Behavior, ecology and conservation of Western Hemisphere shorebirds

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PREY-MEDIATED HABITAT SELECTION BY POST-BREEDING ARCTIC SHOREBIRDS

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By mid-summer, many arctic nesting shorebirds move from upland tundra breeding sites to coastal staging and migration sites. Few studies have determined which habitat features best explain the patterns of distribution and densities of post-breeding shorebirds. Additionally, few studies have examined the behaviour of foraging shorebirds in environments that lack daylight and tidal constraints. Using a vegetation covermap derived from LANDSAT imagery as a spatial sampling frame, I measured the abundance of migrating shorebirds and their use of available habitats along the coastal zone of the Colville River delta, northern Alaska. I also quantified the behavior of migrants, various characteristics of the micro-habitats and the densities of benthic and surficial prey.

The Colville River delta forms the most extensive area of coastal silt barrens and saltmarshes on the Beaufort Sea coast. Within the 68.3 km^2 of silt barren and saltmarsh habitats I surveyed, calidrid sandpipers, primarily Dunlins *Calidris alpina* and Semipalmated Sandpipers *C. pusilla*, constituted 87% of the birds observed. Dunlins were most abundant along silt barrens, whereas Semipalmated Sandpipers were most abundant in saltmarshes. Shorebird densities varied markedly among silt barren and saltmarsh habitat types. The amount of coverage of substrate vegetation and the substrate moisture levels determined delta-wide patterns of shorebird habitat use.

On silt barrens, the variability in shorebird density was related to physical features of the shoreline. Moisture level and substrate grain size influenced the density of benthic prey (oligochaetes and chironomid larvae). Shorebird use of silt barrens, estimated by track counts, was positively correlated with benthic prey density. In saltmarshes, post-breeding shorebirds were densest on wet, sparsely vegetated substrates. Differences in substrate moisture level, in turn, were related to differential benthic and surficial prey densities. Besides higher prey densities, sparsely vegetated substrates allowed shorebird consumers easy access to prey resources.

The majority of shorebirds encountered in the delta were foraging (89%, n = 30,754). The average attack rate of shorebirds feeding on adult insects exceeded 70 pecks per minute. Foraging birds tracked prey resources and switched feeding behaviors, from pecking to jabbing, as prey availability shifted from the surface to the benthos. Within saltmarshes, the proportion of birds observed foraging was related to moisture level and vegetation coverage of the substrate. During continuous daylight, shorebirds foraged at high levels throughout all hours of the day.

My study, by linking micro-habitat features that influence the distribution and density of shorebird prey to coastal habitats, enabled me to explain patterns of density and distribution of post-breeding shorebirds. Post-breeding shorebirds selected coastal habitats that maximized energy accumulation during their initial stages of migration.

CONSERVATION GENETICS OF SHOREBIRDS

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Although many shorebird species presently have moderate to large population sizes, genetic assays of allozymes and mitochondrial DNA reveal that they are commonly genetically depauperate. For example, the number of alleles per locus and average heterozygosity at allozyme loci are much lower in most shorebirds than mean values of these parameters in other bird species. The diversity of mtDNA sequence variants is also correspondingly lower in shorebirds. These observations jointly suggest that many shorebird species have experienced relatively recent population bottlenecks that have resulted in various degrees of loss of genetic variation within populations. Although the results pertain to putatively neutral gene loci and thus are not affecting the fitness of individuals, they do provide an index of past demographic processes that have operated on populations. The next and urgent step in conservation genetics of birds in general, and shorebirds in particular, is to determine to what degree these population contractions have affected variability at MHC loci in the immune system which are known in chickens to function in protection against viral induced tumors and other pathogens. Severe loss of variability in these loci would expose shorebirds to the ravages of periodic epizootics that have been shown to decimate endangered populations of mammals with low MHC variability.

