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Western Sandpipers and more: an informal account of the 6th WESA-workshop in Vancouver

Over the last decade, shorebird studies in the America's received a big boost as a consequence of the Western Sandpiper initiative of the *Centre for Wildlife Ecology*, a collaborative effort of Simon Fraser University and the Canadian Wildlife Service, both based in the proximity of Vancouver, BC, Canada. A wide range of detailed studies centred around the life-history of Western Sandpipers *Calidris mauri* were initiated, carried through, or were supported by SFU/CWS if carried out in other institutions. The exciting two-days meeting convened by Dov Lank at Simon Fraser University on 20 and 21 October 2000 was the 6th in the series. Increasingly, these meetings have brought together shorebird enthusiasts from Canada and the western USA, including Alaska. Although the focus remains firmly on Western Sandpipers, presentations on other shorebird species were liberally admitted (as is testified by the abstracts printed below) and added intellectual scope to the species-centred discussions during the meeting.

A few topics appeared central to the presentations and discussions. (1) The specific problems of becoming an adult and mature Western Sandpiper were discussed in papers on morphology, physiology, moult, habitat selection, diet, reproductive performance and survival. Although first-winter and one year old birds usually show lower performance than adults, the extent to which this is reflected in lower survival remains to be documented.

(2) Differential migration of males and females. Female Western Sandpipers migrate earlier, further away from the breeding grounds and they may end up in more enclosed (e.g. mangrove rimmed) habitats than do males. These behavioural characteristics are correlated with lower wing loading (body mass relative to wing area) and take off speeds (females are faster). The possible structuring role of season- and site-specific raptor predation risk came to the fore in several presentations. However, the extent to which the sexual differences in morphology and performance are functionally related to each other and to the selection pressure exerted by raptors still requires intense studies by the students at SFU/ CWS.

(3) Habitat selection and the critical role of linked habitats for sandpiper survival. Depending on the quality of the intertidal habitat that they find at the northern edge of their winter distribution (the Fraser River delta), individual Dunlins *Calidris alpina* use agricultural fields to a variable degree. On (semi)continental scale, Western Sandpipers similarly depend on the distribution of habitats and their quality. Insights into the factors determining habitat use is likely to increasingly inform management and conservation strategies.

(4) It became clear that there is mounting evidence for wide-scale and long-term declines in shorebird populations in the Americas. An evaluation by the CWS shorebird specialists that convened earlier that week, indicated that 28 of 35 North American shorebird species (80%!) may now be in decline. As declining shorebird populations are not unique to North America, there is an increasing urgency for shorebird studies worldwide!

The quality of presentations was outstanding and the discussions were profound. The enthusiastic and congenial atmosphere was typical of gatherings of wader people wherever they take place in the world. Few shorebirds may be as numerous as Western Sandpipers (they still number in the millions) and few shorebird species are now as intensively studied. It was a great privilege to be able to take part in the 6th WESA workshop and I look forward to hear more from this dedicated and talented band of shorebird scientists.

Theunis Piersma

ABSTRACTS OF PRESENTATIONS AND POSTERS

Keynote

Daily energy expenditure of arctic shorebirds: Where, when and why do they hit metabolic ceilings?

Theunis Piersma

Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, and Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands. email: theunis@nioz.nl

Based on doubly-labeled water measurements in 30 incubating individuals of 8 shorebird species in the 28-150 g body mass range at various sites in the Eurasian and Canadian High Arctic, daily energy expenditure (DEE) of tundra-breeding shorebirds was estimated and compared with literature data for birds during the incubation phase at lower latitudes and for shorebirds at other times of the year. During incubation in the High Arctic, tundra-breeding shorebirds appear to incur DEE levels that are among the highest reported in the literature so far, well reaching inferred ceilings of sustainable energy turnover rates. Foraging away from the nest on the cold and windy open tundra seems the most costly element of the time budget; in Red Knots (*Calidris*

canutus) this is almost two times as costly as incubating a four-egg clutch in mid-incubation. Nevertheless, similarly high rates of energy turnover were also found in molluscivore shorebirds in temperate areas during the non-breeding season. In this case the processing of shell-encased watery prey in combination with the cold and windy environment seem responsible for the high cost levels.

Migration, Moult, and Life History Strategies

Is migration a journey or a destination? migration hops and wing shape in calidridine sandpipers

James Burns

Centre for Wildlife Ecology, Simon Fraser University, Burnaby BC V5A 1S6, Canada. email: jgburns@sfu.ca.

Avian wingshape has been cited for over a century as a classic example of the relationship between morphology and ecology. However, the predicted correlation between migratory behaviour and pointed wing tip shape has rarely been demonstrated. This study uses a novel variable, mean fuel load, as a measure of migration of *Calidris* sandpipers. Mean fuel load uses the masses of birds caught at migratory stopover sites over an extended period as an indicator of the departure fuel load. Species values were averaged over several sites. Using the method of evolutionarily independent contrasts to account for species not being independent data points, I found a significant positive correlation between high mean fuel load and pointed wing shape. There was no relationship between wing shape and the traditional measure of migration, total migration distance.

Disruptive Selection for Migration and Life History Strategies of Western Sandpipers?

Dov Lank

Centre for Wildlife Ecology, Simon Fraser University, Burnaby BC V5A 1S6, Canada. email: dlank@sfu.ca.

Nine to ten month old Western Sandpipers living in central and northern Mexico prepare for northward migration and attempt to breed as one year olds (see Fernandez). Their counterparts living in Panama, which include a higher proportion of females, do not, and instead spend their first boreal summer at tropical latitudes (see O'Hara). Successful breeding by first year males and females has been documented on the breeding grounds (see Sandercock, Neville). As seen among species of shorebirds, longer migration distances apparently change payoffs for northward migration in a bird's first spring. Possible mechanisms involved in these differences include: local adaptation (e.g. population differentiation), within population variation (e.g. polymorphism in migration and life history strategy), and conditional decision making (e.g. based on latitudinal cues or flight feather condition). If northward migration is avoided because of feather condition (see Yen, O'Hara), oversummering is an evolutionary alternative to partial (or complete) post-juvenile wing moult (see Gratto-Trevor). Or perhaps the whole thing is driven by predation (see Ydenberg).

