (B) and non-breeding sites (N).

Location	Season	Estimates of ϕ or return	
		rates (rr)	Source
Nome, Alaska	B	0.62, 0.57 males* 0.59, 0.55 females*	Sandercock <i>et al.</i> 2000
Yukon-Kuskokwim Delta, Alaska	B	rr = 0.58 males rr = 0.49 females 0.67 males** 0.40 females**	Holmes 1971, Oring & Lank 1984 Ruthrauff & McCaffery, pers. comm.
Cabo Rojo, Puerto Rico	N	0.56 adults 0.61 juveniles	Rice 1995
Chitré, Panama	N	0.54 males 0.62 females	O'Hara <i>et al.</i> 2002
Punta Banda, Mexico	N	0.49 adult males 0.45 juvenile males	Fernández <i>et al.</i> 2003

* estimates from two years, samples of nearly all adults

** data from 1998-2002

populations of marked individuals. Sillett & Holmes (2002) obtained estimates of seasonal and annual survival rates from separate local populations of Black-throated Blue Warblers *Dendroica caerulescens* on the breeding grounds in New Hampshire, USA, and on the wintering grounds in Jamaica. Under the assumption that the individuals studied were representative of summer and winter populations, they combined their seasonal estimates with estimates of annual survival rates, and calculated survival rates during the migratory periods, which could not be studied directly. They concluded that the daily mortality rate during migration was 15 times higher than during the two residency seasons. Multiple mark-recapture data sets are becoming available for many non-game species, and comparisons among them may permit additional analyses along these lines. With Western Sandpipers, for example, we hope to develop techniques for combining information from the mark-recapture studies shown in Table 1 to address questions about seasonal survival rates and relative habitat quality.

CUTTING ACROSS DISCIPLINES

Wildlife managers are often called upon to act in response to changes in local population size. Over the past decade, the cumulative number of Western Sandpipers counted during southward migration at the Sidney Island lagoon, a small stopover site in British Columbia, Canada, declined drastically from c. 16 000 to 4 000 (Ydenberg *et al.* 2004), creating a strong incentive to understand the factors causing this change. Members of the Western Sandpiper research group have collaborated, integrating behavioral, ecological, demographic and physiological studies to address this question.

The Sidney Island lagoon includes c. 100 ha of mudflat, surrounded on three sides by a forest and beach. Across the Strait of Georgia, 40 km east of Sidney Island, is the Fraser River estuary, the major stopover site in British Columbia, with over 5 000 ha of open mudflats that are used by up to a million shorebirds every autumn and spring. We do not know whether population changes have also occurred at the Fraser estuary because the size of the site makes it difficult to census. However, comparisons of attributes of both areas, and of birds captured at them, have

been useful in our analysis of this situation (Lissimore *et al.* 1999, Ydenberg *et al.* 2002, Ydenberg *et al.* 2004).

At Sidney Island, migrating Western Sandpipers were captured, measured, individually marked, and re-sighted daily during the years of population decline; birds were also captured and measured at the Fraser estuary. At Sidney Island, the body mass of captured birds decreased by c. 10% during this period, while no change was observed at the Fraser estuary. Mark-recapture analysis showed a decline in the length of stay of south-bound Western Sandpipers using Sidney Island, falling from about eight days in 1992 to about three days in 2001. These changes suggested that deteriorating food conditions at Sidney Island might cause changes in sandpiper numbers.

Western Sandpipers feed on soft-bodied macro-faunal and meio-faunal invertebrates (Sutherland *et al.* 2000, Wolf 2001), making it difficult and time-consuming to measure food abundance directly. However, recent advances in physiological methods offer novel ways to obtain indicator values for the quality of the resources at a site. Blood plasma triglyceride levels in Western Sandpipers correlate with fattening rates as well as with direct measures of food abundance (Williams *et al.* 1999, Guglielmo *et al.* 2005, Seaman 2003). Triglyceride levels of Western Sandpipers caught at Sidney Island in 1996 were twice as high as at the Fraser estuary (Ydenberg *et al.* 2002), casting doubt on lower food availability as an explanation for decreased usage of Sidney Island. Why, then, did Western Sandpipers leave Sidney Island before reaching a body mass comparable to birds at the nearby Fraser Estuary?

The past two decades have seen a steady increase in populations of the Peregrine Falcon *Falco peregrinus* in western North America (Hoffman & Smith 2003), following severe declines caused by the extensive use of DDT after the Second World War. Daily Peregrine sightings during southward migratory periods in the Strait of Georgia increased steeply since at least 1985 (Ydenberg *et al.* 2004). Western Sandpipers are preyed upon by Peregrines, and their escape performance decreases with increasing body mass (Burns & Ydenberg 2002). Individuals accumulating fat for onward migration are therefore especially vulnerable to predators. Peregrines are most successful when