A second aspect of the conservation genetics of shorebirds that is important to their management is their biogeographic history or phylogeography. For example, genetic analyses of populations of Dunlins *Calidris alpina* sampled throughout their circumpolar breeding distribution has demonstrated that their intraspecific variability emanates from isolation in Pleistocene refugia, and that this imprint of history has been maintained today by breeding site philopatry in extant populations. Calculations based on the fast evolving D-loop region of mtDNA suggest that populations have been only moderately bottlenecked in the past. Conversely, similar analyses of Turnstone *Arenaria interpres* and Knot *Calidris canutus* have revealed that these species have each recently expanded from single genetically depauperate refugial populations, and thus have not had time yet to recover genetic variability lost in past 'bottleneck' episodes. However, the conclusion that the latter two species are globally panmictic seems an unlikely one because very fast evolving quantitative genetic characters such as body size and plumage color are already differentiated in some populations. Because of their low genetic diversity, Turnstones and Knots are potentially more sensitive to etiologic agents, pollutants, and habitat disturbance, and should be the focus of future genetic investigations of their MHC diversity and its biological consequences.

SPRING SHOREBIRD MIGRATION ON THE COPPER RIVER DELTA, 1991-92

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Aerial and ground shorebird surveys were conducted on the Copper River Delta, Alaska in spring 1991 and 1992. Aerial surveys in 1992 were conducted every 2-3 days from 25 April to 17 May. Two simultaneous flights were conducted during the two hours before high tide covered the intertidal mudflats and selected outer beaches from Controller Bay to Orca Inlet, a straight line distance of 120 km. The 1992 aerial shorebird survey estimates ranged from 42,000 birds on 25 April to 564,000 on 9 May. Mean estimate per survey was 279,000 ± 54,000 birds (n = 10). We detected 2 peaks: 459,000 birds on 4 May and, after a drop to 271,499 birds on 7 May, a second peak of 564,000 birds on 9 May. On our final 17 May flight, an

estimated 125,000 shorebirds were observed. Highest concentrations of shorebirds occurred at the far eastern and western ends of the Delta. Outer beaches on barrier islands received minimal use. Species composition on ground transects indicated that Western Sandpipers *Calidris mauri* comprised 77 and 82% and Dunlins *Calidris alpina*) 21 and 17%, of the total numbers of migrant shorebirds in 1991 and 1992, respectively.

In 1992, Western Sandpipers were radio-tagged by co-operators at San Francisco Bay, the Fraser River Delta, British Columbia, and the Stikine River Delta, Southeast Alaska. A total of 48 or 80 radio-tagged Western Sandpipers were detected during aerial telemetry flights over the Delta. Telemetry flights were conducted every morning from 29 April through 24 May. Length of stay on the Delta averaged 3.06 ± 0.25 days (n = 48) with a mode of 1 and a range of 1 to 8 days.

We used aerial survey estimates (both actual and interpolated), length of stay curves with means ranging from 2.3 days to 3.7 days, and a range of % composition values (65-81.5%) to estimate the total number of Western Sandpipers staging on the Copper River Delta. The total population estimate ranges from 1.2 to 2.3 million Western Sandpipers. These numbers are markedly lower than Islieb's 1973 estimate of 6.5 million Western Sandpipers. That estimate was based on ground surveys and a 36-hr length of stay. Further refinement of species composition data will increase the accuracy of our estimates. We intend to use the data and techniques we are developing to establish a permanent shorebird monitoring program on the Copper River Delta.

VARIATION IN DISTRIBUTION BETWEEN SEXES IN NON-BREEDING AMERICAN AVOCETS *Recurvirostra americana*

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Changes in environmental conditions often evoke shifts in the distribution on non-breeding shorebirds at a particular site. Examining the effects of changing conditions on these birds will make a significant contribution to understanding winter survivorship. Furthermore, addressing these issues between sexes may shed light on intraspecific dependence on local resources. In this study, I examined the effects of temporal, weather, and habitat-related variables on the distribution of male and female American Avocets *Recurvirostra americana* by addressing the following null hypotheses: i) males and females do not differ in their distribution as a result of temporal variation during the non-breeding season; ii) males and females do not differ in their distribution as a result of variable habitat availability during the non-breeding season; iii) males and females do not differ in their distribution as a result of variable weather conditions during the non-breeding season. Rejection of any one of these hypotheses may suggest that male and female American Avocets exhibit differences in site selection to ensure their survivorship during the winter season.