Sex and age ratios of wintering western sandpipers.

Silke Nebel

Behavioural Ecology Research Group, Dept of Biological Sciences, Simon Fraser Univ., Burnaby BC V5A 1S6, Canada. email: snebel@sfu.ca.

Based on 13 unpublished data sets (British Columbia to Ecuador on the American west coast and South Carolina to Venezuela on the east) the differential distribution of age and sex classes of Westerns Sandpipers during the non-breeding season was documented. Across the latitudes, there are two rather distinct groups with regard to sex ratios. Birds wintering in the northwest (Canada, US and Mexico) are dominated by males, while most females migrate further to the southeast (Central and South America). Strong distributional patterns also emerge within the four age and sex classes. In juvenile males, there is a strong decline in numbers within the northwest with increasing distance from the breeding grounds in Alaska, while few of them winter in the southeast. A different pattern appears in adult males whose proportion increases with distance within the northwest, while their total proportion in the southeast is higher than that of juvenile males. Few juvenile females winter in the northwest, and there is only a slight decrease with distance; most are found in the southeast. Adult females show a rather linear increase with overall distance from Alaska, with the highest proportions in the southeast.

Although the patterns are quite obvious, the reasons underlying these distributions are not. Possible explanations were discussed, including the influence of arrival time, competition, predation risk, different migratory routes, inexperience of juveniles and higher juvenile mortality.

PPW Moult: What Is It and Why Look for It?

Cheri Gratto-Trevor

Canadian Wildlife Service, 115 Perimeter Rd, Saskatoon, SK S7N 0X4, Canada. email: cheri.gratto-trevor@ec.gc.ca

(title only)

Geographical Comparison of Primary Flight Feather Wear in Western Sandpipers.

Peggy Pei-Wen Yen

Centre for Wildlife Ecology, Simon Fraser University, Burnaby BC V5A 1S6, Canada. email: ppyen@sfu.ca

Western Sandpiper primary feathers collected January to March from wintering sites in northern Mexico and Panama were assessed for ultraviolet radiation wear. Ultraviolet radiation has the ability to degrade keratin, a fibrous protein molecules that serve as structural units for feathers. The two wintering grounds differ latitudinally by 24 degrees and the rate of difference in wear between the outer vane, which is exposed to UV, and the inner vane, which is shaded by the adjacent feather, was greater in Panama. The birds wintering farther south, closer to the equator have a faster rate of feather degradation, but may live in a more 'benign' site. Migratory birds flying long distances are exposed to various mechanisms of feather degradation, therefore, I also consider other covarying factors in addition to UV, such as differential pigmentation, the mechanics of flight, and environmental elements, that may also contribute to wear.

Latitudinal distribution and wing feather wear in the Western Sandpiper.

Patrick O'Hara

Centre for Wildlife Ecology, Simon Fraser University, Burnaby BC V5A 1S6, Canada. email: pohara@sfu.ca.

Sex-dependent differential migration is strongly expressed in the Western Sandpipers, with 80% male biased populations in the northern end of the wintering range and 80% female biased populations in the south. Because adults show a high degree of site fidelity, factors influencing settlement decisions in young birds are probably important in determining adult wintering distributions. Social dominance and other hypotheses explaining differential migration predict larger birds winter closer to the breeding grounds because of competitive superiority or tolerance to harsher climates. Using both culmen length and wing chord as indices of size, we compared sizes of birds wintering in Ecuador, Panamá and México and found that larger Western Sandpipers in both sexes winter further south regardless of age. Since larger birds are found further south in their first winter, factors influencing settlement may be occurring very early in a bird's life, perhaps during the first migration southward.

Wing wear is a potential factor influencing settlement patterns. Western Sandpipers apparently lack partial post-juvenile wing moults (PPW), and thus flight feathers have to sustain 3 full migrations if birds migrate north in their first spring. We collected 9th primary flight feathers from birds wintering in Panamá and México and quantified wear in the inner and outer vanes along the rachi of each collected feather (Sæther *et al.* 1994, Condor 96: 959-972). Primaries of first-winter birds in Panamá were much more worn than for those wintering in México, whereas adult feathers, grown after southward migration, do not differ between countries. Controlling for structural size, there was significant loss of wing chord length with wing wear. An intriguing latitudinal pattern in wing chord length is that both adults and first-winter birds wintering further south have disproportionately longer wing chords. Finally, we experimentally tested for the influence of changes in wing chord on migratory behaviour by clipping the 7th, 8th, 9th and 10th primary, 2, 3, 4,3 mm respectively. Birds with clipped wings were more likely to remain following spring departure date and that clipped birds gained less mass during pre-migratory mass gain than control birds. It appears that there is an interplay between feather wear, migration behaviour and partial post-juvenile wing moult.

HABITAT CHOICE, SANDPIPER MASS AND PREDATION RISK

Do Lighter Weight Sandpipers Indicate Healthier Ecosystems?

David B. Lank and R. C. Ydenberg

Centre for Wildlife Ecology and Behavioural Ecology Research Group, Dept. Biol. Sci., Simon Fraser U., Burnaby BC V5A 1S6, Canada; **R.W. Butler** CWS, Delta, BC, Canada; **K. O'Reilly** Biology Dept., Univ. of Portland, Portland OR, 97203, USA; **J. Ireland, G.C. Reifel** Migratory Bird Refuge, Delta BC, Canada. email: dlank@sfu.ca.