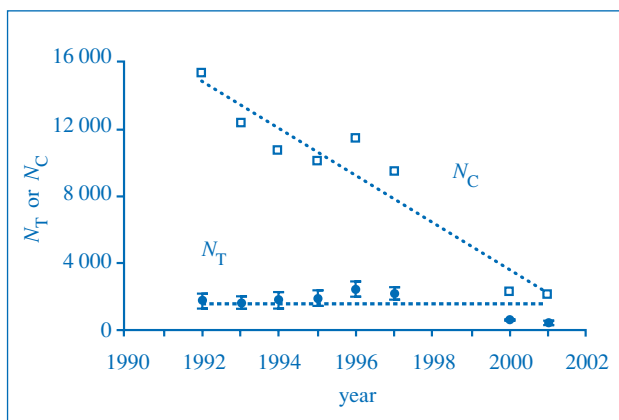


Fig. 3. Comparison of annual cumulative daily counts (NC) of Western Sandpipers *Calidris mauri* stopping over at Sidney Island with estimates of the true number (NT), which take into account the estimate of length of stay. The values for NC indicate a significantly declining trend of c. 18% per year. In contrast, estimates of NT indicate no significant ($P = 0.24$) decline (after Ydenberg *et al.* 2004; reproduced with permission from The Royal Society of London).

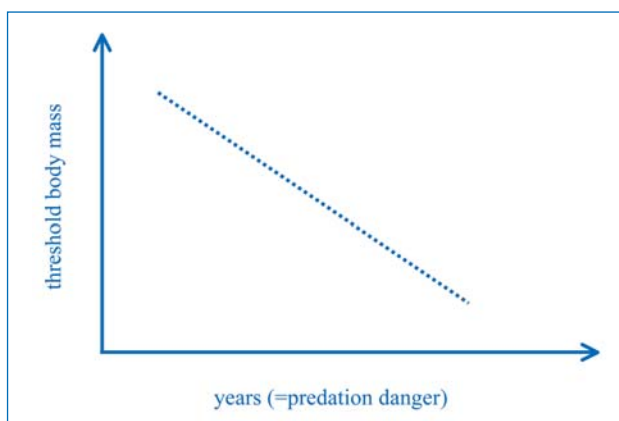


Fig. 4. A bird should switch from a more dangerous but more profitable site to a safer but less profitable site as a function of body mass, which determines its relative escape performance. With increasing predation danger over time, the threshold body mass for changing habitats decreases.

attacking by surprise, which is facilitated by cover, such as high vegetation. The Fraser estuary is large and open, and therefore a relatively safe place for a foraging sandpiper, while Sidney Island is small, enclosed, and inherently more dangerous (Ydenberg *et al.* 2002).

Within this context, Ydenberg *et al.* (2004) developed a hypothesis to explain the change in census numbers at Sidney Island: site choice is driven by a mass-dependent trade-off between local predation danger and foraging profitability. An individual is predicted to switch from a profitable, but dangerous site, to a less profitable, but safer site, contingent on relative marginal fitness values which may be represented as a threshold mass (Fig. 4). With increasing falcon abundance, this trade-off is thought to have led to the following dynamics at Sidney Island: increased danger \Rightarrow lower mass departure threshold \Rightarrow shorter length of stay \Rightarrow fewer birds counted.

Estimates of the true population size of migrants based on census data are particularly sensitive to length of stay. Ydenberg *et al.* (2004) used the mark-recapture data to estimate the actual annual number of birds moving through Sidney Island, incorpo-

rating information on length of stay. There was no evidence that fewer individuals passed through the site in later years (Fig. 3); instead, the steep census decline was accounted for almost entirely by the shortened length of stay. Thus, a change in behaviour, rather than a decrease in local population size, was responsible for the apparent decline.

Recoveries in raptor populations are taking place on continental scales in both the eastern and western hemispheres (Cade *et al.* 1988, Kjellén & Roos 2000, Hoffman & Smith 2003), and must have direct effects on mortality rates of their prey. More important, however, may be indirect effects, such as the changes in habitat usage as illustrated here, in response to changes in environmental danger (*sensu* Lank & Ydenberg 2003). The evidence for declining shorebird populations in North America comes primarily from counts made during migration (Morrison *et al.* 2001). Changes in length of stay alter the cumulative number of birds censused and peak counts, both of which are commonly used as indices in analyses of trends in population size. If changes in the use of smaller stopover sites, which are more easily monitored with precision, are taking place elsewhere, behavioral changes could account for part of the perceived population declines (Ydenberg *et al.* 2004). Other behavioral variables that could affect census data include changes in the timing or route of migration, which also may be influenced by predation danger (Lank *et al.* 2003). The potential effects of habitat or other behavioral changes should be taken into account when designing monitoring programs and interpreting data from them.

CONCLUSION

The potential benefits of “cross-cutting” approaches to studies of the population ecology of migratory species may seem obvious, but what are the additional costs associated with this approach? These include generating and adopting common protocols for gathering data, steering students towards projects suitable for thesis topics, and spending far more time in the production of multi-authored reports than might be the case for more independent research. Enticing researchers who work in related fields to address questions of interest is potentially a highly cost-effective approach, as these researchers may subsequently bring more resources to the table as their interests grow, but it has the disadvantage that progress with a project will be limited by the schedules of multiple collaborators, each of whom can slow things down. We have invested considerable time in organizing meetings; this time paid off not only with exchange of information, but also in fostering a sense of common purpose and identity that kept participants engaged with the work. But fundamentally, we have found that collaborations are most likely to prosper if they take advantage of pre-existing interests in the populations or topics being addressed. Much of the success of our network came simply by identifying persons already enthusiastic about a question, supporting their individual efforts, and fostering communication and collaboration among them and with ourselves.

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