The study was conducted from mid-January to mid-may, 1991 and 1992, on South Island, South Carolina. Ten sites (eight brackish water impoundments and two natural tidal area) were sampled. Scan sampling was used to record the following information: plumage color, sex, nearest neighbour distance, behavior, and individual water depth (i.e., dry mud, wet mud, water above the foot, water belly deep). Cloud cover, wind speed, wind direction, ambient temperature, water level, tide stage, percentage of exposed mudflat, and time were recorded along with each scan. Additional site information collected included weekly measurements of salinity and identification of vegetation and available prey. General linear models for unbalanced ANOVAS (SAS) were used to determine which environmental variables contributed most to variation in the number of males and females occurring at each site. These variables were considered significant at $p \leq 0.05$.

American Avocets were observed in seven of the nine sites sampled in 1992. Six sites were impoundments and one was a natural tidal area. Of 14,443 individual observations, 26% (n=3,736) were on females and 17% (n=2,480) were on males. Site was significant for all models indicating nonrandom distribution among sites ($p<0.0001$). Interactions between site and the temporal variables month, period (approximately three-week time blocks), week, and time of day were significant for all birds ($p<0.0001$) suggesting that differences in the number of American Avocets between sites varied daily as well as seasonally. The effects of exposed mudflat (independent of site and interaction with site) and interaction between site and water level were significant for all American Avocets as well ($p<0.0001$). Interaction between site and salinity was only significant among females ($p<0.0005$) indicating that salinity may differentially influence distribution of males and females. All weather variables except wind direction were significant for females (temperature: $p<0.004$, cloud cover: $p<0.0001$, wind speed: $p<0.0001$). Males were not significantly influenced by any of the weather variables, once again suggesting the possibility of differential distribution between sexes.

Despite the preliminary nature of these results, some interesting trends were revealed. The data indicated that temporal variation, habitat, and weather did influence the distribution of American Avocets among sites and that some variables such as salinity and weather may have resulted in differential distribution between sexes. A closer look at the effects of time on habitat and weather variables is required before any firm conclusions can be drawn. Future analyses will include examining the effect of environmental conditions on behavioral differences between males and females.

DIETARY ECOLOGY OF BREEDING RECURVIROSTRIDS IN HYPERSALINE ENVIRONMENTS

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A proposed means of reducing the risk of selenium contamination to breeding shorebirds in hypersaline evaporation ponds in the San Joaquin Valley is by disrupting the invertebrate food chain by pesticide application or other such treatments. We studied the patterns of invertebrate abundances and examined the foraging behaviors and diets of American Avocets *Recurvirostra americana* and Black-necked Stilts *Himantopus mexicanus* related to those patterns with respect to the evaporation pond systems selected by these species from March-June, 1991-92.

The foraging behaviors of American Avocets differed from those of Black-necked Stilts; >30% of American Avocet maneuvers were directed against pond substrates, whereas <5% of stilt maneuvers were directed against substrates. Both species primarily directed attacks against invertebrates in the water column. Foraging differences, however, did not translate into dietary differences. Invertebrate abundance was variable but species richness was always low due to the high salinity.

The most common invertebrate taxa in evaporation ponds were midge larvae and adults (Diptera: Chironomidae), brine fly larvae and adults (Diptera: Ephidridae), and water boatmen (Hemiptera: Corixidae). These also were the most common taxa in recurvirostrid diets. The percentage each taxon comprised of total invertebrate abundance often differed from percentages in bird diets, so that use was significantly different from availability. However, the most common prey available to shorebirds usually was the most common prey in diets. Notable exceptions occurred when birds were collected during a hatch of adult flies. Birds commonly fed on newly-hatched adults but invertebrate sampling methods (column sampling) were not efficient at collecting adults. Dietary comparisons among species revealed that American Avocets and Black-necked Stilts often fed on similar prey at any given time and pond.

We conclude that recurvirostrids feed opportunistically in evaporation ponds largely eating the most abundant prey at any given time. This behavior probably has evolved in response to the high abundance but low diversity of prey available in these simple systems. Thus, if pesticides or other means are to be used to disrupt evaporation pond food chains, those means must be successful in reducing all prey types found in the ponds. Otherwise opportunistic shorebirds will probably switch to feeding on invertebrate types unaffected by the treatment.