Birds regulate their body mass carefully. A growing body of literature suggests that overwintering songbirds maintain themselves at lighter weights when predator numbers increase. This indicates that a bird's "optimal" mass in the absence of predator includes a buffer against poor feeding or poor weather, which birds give up when predators are present because predation risk increases with a bird's mass: a predation-starvation risk tradeoff. We present data suggesting that predation risk may also influence habitat choice and/or the level of fat stores carried by migrant sandpipers. During southward migration, both the number and the body masses of Western and Least Sandpipers (*Calidris mauri* and *C. minutilla*) captured at a small staging site in coastal British Columbia, and of Semipalmated Sandpipers captured at a small site in the Bay of Fundy, have declined throughout the 1980s and 1990s. Concurrently, falcons increased in abundance, due to lower environmental levels of DDT and successful captive rearing and reintroduction programs. In

contrast, sandpiper masses at a large, open, and presumably safer site on the BC coast have remained unchanged throughout the period. We suggest that changes in predation risk led to changes in mass-specific habitat choices by migrants, resulting in abandonment of more risky sites, especially by heavier birds. In addition to behavioural ecological questions, such a process should be considered in the design of, and will affect the interpretation of, population monitoring schemes for migrant shorebirds, including those proposed in the US and Canadian National Shorebird Plans.

Declines in abundance and spring mass of Western Sandpipers on the Fraser River Delta.

Rob Butler and Moira Lemon

Canadian Wildlife Service, Pacific Research Centre, RR1, 5421 Robertson Rd., Delta BC V4K 3N2, Canada. email: rob.butler@ec.gc.ca.

The mass of female and male Western Sandpipers has declined since 1979, with female mass falling most sharply. It was hypothesized that the change in mass of Western Sandpipers might be in part related to the presence of falcons. Peregrine Falcon *Falco peregrinus* abundance during the spring migration of shorebirds increased by about 3.5 fold since 1986.

Differential Timing of Southward Migration by Male and Female Western Sandpipers.

Ron Ydenberg

Behavioural Ecology Research Group, Simon Fraser University, Burnaby BC V5A 1S6, Canada. email: ydenberg@sfu.ca.

It has been known for more than a decade that female western sandpipers precede males on southward migration. I used a statistical procedure developed by Morbey (2000. Can J Fish Aquat Sci 57:1252-1257) to estimate the degree of difference, based on mist net captures of southward migrating western sandpipers in the Strait of Georgia between 1978 and 1997. Overall, the difference is highly significantly biased toward protogyny (females first) but annual values range from 6.5 days to males ahead (protandry) by 2 days. It is striking that protogyny is even greater among juveniles (who migrate a month later than do adults), even though females are larger. Annual values of adults and juveniles are positively correlated. Existing hypotheses for differential migratory timing are not well developed, but usually assume that events during breeding drive migratory patterns. I propose a hypothesis based on predation danger: as falcons complete breeding across the continent, their presence rises in late July along coastal migration routes. I suggest that the danger posed by these important predators has selected for western sandpipers to depart breeding areas in June, often before their offspring have fledged. Further, I suggest that females are in greater danger from falcons than are males, and hence have been selected for even earlier departure than males, among both adults and juveniles. Thus, selective pressures on the migration route may have driven the evolution of parental care patterns, rather than the reverse.

Monitoring the Semipalmated Sandpiper and its Prey in the Bay of Fundy: A 25-year Perspective.

Peter Hicklin

Canadian Wildlife Service, Atlantic Region, PO Box 6227, 17 Waterfowl Lane, Sackville, NB, E4L 1G6, Canada. email: peter.hicklin@ec.gc.ca.

In the mid-1970s, I undertook field research on a) the numbers and distribution of roosting Semipalmated Sandpipers in the Bay of Fundy during the fall migratory period by conducting ten aerial surveys over the bay during high tides, b) the abundances and distributions of intertidal invertebrates on 11 mudflats in the two main branches of the Bay of Fundy, Minas Basin and Chignecto Bay, on a year-round basis and particularly the birds' main prey species, the burrowing amphipod *Corophium volutator* and c) initiated a shorebird-banding program to determine i) the birds' body condition while staging in Fundy and ii) where the birds staged and/or overwintered once they left the bay. Consequently, we have continued to monitor the annual abundances of *Corophium* and the body condition of the sandpipers to the present time. The results have shown that i) in 1997, the sandpipers were in similar abundances as in 1976 but appeared to arrive later and stay longer than was shown in the earlier aerial surveys, ii) the densities of *Corophium* fluctuated considerably between 1978 and 1997 with significant reductions on some mudflats in the later years and iii) the birds' body condition significantly declined beginning in 1997 with the lowest body masses recorded in 1999. Data collected in year 2000 suggests that the birds' body condition has improved although statistical analyses have not yet been undertaken on these data.

Sex and age segregation of Western Sandpipers on the wintering Grounds at Bahia Santa Maria, Western Mexico

Guillermo Fernández

Centre for Wildlife Ecology, Simon Fraser University, Burnaby BC V5A 1S6, Canada. email: gjf@sfu.ca.

Bahia Santa Maria is located in western Mexico. This region may support over 30% of the shorebird population wintering in North America, and the Western Sandpiper

is the most abundant species. During the winter 1999-2000, I estimated over 300,000 wintering sandpipers. From the landscape point of view, I categorized three groups of sites: 1) Lagoon sites with open big areas and brackish flats, 2) Lagoon sites with moderate open areas and mangroves, and 3) Freshwater marsh sites with small beaches. Each of these sites has different bird abundance: sites type 1 had the highest and sites type 3 had the lowest numbers of birds. I captured and banded Western Sandpipers at different sites. During the winter, sites type 1 had over 80% of adults and males; sites type 3 had over 30% of adults and males. Age and sex ratios of sites type 2 were more variable. The population structure differs between winter and migration period; females and first-year birds were more common in April than during the winter. Birds were disprortionally heavier and had longer wing chord as adult and male ratio increased among sites. Although feeding rates did not differ between sites, the vigilance rate was higher in the single type 3 site. Also, some birds in type 1 sites showed territorial and non-territorial behaviour. Prior spring migration, adults gained weight faster than first-year birds and adult males leave earlier and proportionally lighter than adult females. Two possible mechanisms may explain this kind of site segregation: a) intraspecific competition hypothesis, and b) condition dependent habitat use hypothesis. Bird distribution and settlement decisions during the non-breeding season should be affected by birds' performance due to age (experience and wing moult) and sex (body size), as well as by sites attributes (food resources, number of birds, and predation risk).

Use of space by individual non-breeding Dunlin (*Calidris alpina pacifica*) in relation to prey availability.

Pippa Shepherd

Centre for Wildlife Ecology, Simon Fraser University, Burnaby BC V5A 1S6, Canada. email: pshepher@sfu.ca.

Prey availability can be an important factor affecting the distribution of non-breeding shorebirds (Goss-Custard 1970a, Goss-Custard et al. 1977 and 1991, Bryant 1979, Rands and Barkham 1981, Hicklin and Smith 1984, Colwell and Landrum 1993, Piersma et al. 1993, Yates et al. 1993). Distribution models usually assume that the mechanism by which patterns are achieved is through individual behavioural responses to stimuli (Fretwell and Lucas 1970, Fretwell 1972), however, due to logistical constraints, emipirical investigations have largely been restricted to individuals of species that use small areas and/or exhibit territoriality. We used radio telemetry, GIS applications, regression analyses, and randomization models to perform the first study directly relating the magnitude of space used by individual non-territorial far-ranging shorebirds to the density of invertebrate prey within that space. We predicted that space use would decrease with increasing prey density. Space use was quantified using estimates of marine home range and core area sizes, and marine invertebrate samples were collected to quantify the densities of four categories of invertebrate prey (large annelids (> 1 cm long), small annelids (< 1 cm long), crustaceans, and molluscs). There was a statistically significant decrease in Dunlin home range size ($F_{4,24} = 13.9$, $r^2 = 0.70$, $P < 0.001$) but not core area size ($F_{4,24} = 1.9$, $r^2 = 0.24$, $P = 0.15$) as the density of invertebrates (all four types) within them increased. Dunlin were trapped at three separate sites throughout the Delta, and there were significant differences in home range size ($F_{2,24} = 14.1$, $P < 0.001$) and core area size ($F_{2,24} = 5.5$, $P = 0.007$) among sites. In order to be certain that the significant relationship between home range size and invertebrate density was not simply due to differences among sites (essentially a three-point regression with pseudo-replication), we repeated the analyses within the site with the largest sample of Dunlin. Within that site, both home range ($F_{4,11} = 22.8$, $r^2 = 0.89$, $P < 0.001$) and core area ($F_{4,10} = 9.1$, $r^2 = 0.78$, $P = 0.002$) size decreased as invertebrate density increased. Crustacean density alone explained 59% of the variation in home range size across sites, 60% of the variation in home range size within a site, and 73% of the variation in core area size within a site. Individual Dunlin made fine-scale decisions about their use of space that were significantly and closely related to prey density.

The contribution of agricultural land to the diet of shorebirds wintering in the fraser river delta: Evidence from stable isotope analysis.

Lesley J. Evans Ogden

Centre for Wildlife Ecology, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada. email: ljevanso@sfu.ca.

The Fraser River Delta represents the only major over-wintering habitat in Canada for shorebirds. Adjacent to the vast food-rich area of intertidal mudflats is an extensive area of farmland used for feeding and roosting. The relative dietary importance of farmland versus mudflats to local shorebird populations has not been previously established, and is being determined by means of stable isotope analysis. Comparing blood and tissue samples from Dunlin with those of terrestrial-exclusive American Robins, (*Turdus migratorius*) and marine-exclusive

White-winged Scoters, (*Melanitta perspicillata*), preliminary analysis of Carbon-13 indicates considerable variation between individuals in the relative contribution of terrestrial prey to overall diet. Individual values range from highly marine signatures to highly terrestrial ones, and the population average varied significantly between years, suggesting that use of field varies both within populations and over time. No significant differences in food origin were found between sexes and age classes. Since the use of fields to at least some extent is widespread throughout the population, I propose that land stewardship programs are necessary to ensure the future conservation of this important and previously undervalued shorebird habitat.

BREEDING BIOLOGY

Breeding Ecology of Western Sandpipers on the central Yukon-Kuskokwim Delta, ALASKA.

Dan Ruthrauff

Humboldt State University, PO Box 4212, Arcata, CA 95518, drr6@humboldt.edu, and **Brian McCaffrey** Yukon Delta National Wildlife Refuge, PO Box 346, Bethel, AK 99559. email: brian_mccaffery@fws.gov.

We studied the breeding ecology of the Western Sandpiper (*Calidris mauri*) from 1998 through 2000 at a permanent Yukon Delta National Wildlife Refuge field site in western Alaska. The density of nesting pairs in 1999 and 2000 was 2.95/ha. and 3.01/ha., respectively, among the highest densities recorded for this species. Mayfield nest success on a 16 ha. plot from 1998 to 2000 was 0.56, 0.24 and 0.35, respectively. Fledging success, defined as a nest fledging one or more young, was 75% (12 of 16 hatched nests) in 1999 and 68% (19 of 28 hatched nests) in 2000. Chicks were observed to fledge as soon as day 13, but often required up to 18 days to achieve sustained flight. Among 12 and 19 broods observed in 1999 and 2000, respectively, males tended broods a mean of 11.75 days and 13.2 days after hatch, while mean female attendance was 8 and 6.4 days in those two years. Males and females did not differ significantly in the length of attendance in 1999, but males remained with broods significantly longer than females in 2000. Males demonstrated significant seasonal declines in duration of attendance in both years, while females exhibited significant seasonal declines only in 2000. Finally, survival estimates based on resightings of banded adults were extremely low for females relative to males at our study site, as well as to breeding female survival estimates from other studies. Of 21 females banded in 1998, only 5 (23.8%) were resighted in 1999, only 1 (4.7%) of which was subsequently resighted again in 2000. Of 31 males banded in 1998, 23 (74.2%) were resighted in 1999, and 20 (64.5%) were again resighted in 2000. Despite finding a combined 99 nests on an additional 35 ha. area surrounding our core study plot in 1999 and 2000, we observed no additional banded females. Further, females who bred successfully in 1998 were less likely to be resighted in both 1999 and 2000 than unsuccessful females. We therefore suspect that the low survival estimate is primarily the result of mortality rather than emigration.