SPRINGTIME FORAGING OF SANDERLING *Calidris alba* FLOCKS IN RESPONSE TO AGGREGATIONS OF POST-LARVAL MOLE CRABS IN MONTEREY BAY, CALIFORNIA

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Large flocks (ca. 250-300 individuals) of Sanderling *Calidris alba* were commonly observed foraging in the mid-intertidal zone of fine sand beaches in Monterey Bay, California, on the lowest spring tides of February-April 1989 and 1990. The areas in which they foraged lay parallel to the water and were in the drier portions of the mid-intertidal.

As Sanderling flocks foraged, they completely pecked and overturned long, narrow portions of beach (e.g. up to 64 m long and up to 3 m wide), herein called "foraged areas". I commonly observed a string of foraged areas along as much as one kilometer of beach during a single low tide. Individuals within flocks foraged close together without exhibiting territorial displays. Flocks were observed foraging in this manner throughout a set of low tides.

In order to determine whether Sanderlings foraged on patches of prey and to identify changes in the relative abundances of prey types associated with these areas, 14 foraged areas were sampled inside and outside during 1989 and 1990. Additionally, an exclusion experiment was conducted as flocks foraged to determine the abundance of each prey type before and after foraging.

Prey types identified in the foraged areas were post larval Mole Crabs *Emerita analoga* and isopods *Excirolana* spp. After Sanderling flocks foraged in an area, the mean abundance of *E. analoga* post larvae was greater inside a foraged area than outside it and the mean abundance of *Excirolana* spp. generally showed no difference between inside and outside a foraged area. According to the results of the exclusion experiment, the mean abundance of post larval Mole Crabs was 36% less in foraged areas after they were foraged than before ($p=0.0004$). The mean abundance of *Excirolana* was only 9% less in a foraged area after foraging than before ($p>0.20$). Sanderling flocks seemingly located patches of prey dominated by post larval Mole Crabs and although they consumed a statistically significant proportion of this prey type, the flocks did not reduce the mean abundance of post larval Mole Crabs to their background (outside) levels. Results of the exclusion experiment support the interpretation that Sanderling flocks did not feed extensively on *Excirolana* in the foraged areas.

Post larvae of *E. analoga* were found in largest concentrations on fine sand beaches in Monterey Bay at a time coincident with the spring migration of Sanderling. It appears that Monterey Bay may offer a unique setting for migrating Sanderling flocks to forage on a highly abundant prey item. Additional sampling of foraged and nonforaged areas before and after foraging and further investigation as to the metabolic efficiency of sanderling foraging on post larval Mole Crabs should be conducted to determine the potential importance of Monterey Bay as a stopover site for migrating Sanderling.

CAN LANDSAT TM IMAGERY BE USED TO IDENTIFY PRIORITY SHOREBIRD HABITAT IN THE MACKENZIE DELTA LOWLANDS?

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Most species of North American shorebirds breed in the arctic yet our information on breeding densities and distributions is sparse throughout northern Canada. Due to logistical constraints in censusing the entire region, we need a technique to quickly identify habitat types important to breeding shorebirds without extensive ground-truthing. A previous Canadian Wildlife Service study examined the use of Landsat TM imagery in a small study area in the Mackenzie Delta lowlands from 1985 to 1987. By analyzing the visible red, reflective infrared, and mid-infrared bands using an unsupervised classification algorithm of Maximum Likelihood Rule and relating to the resultant Landsat Classification Units (LCUs) to vegetation cover types by extensive ground-truthing, the study identified a Landsat Classification Unit (LCU) type that appeared to characterize priority shorebird nesting habitat in that area. I extended the Landsat TM analysis to the entire outer Mackenzie Delta and had the area mapped using the same general LCU types and same satellite images of the previous study.

I tested the accuracy of the relationship between mapped LCUs and observed habitat in 1992 by censusing fifty-two 200x200 m^2 plots for breeding shorebirds and identifying habitat type. Of these 52 plots, according to the satellite maps, 19% were type II or III (wet emergents or wet sedge/willow), 17% were type IV (dense willow), 27% type V (upland tundra) and 37% type VI (proposed priority shorebird habitat: damp sedge or low centre polygons). These plots were spread throughout the study area but clustered in three regions: one that included the original study area, another approximately 10 km away, and the third 30 km away. Accuracy of the LCU types (relationship of mapped to actual vegetation type) was highest (89%, 16/18) in the area closest to the original study site, lower (58%, 14/24) in the second area and lowest (20%, 2/10) in

the farthest plots.

Preliminary analysis has indicated that, according to mapped LCU types, type VI plots were not more often used than types IV and V or II and III. However, using observed habitat type, type VI was used approximately three times more often by breeding shorebirds than were types IV and V or types II and III. These results suggest that Landsat TM analysis, while correctly identifying priority shorebird habitat in areas intensively ground-truthed, may not always be readily extrapolated to surrounding areas particularly in regions subject to rapid habitat change (e.g. irregular flooding of the delta). This limits the use of the technique in estimating shorebird breeding densities in large regions of the arctic although it may be useful in roughly identifying potential shorebird habitat and at least eliminating obviously unsuitable areas.

BROOD AMALGAMATION IN BRISTLE-THIGHED CURLEWS *Numenius tahitiensis*: PROCESS AND FUNCTION

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Alloparental care has generally been restricted to cases in which non-breeding adults help at nests or co-breeding adults raise young in communal nests. Alloparental care may also include the amalgamation of broods wherein one or more adults care for young that are not their own with these young added to the brood after hatch. We observed the amalgamation of Bristle-thighed Curlew *Numenius tahitiensis*: broods in western Alaska during 1990-1992. Amalgamation began with the incidental mixing of broods as they left their nests and moved to higher elevations. These associations were short-lived and comprised of only 2-3 broods. At 2-3 weeks of age, broods joined extended associations wherein each brood occupied a unique area that was defended by its parents. At 3-4 weeks, these associations coalesced into aggregations comprised of 5-10 broods wherein young intermixed and parents defended a common brood-rearing area. Young within these aggregations generally remained together until migration.

Virtually all broods (38 of 42) that survived to fledging joined aggregations. Generally, brood aggregations consisted of young of similar ages although in 1992 young from two distinct hatching periods, separated by 13 days of age, amalgamated. Most evidence suggests that adults attending aggregations had young present. Alloparental care was restricted to antipredator defense (e.g., mobbing, circling, and alarm-calling); other forms of care such as feeding and brooding were not observed. The intensity of antipredator defense and the number of adults defending young gradually decreased as young matured and aggregations formed. Desertion by female parents coincided with the formation of extended associations (20-27 days post-hatch) and most males deserted 1-8 days later when young began to fly and aggregations formed. Eventually, only one or two males remained with each aggregation giving alarm-calls as predators approached.

Temporary associations also formed among Bristle-thighed Curlews and American and Pacific Golden Plovers *Pluvialis dominica* and *P. fulva*, Whimbrels *N. phaeopus*, Bar-tailed Godwits *Limosa lapponica*, Western Sandpipers *Calidris mauri* and Long-tailed Jaegers *Stercorarius longicaudus*. Most heterospecifics associated with curlew broods less than 3-6 days although Bar-tailed Godwit and Whimbrel young often participated in aggregations for longer periods.

Bristle-thighed Curlews did not appear to form aggregations because food and cover was patchily distributed or limited. These resources were distributed in large expanses over the study area and aggregations were seldom seen in the same spot from day-to-day or year-to-year. Similarly, we did not find evidence that aggregations formed because adults were exchanging parental care (i.e., reciprocal altruism) or because certain males fathered offspring in multiple broods. Aggregations may, however, allow parents to "share" predator defense during early to mid brood-rearing and allow older, abandoned young to benefit by diluting predation risk and by confusing and disrupting predator attacks. Aggregations may also be important in allowing females, and some males, to desert their young earlier. The need to accumulate energy reserves for their long migration (up to 10,000 km) may force parents to desert their young before they are fully dependent. Juveniles may also benefit directly from aggregating by providing a flock with which they can migrate.