Division of parental roles in breeding western sandpipers.

Julie A. Neville

Department of Biology & Wildlife, University of Alaska-Fairbanks, Fairbanks, AK 99775. e-mail: ftjan@uaf.edu

Previous observations of Western Sandpipers (*Calidris mauri*), a monogamous shorebird, suggested differences in parental care may exist (Holmes 1973, Erckmann 1981). To determine parental roles of Western Sandpipers on their breeding grounds near Nome, Alaska, I repeatedly documented which mate was present at the nest during the incubation period, and which mate remained with the brood in 1998 and 1999. There was a clear temporal division of parental roles during incubation. Males were observed incubating more often (57 % of time) than females (43%). Males were more likely to be incubating between 0700 - 1900 h (ADT) while females incubated from 2000 - 0600 h (ADT). This within-day pattern of incubation between the sexes did not change during the three week incubation period. During the brood care period, most males remained with their brood until fledging. Females deserted their brood prior to their mates (22 of 24, 91.6%). The number of days that a female remained with her brood was negatively correlated with hatch date ($r = -0.66$, $P < 0.001$). These results suggest that male Western Sandpipers contribute significantly more during the incubation and brood care periods, providing strong evidence that the sexes differ in parental care.

Age-specific variation in the reproductive performance of western sandpipers.

Brett K. Sandercock

Dept. of Forest Sciences, University of British Columbia, Vancouver BC, Canada. email: bsanderc@interchange.ubc.ca.

Research in the past decade has shown that juvenile Western Sandpipers (*Calidris mauri*) face many ecological and physiological challenges during their first year of life. Compared to adults, juveniles depart breeding areas at later dates and with lower fat reserves, maintain a larger gut during fall migration, and have larger home ranges at more northerly wintering sites. If these

events have long-term effects, Western Sandpipers and other migratory shorebirds might be expected to exhibit age-specific variation in their vital rates (i.e., breeding propensity, fecundity and survivorship. Indeed, some yearlings oversummer at equatorial latitudes in their first spring, whereas others migrate to arctic areas to breed. The objective of this study was to investigate age-specific variation in the reproductive performance of female Western Sandpipers. Birds were classified as yearlings, newly banded adults or old returning adults on the basis of plumage coloration and previous banding information. A subset of known-age birds showed that coloration of the inner tertials and upper wing coverts was a reliable character for aging Western Sandpipers. In newly formed pairs, yearling and adult females mated assortatively with birds of the same age-class. Yearling females nested significantly later (by 6 d), and laid eggs that were 5% smaller than those of old adults. Clutch size did not vary with age-class; a majority of clutches contained 4 eggs. Yearlings had lower rates of nest success, higher rates of partial clutch failure, and lower rates of renesting than old adults. In all components of reproduction, new adults had performance that was intermediate to yearlings and old adults. Overall, the mean number of nestlings leaving the nest was 2.07 per yearling female, 2.93 per new adult, and 3.66 per old adult. For the same population, minimum estimates of survival for adult females range from 0.55 to 0.59. Preliminary population modeling with an age-structured matrix model indicated that the observed levels of productivity would be adequate to maintain stable population numbers, but only if survival of juveniles is relatively high (ca. 70% of adults). Comparative data for other populations of shorebirds are few because most species have strong natal dispersal and are otherwise difficult to age. The results of this study suggest that the potential effects of age should receive greater attention in future studies of shorebird biology.

Feeding and Physiology

The Role of Corticosterone in the Orchestration of Long- Distance Shorebird Migration.

Meta M. Landys

Dept. of Zoology, Univ. of Washington, Seattle WA 98195, USA. email: meta@u.washington.edu

Avian species migrate long distances between summer breeding localities and distant wintering sites to take advantage of seasonal cycles in food abundance. Many of the behavioral and physiological processes expressed during migration include those that glucocorticosteroid hormones regulate, e.g., metabolism, feeding and activity. Corticosterone, the glucocorticosteroid found in bird species, may therefore play a primary role in the orchestration of migration. In fact, levels of this hormone increase specifically during the migratory period in many bird species.

To investigate which particular processes of migration corticosterone may regulate, I examined the pattern of corticosterone secretion across different migratory sub-stages in a long-distance shorebird migrant, the Bar-tailed Godwit *Limosa lapponica*. Elevated levels of corticosterone were found only immediately prior to and during migratory flight. Corticosterone may therefore regulate processes expressed specifically during the flight stage, which may include energy mobilization, organ reconstruction, *Zugunruhe*, and exploratory movement – a behavior that would adaptively increase awareness of rapidly changing environmental conditions.

To further explore the regulatory role of corticosterone during migration, I experimentally manipulated corticosterone levels during the migratory period and monitored resulting behavioral differences in captive Red Knots *Calidris canutus*, also a long-distance migratory shorebird. Red Knots were chosen as the model species because they perform well in captive conditions, and because they display an association between corticosterone and migratory sub-stage that is similar to that seen in godwits. Only probing behavior differed between groups; Red Knots with artificially lowered corticosterone titers tended to investigate the mudflat and cage floor less than did control birds. In addition, birds with artificially low corticosterone titers significantly decreased in mass, even though feeding behaviors were not affected. These results suggest that corticosterone assists birds in perceiving the environment during flight, and also allows birds to maintain the heavy mass typical of departure – perhaps through lowered metabolic rate or increased digestive efficiency. On-going studies will determine whether corticosterone also plays an energy-mobilizing role during migration, and whether measured effects are specific to the migratory stage.