MIGRATORY FLIGHT THRESHOLDS RELATIVE TO ESTIMATED FAT STORES IN SEMIPALMATED SANDPIPERS *Calidris pusilla*

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Physiological and aerodynamic theories of the potential maximum flight times and distances of shorebirds as a function of their fat stores produce a range of predictions. It would be helpful to know how the birds themselves assess their flight capacities. How fat are birds when initiating migratory flights of a given distance and how fat are birds when they end flights? Intelligent management requires answers to these questions. Migrants' abilities to cope with the elimination of a site, or their benefit from using a new or restored site, depends in part on these numbers.

I measured the probabilities of migratory arrival and departure relative to estimated fat levels of adult and juvenile Semipalmated Sandpipers at fall staging areas in North Dakota and coastal New Brunswick where the birds differed in their origins and destinations. North Dakota birds were arriving from Alaska and/or the western Canadian arctic. Migrants in New Brunswick were largely from the central and eastern arctic. New Brunswick birds were preparing for a transoceanic flight to the Caribbean or South America. The direct destinations from North Dakota are unknown.

I captured samples of ca. 40 Semipalmated Sandpipers *Calidris pusilla* daily, and estimated fat stores for each bird from a regression on wing length. Estimated stores ranged from -6 g to 25 g. Negative values suggest non-linearity towards extreme values and/or systematic under-estimation of real fat stores. A migration index for 2-g fat classes was calculated by comparing the fat distributions of samples of birds captured at the staging areas on days prior to major migratory movements versus distributions on days following movements. Changes in distributions reflect net relative immigration and emigration from the site at each fat class. To compare daily distributions, estimated fat levels were adjusted for differences in the time of day samples were taken and for changes in mass during days and overnight. Days without migratory movements were used as methodological controls. No changes in fat distributions were seen across such days.

Following nights with migration, birds with less than ca. 6 g of fat were strongly over-represented in North Dakota adults and juveniles and for juveniles in New Brunswick. New Brunswick adults apparently arrived carrying greater fat stores. Thus, North Dakota migrants may have less flexibility and be more sensitive to the elimination of stopover sites and juveniles may be more sensitive than adults.

Adults had strong departure threshold probabilities at ca. 14-18 g in North Dakota and ca. 16-18 g in New Brunswick. North Dakota adults were thus nearly as well provisioned as those facing transoceanic flights from New Brunswick suggesting that long distance flight is the norm for inland birds as well as those on the coast. Juveniles showed more linear departure probabilities apparently leaving staging areas in poorer average condition. The

flight strategy and survival consequences of this difference are unknown but young birds are apparently less well prepared to deal with poorer conditions *en route*.

ESTIMATION OF LEAN AND LIPID MASS IN SHOREBIRDS USING TOTAL BODY ELECTRICAL CONDUCTIVITY (TOBEC)

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Many phases of the avian life cycle produce periods of high energy demand that are often met by storing lipid during times of energy surplus. Accurate quantification of lipids in free-living birds has proven difficult. The most accurate method of quantifying lipids, solvent extraction, requires sacrificing the bird and this is undesirable under a variety of conditions. Total body electrical conductivity (TOBEC) is a non-invasive technique used to measure body composition. TOBEC has recently been used to predict lean mass and lean mass estimates are subtracted from total body mass to estimate fat content.

Important considerations in the application of TOBEC measurements include the order of the predictive equation used (linear or quadratic) and the relative error associated with fat content predictions using lean mass estimates. Regression analyses were used to determine variations in body composition explained by TOBEC and to produce predictive equations for lean and lipid mass. These predictions were then compared with values determined by solvent extraction of carcasses. Predictions of lean and lipid mass from previously published predictive equations were also compared to the laboratory values.

Eighteen Dunlins *Calidris alpina*, 20 Semipalmated Sandpipers *C. pusilla*, and 20 Short-billed Dowitchers *Limnodromus griseus*, were collected between 29 April and 2 June, 1992, from South Island, Georgetown, South Carolina. Birds were weighed to the nearest 0.5 g and the mean of three scans in an EM-SCAN SA-2 body composition analyzer was recorded as the TOBEC index (*I*). Water content was determined by freeze-drying carcasses for 48 hours. Lipids were extracted using petroleum ether and weighed to the nearest 0.1 g. Lean mass (LM) was defined as the sum of the lean dried carcass mass and water content. Normalized TOBEC indices were regressed on lean mass and lipid mass independently. To test model predictions, individuals were randomly assigned to either a calibration set (n=44) or a verification set (n=14).

TOBEC measurements were significantly correlated with lean body mass in a linear interspecific model and explained 99% of variation in lean mass (R^2=0.99, F=8091.7, p=0.0001, n=44) when body size was included in the regression. Estimated lean mass (ELM) can be calculated using the equation, ELM = 152(I^2BL) - 1.29, where BL is body length. Using the verification set of individuals, the mean difference between ELM and LM was 1.97 g (SE=0.72, n=14), a 4.3% relative error (SE=1.18). Lean mass was also estimated using linear and quadratic TOBEC equations from other studies that do not incorporate body size. The relative error of these equations when predicting lean mass with the verification set was 17.4% (SE=2.55) and 11.2% (SE=2.29) for the linear and quadratic, respectively. In this study, linear and quadratic models using only log-transformed TOBEC indices explained a significant amount of the variation in lean mass (linear: R^2=0.95, F=742.85, p=0.0001, n=44; quadratic: R^2=0.99, F-2847.28, p=0.0001, n=44), but these models produced wider confidence intervals for predicted lean mass than the model above. Within species, the body size model produced the most accurate estimates of lean mass. TOBEC explained the most variation in lean mass in Short-billed Dowitchers (R^2=0.96, F=289.92, p=0.0001, n=15) and accounted for the least variation in Semipalmated Sandpipers (R^2=0.51, F=13.51, p=0.0028, n=15).

TOBEC measurements were correlated with lipid mass in an interspecific linear model when body mass was included as an independent variable (R^2=0.89, p=0.0001, n=44). Lipid mass (ELI) was estimated using the equation, ELM = 39.51 + 0.87 (BM) - 20.25(*I*), where BM is body mass. With the verification set, this equation produced a relative error of 58.6% (SE=11.38, n=14) in lipid estimations. For the sandpipers used in this study, variation in lipid mass and TOBEC were related in the following ways: Short-billed Dowitcher, R^2=0.97, F=143.31, p=0.0001, n=15; Semipalmated Sandpipers, R^2=0.91, F=60.78, p=0.0001, n=15; and Dunlin, R^2=0.87, F=34.16, p=0.0001, n=14.

The TOBEC method produces highly accurate estimates of lean mass. These estimates are improved when body size is incorporated in the regression model. In addition, TOBEC-estimated lipid predictions are possible when body mass is incorporated into the regression model. Fat content was predicted more accurately with a regression of lipid mass on TOBEC than with the two-step process previously suggested. The TOBEC method is a potentially valuable tool in studies of ecophysiology and energetics and is especially useful for monitoring nutrient reserve dynamics over time in free-living birds.

OPTIMAL SHOREBIRD MIGRATION: WILL WE RECOGNIZE IT WHEN WE SEE IT?

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I discuss a dynamic programming model of the spring migration of Pectoral Sandpipers *Calidris melanotos*. The purpose of the model is for planning wetland creation on a regional scale and it allows me to ask two questions: 1) how might the spatial distribution and quality of wetlands affect optimal migration behavior? and 2) where would one choose to construct new wetlands in order to have the largest positive effect on fitness?

The dynamic model is based on a fundamental tradeoff that migrating birds must make between a) feeding at migration stopover (i.e., wetlands) thereby increasing energy reserves and/or b) continuing to fly towards the breeding grounds thereby depleting energy reserves. A bird must balance these decisions such that it arrives on the breeding grounds within a specified window of time to successfully reproduce. If it arrives too early, there may not be adequate food resources and if it arrives too late there will not be sufficient time to rear young to fledging before the onset of winter. A bird that behaves optimally will maximize its expected reproductive output: a function of its time of arrival and its energy reserves upon arrival.

Analyses of spring migration data for Pectoral Sandpipers suggest a much richer set of possible optimal behaviors than is recognized by contemporary migration theory. Energy-optimal migration behavior is highly dependent on the spatial distribution and quality of potential stopovers. Three regimes of stopover density are recognized. At higher stopover densities (regime I) there is a range of equally optimal migration behaviors and selection pressures on migration behavior may have been light or non-existent. At lower wetland densities (regime II) there may be a unique optimal behavior but the optimal behavior changes with wetland density. At still lower wetland densities (regime III) there are insufficient energy and time resources to complete the migration; expected fitness is zero and birds will either die during migration or stop short of the breeding grounds.