Foraging ecology of juvenile WESAs in southwestern BC during their first fall migration.

Nicholas Wolf

Behavioral Ecology Research Group, Simon Fraser University, Burnaby, BC, V5A 1S6, Canada. email: nwolf@sfu.ca.

The goal of this project was to determine (1.) what juvenile Western Sandpipers are eating when they forage on two mudflats near the Fraser River estuary in British Columbia, and (2.) whether the rate

at which they put on weight while foraging differs between the two sites, which are Sidney Island and Boundary Bay. To identify prey types, mud and poop samples were collected in areas where birds were feeding in August of 1999 and analyzed using a dissecting scope. The most abundant prey in both mud and poop were Gammarid and Corophium amphipods. Of the latter, only individuals in the 2.75-4.75 mm size range were consumed. Other crustaceans, snails, bivalves, polychaetes, and foraminifera were also apparently taken. To compare mass gain rate between sites, juvenile males were mist-netted in August of 2000 and held for approximately 2.25 hours in a floorless mesh enclosure on one mudflat or the other. Birds were weighed repeatedly before and after foraging in the enclosure, allowing mass gain rate to be estimated as the difference between the intercepts of the "before" and "after" mass trajectories. At both sites, mass gain rate was negatively correlated with initial mass, except that it appeared to level off for very low initial masses - presumably reflecting the maximum intake rate achievable at each site. On average, mass gain rates were 0.3 g/h higher on Sidney Island (by ANCOVA, with initial mass as the covariate, $p = 0.214$, $n = 45$), and the maximum there was about 0.75 g/h. These results are very preliminary because the sample size was small, and because we don't yet know the extent to which the mass gained represents assimilation, rehydration, or retention of gut contents.

Busting a Gut: Age-related Differences in Digestive Tract Function During Migration.

R. Will Stein and Tony D. Williams

Centre for Wildlife Ecology, Dept. Biol. Sci., Simon Fraser U., Burnaby BC V5A 1S6, Canada.

The absorptive components of the digestive tract, i.e. small intestine, large intestine, and ceca, are disproportionately large (wet mass) in juvenile Western Sandpipers (*Calidris mauri*) during the first migration south. In fact, the small intestine is at its highest mass of the entire life cycle during the first migration. Due to the importance of juvenile recruitment to population stability, we examined the functional importance of this structural difference to the survival strategy of migrating juveniles. The small intestine is used as a model system to assess performance in meeting energy demands during migration. The structure and function of the small intestine are assessed at three levels: 1) morphology as it relates to digestive function; 2) nutrient uptake efficiency measured *in vitro* using the 'everted sleeves' technique; and, 3) activities of two modulated digestive enzymes, pancreatic lipase and aminopeptidase-N. The role of endoparasite prevalence rates and diet sediment loads was evaluated in regards to the functional significance of this marked age-related difference in digestive tract mass. Preliminary results demonstrate that there is no age-related difference in small intestine mass prior to departure from the breeding grounds, and that the mass of the small intestine increases after migration commences for juveniles, but not for adults. In addition, juveniles have higher tapeworm (*Cestoda* sp.) prevalence rates and lower lung fluke (*Trematoda* sp.) prevalence rates during migration than adults.

Age Effects in Migration Physiology: Future Directions.

Chris Guglielmo

Department of Zoology, University of British Columbia. email: cgugliel@sfu.ca

Age Effects in Migration Physiology: Future Directions. Christopher G. Guglielmo.

Young Western Sandpipers making their first migration differ physiologically from adults in ways that may affect their migration performance, for example by having larger guts, less flight muscle fatty acid binding protein, and a higher index of flight-induced muscle damage. Research presented at this meeting by several members of our group indicates that first-year birds wintering in the southerly part of the range defer migration in their first spring, and that yearlings that do breed have lower reproductive performance than adults. I suggest four future research directions to expand on what we have learned thus far: 1) a study of the genetic structure (if any) of breeding and wintering WESA populations to determine whether deferred migration by first-year birds is a reproductive strategy of particular populations, or a facultative decision made by individual birds in response to their perceived distance to the breeding area; 2) assuming no genetic structure is found, a common garden study of first-year birds brought from different latitudes to explore the proximate mechanisms of deferred migration (e.g. light cycle cues, food conditions); 3) renewed radio telemetry studies to determine the migration performance (i.e. flight distances, stopover times, survival) of first-year birds migrating north from different latitudes, and of juveniles, first-year breeders and adults migrating south from the arctic; and 4) studies of the functional significance for migration success of behavioural, physiological and biochemical differences between juvenile and adult sandpipers, and the effects of learning and training (use/disuse).

POPULATION DEMOGRAPHY, MONITORING, AND CONSERVATION

The Unrealized Potential of Shorebird Vocalizations in Management and Conservation.

Ted Miller

(Memorial University, St. John's, Newfoundland, Canada). email: tmiller@morgan.ucs.mun.ca

Coastal Zone Productivity and the Distribution of the World's Shorebirds

Rob Butler

(Canadian Wildlife Service, Pacific Research Centre, RR1, 5421 Robertson Rd., Delta BC V4K 3N2, Canada), Guy Morrison and Nick Davidson (Canadian Wildlife Service, Ottawa): email: rob.butler@ec.gc.ca.

The density of shorebirds around South America was positively related to coastal zone productivity in adjacent waters. Moreover, the distribution of beaches with >100,000 shorebirds world wide were adjacent to coastal regions with high coastal zone productivity. Changes in wind strength as predicted by climate models with 2XCO2 atmosphere had a small (-3%) effect on the predicted fitness in Clark and Butler's (2000) dynamic model of Western Sandpiper migration. The strength of upwelled ocean water in the Gulf of Panama is positively correlated with the strength of winds. It is hypothesized that pre-migratory fattening by Western Sandpipers in Panama might be determined by trophic processes that link the seasonality of winds with phosphorous concentrations in upwelled water, and invertebrate abundance on mudflats.

Westerns, Waterbirds, and Salt Ponds along the Pacific Flyway: a Critical Relationship?

Nils Warnock

Point Reyes Bird Observatory, 4990 Shoreline Hwy., Stinson Beach, CA 94970. email: nilsw@prbo.org.

Commercial salt ponds, active and inactive, are important habitat for waterbirds, especially Western Sandpipers *Calidris mauri*, in coastal California and Mexico. Recently, proponents have proposed restoring large areas of salt ponds to tidal marsh, a threatened habitat on the West Coast. We review the historical importance of salt ponds to Pacific Flyway waterbirds and present results from current work in San Francisco Bay. We found that use of salt ponds by waterbirds and behavior of waterbirds in salt ponds varied with tide, pond salinity, and time of year. Between October and February, we recorded 51 species of waterbirds using nine salt ponds we surveyed (n = 6 high tide surveys per pond and 6 low tide surveys per pond), with over 180,000 bird sightings. On the high tide, Dunlin *Calidris alpina* (n = 30,239) and Western Sandpipers (n = 19,512) were the two most abundant species, while on the low tide Northern Shovelers *Anas clypeata* (n = 19,204) and American Avocets *Recurvirostra americana* (n = 5,688) were the two most abundant species. Use of salt ponds by radiomarked shorebirds varied significantly. Black-necked Stilts *Himantopus mexicanus* heavily relied on salt ponds on low and high tides, and Western Sandpipers heavily relied on salt ponds on high tides and switched to tidal mudflats on low tides. A high proportion of both of these species were observed to feed in the salt ponds (65% of Western Sandpipers, 63% of Black-necked Stilts). The future management of salt ponds in California will be critical to maintain current populations of waterbirds using the Pacific Flyway.

Spatial dispersion of migratory shorebirds at the continental scale: Implications for conservation.

Laura X. Payne

[1,3]Department of Wildlife Ecology, University of Wisconsin, Madison WI 53706, USA. [2]Manomet Center for Cons. Sci., Manomet, MA 02345, USA.
email: lxpayne@calshp.cals.wisc.edu.

To date, most efforts to protect migratory shorebirds have been site-based, with emphasis on identification and protection of traditional migratory 'hotspots.' While practical from a conservation standpoint, this classic approach under-represents species that are dispersed, or those that are distributed on the landscape in different ways during different years. Currently, the extent to which shorebird species are included under the hotspot approach is unknown; our work seeks to examine the overlap between current conservation approaches and the underlying spatial ecology of migrant shorebirds. Using 20 years of International Shorebird Survey data collected at 1000 wetlands in the conterminous United States, we quantified landscape-scale dispersion patterns for 30 species during fall and spring migration. Species differed in degree of dispersion, ranging from highly aggregated to highly dispersed. Additionally, most species exhibited a seasonal shift in dispersion, being more dispersed in fall. Interspecific dispersion differences may arise from spatial constraints (habitat preference or feeding specialization), or temporal constraints (migration distance), since availability and number of sites differs with habitat type, and time available for migration varies with distance traveled. We regressed dispersion on migration distance and found that long-distance migrants were significantly more aggregated than shorter

distance migrants. Overall, we identified several types of migration strategies that relate to conservation and management: a) consistently aggregated species, b) consistently dispersed species, and c) species that exhibit inconsistent dispersion patterns (aggregated in some years, dispersed in others). In addition, we found a tendency for aggregated species to exhibit greater variation in spatial pattern across years. Our results suggest that 1) broader management strategies are needed to effectively protect most migratory shorebirds; and 2) for hotspots that have already been identified, knowledge of the landscape-scale dispersion patterns of species using that site could help managers to rank the importance of that site to many species, and to evaluate the site within a continental context. This work represents the first part of a continuing study; subsequent work will address conservation/ management approaches for specific species and sites.

Declines in North American shorebird populations.

Morrison, R. I. G., Aubry, Y., Butler, R. W., Beyersbergen, G. W., Donaldson, G., Hicklin, P.W., Johnston, V.H., Ross, R. K., and Gratto-Trevor, C. L.

Canadian Wildlife Service Shorebird Committee. email: guy.morrison@ec.gc.ca.

Recent preliminary analyses of shorebird survey data from across Canada provide very strong evidence that declines in shorebird populations may be much more widespread and pervasive than previously thought. Analyses involved data from volunteer count programs on the Atlantic coast of Canada and in Ontario, a checklist program in Quebec, roadside counts conducted as part of the Breeding Bird Survey in the USA and Canada, counts conducted during research projects on the Pacific coast, and comparisons of survey plot data from Arctic locations. Results from all individual survey projects showed statistically significant disproportionate numbers of negative trend values. Overall, of the 35 species of shorebirds covered by the analyses, 28 (80%) were negative: this included 19 species with statistically significant or persistent negative trends and only one with a positive trend. The pattern of declines is especially notable given that methods of data collection and analysis vary across the different regions and projects. A variety of factors is likely to be involved in the observed declines. Shorebirds, along with grassland species and sea-ducks, stand out as groups that are currently particularly threatened. These results underline the importance of taking action on conservation issues addressed in the Canadian and US Shorebird Conservation plans.

Long-term Population Changes Reflected in Changing Balance Between Mortality and Recruitment in UK-Wintering Red Knots.

Theunis Piersma and Hugh Boyd

Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, & Centre for Ecological and Evolutionary Studies, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands. email: theunis@nioz.nl, and National Wildlife Research Centre, Canadian Wildlife Service, Environment Canada, Ottawa K1A 0H3, Canada.

The demography of Red Knots *Calidris canutus islandica* wintering in Britain from 1969 to 1995 was examined using published data on winter numbers, unpublished ringing data, and information on the percentages first year birds in late autumn and winter catches (defined here as 'recruitment'). The maximum time between ringing and reporting was 24 years for a Red Knot ringed as an adult. The mortality rate of juveniles during their first winter was four times that of adults, but did not differ later. For three periods, recruitment minus mortality corresponded qualitatively with changes in population size. In 1969-77, when the numbers wintering in Britain were declining by 8.7% annually, the mean percentage juveniles in the wintering population was estimated at 12.1% and the mean adult mortality rate of ringed birds was 23.6%. In 1977-85, when numbers were increasing by 4.6% per annum, juvenile percentages were high (28.8% juveniles) and adult survival rate was also higher than in the previous period (19.6%).

In 1985-95, when wintering numbers showed no clear trend (average +0.9% per annum) but were still below those in 1969-72, juvenile percentages were low again (13.8%) but the mean adult survival rate was still high (14.2%). Cold summers appeared to reduce both recruitment and adult survival. Recovery rates during, and subsequent to, warm winters were reduced. British Knot populations appear to fluctuate as a consequence of factors affecting survival as well as reproduction. There is evidence for density dependent processes that affect overall reproductive success. Although probably acting sometime from late winter to early autumn, the mechanisms causing such density dependence remain mysterious.

A method to estimate shorebird numbers on the Copper River Delta, Alaska.

Mary Anne Bishop, P. Meyers, and P. F. McNeley

(US Forest Service, Cordova). Poster version of: J. Field Ornithol. 71(Autumn, 2000): 627-637. email: mbishop@eagle.ptialaska.net.

We estimated the annual population of Western Sandpipers (Calidris mauri) stopping over on the Copper River Delta during peak spring

migration 1992-1995. Our calculations required four components: total daily shorebird numbers; the daily proportion of each species, average length of stay; and the detection probability. For the 21-day period 26 April-16 May, annual population estimates for Western Sandpiper ranged from 1.2-4.1 million birds per year. For both species, numbers were highest in 1993 and lowest in 1994. Power analysis determined that 15 years of aerial surveys are needed to detect a 10% decline in Western Sandpiper numbers. Based on the proportion of birds in the Pacific Flyway stopping over on the Copper River Delta, we estimated the Western Sandpiper Pacific Flyway population was >2.8 million in 1992 and >4.3 million in 1995. These data indicate that the Copper River Delta continues to support the largest spring concentration of shorebirds in the Western Hemisphere.

Reconstructing foraging paths for red-necked stints using fractal dimensions and pecking success from footprint surveys to describe movements and prey distribution on a mudflat scale.

Falk Huettmann

Centre for Wildlife Ecology, Dept. of Biological Sciences, 8888 University Drive, Simon Fraser University (SFU) Burnaby B.C. V5A 1S6, Canada. email: falk.huettmann@ec.gc.ca.

Foraging paths of Red-necked Stints *Calidris ruficollis* were investigated during fall migration 1999 for fine-sediment mudflats of the Moroshechnaya River Delta, eastern Sea of Okhotsk. Length and angle measurements, and pecking success information from footprint surveys were used. We analyzed the fractal dimensions of foraging paths, and correlated length and turning angles with pecking success, no correlations were found. With increasing scale (size of step) the fractal dimension of the foraging path increases slightly, but insignificant. This indicates for this working scale (grain size 1 cm, extend 511 cm) that Red-necked Stints make their foraging decisions not under energetical considerations but using a systematic approach (appr. 12 cm step-length, and 35° change of angle) ; this might be in accordance with distribution of prey in the mudflat. On a smaller scale (<1 cm grain size), and once prey was located, Red-necked Stints forage intensively in food patches along 'cracks' of the mudflat. I suggest that fractal dimensions of foraging paths can serve as a description for prey patch distribution in mudflats relevant to shorebirds along the flyway, across and within seasons.

Observations Of Shorebirds In The Yucatan Peninsula During Springtime Migration.

Jorge Correa Sandoval

El Colegio de la Frontera Sur. Zona Industrial No.2, Chetumal, 77000, Quintana Roo, México. email: jcorrea@ecosur-qroo.mx.

The Yucatán Peninsula is located in the southeastern part of Mexico. It is utilized by shorebirds both, during migration and as a wintering place. During the spring, in their way to their breeding grounds, birds also gather in the coasts of the peninsula just before flying across the Gulf of Mexico. During springtime of 1991 (from late March to early June) we carried out surveys and censuses of shorebirds in the coast of Yucatán State in the western coast and also in the northern coast of the Yucatan Peninsula at the Ría Celestún Biosphere Reserve (RCBR) and Ría Lagartos Biosphere Reserve (RLBR) respectively. The list of observers also included in Celestún to David Alonzo and Juan José Durán whereas in Lagartos the observers were Eduardo Galicia, Elvia Rodríguez and Roberto Vázquez. In Ría Celestún a total of 1713 individuals of 18 species were seen. In Ría Lagartos a total of 2804 individuals of 16 species were seen. 22 species of Charadriidae, Haematopodidae and Scolopacidae were recorded all together. Looking at the abundances of selected species along the time at both reserves, it seems to be a shift in the period of time where they pass through. For instance, the tendency seems to be that the birds get first to Ría Celestún and keep moving northwards along the coast to arrive to Ría Lagartos a few days latter. Another interesting outcome is to see the concentration of some species. *Catoptrophorus semi-palmatus* is heavily concentrated during April at Ría Celestún and absent after that. *Pluvialis squatarola* show a concentration from late April to mid May. *Calidris pusilla* and *C. mauri* show the same pattern, being extremely abundant during mid April. *Calidris minutilla* was seen but always in mixed flocks with other *Calidris* but the pattern is the same having a peak in Ría Lagartos during April. I suggest to start a banding program to shed light on differential timing of migration by sex and age of selected species (*Calidris mauri*, *C. minutilla* and *C. pusilla*).