Thus, there is a wide range in what would be considered to be energy-optimal migration. However, there appear to be characteristic patterns of fat and movement dynamics associated with migration and each of the wetland regimes. If so, then it may be possible to use observed patterns to diagnose conditions in a migration corridor and to identify appropriate

management strategies.

I discuss use of the model to develop testable hypotheses about optimal migration and management of migration corridors. In particular, I discuss competing ideas from the literature and possible strategies for eliminating incorrect hypotheses.

DIGENEAN TREMATODES AND THE MYSTERY OF SHOREBIRDS SUMMERING: A REVIEW AND A CASE STUDY OF THE GREATER YELLOWLEGS *Tringa melanoleuca*

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The hypotheses proposed to explain why individuals of many shorebird species stay on the wintering grounds in the southern latitudes during the boreal summer instead of migrating north for breeding are briefly summarized. The main hypothesis considers that summering shorebirds are sexually immature first-year birds. Most summering birds are actually juveniles but, in some species, adult individuals were also reported summering. In addition, many boreal shorebirds of the species known to summer in the southern latitudes do return to the breeding grounds and, in many cases, start breeding at the end of their first year.

Why do some individuals, first-year birds and older, over-summer in the southern latitudes while other members of the same species and age class return to the Holarctic region and breed? In summering shorebirds, the pre-migratory molt and fattening do not take place, or are delayed, the birds acquiring an alternate plumage and getting fat by the end of June and the beginning of July. The reasons for absent or delayed molt and fat accumulation are reviewed.

The possible relationship between trematode infestation and the summering of shorebirds in the southern latitudes is tested by the collection of Greater Yellowlegs *Tringa melanoleuca* over a whole year in coastal Venezuela to examine the seasonal variations in the infestation by digenean trematodes and to compare digenean intensity in adult and juvenile hosts. We also compare these data with the digenean infestations of juveniles collected in the Gulf of St. Lawrence in preparation for their first southward migration to the wintering grounds.

Venezuelan Greater Yellowlegs were infested with eleven digenean species or genera in comparison to four in the Gulf of St. Lawrence. The digenean faunas of adult and juvenile Venezuelan yellowlegs were relatively dissimilar with only four species or genera common to both age classes. The trematode diversity and intensity tended to be higher in juveniles than in adults. In Greater Yellowlegs recently arrived on the wintering grounds, the trematode intensity in adults was higher than that in juveniles. In contrast, at the time of the spring northward migration, the intensity of the digenean community in juveniles tended to be higher than in adults and the percentage of the host individuals infested by digenean trematodes in Venezuelan lagoons increased from November to April-May. The detrimental effects of trematode infestations and the reasons for the age differences in digenean infestations are discussed.

It is concluded that in addition to causing enteritis, anemia and some mortality, trematode infestation may prevent or delay normal pre-migratory molt and fat accumulation in some shorebirds, particularly juveniles, and therefore be an important factor responsible for their summering.

RETURN RATES, SITE AND MATE FIDELITY, AND BROOD MOVEMENTS OF SHOREBIRDS BREEDING ON THE NORTH SLOPE OF ALASKA

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Baseline data on breeding birds were collected from 1988 to 1992 on two 1 km^2 study plots in the Kuparuk Oilfield on the North Slope of Alaska. The study was initiated to provide information that could be used to make recommendations for minimizing the impacts of oilfield development on migratory birds and their habitats. In addition to the results reported here, data were recollected on nest and bird densities, nesting phenology, nest success, and the habitat relationships between nest sites and bird sightings. All nests were located and marked during three breeding season censuses. Adult shorebirds were trapped at their nests using drop-box traps and banded with colored plastic leg bands to identify individual birds. Returns, nest locations, and the mates of banded birds were noted in subsequent years. Observations of brood movements and brood attendance were added to the study in 1991-1992.

Ten shorebird species nested regularly on our study plots. Semipalmated Sandpipers *Calidris pusilla* and Pectoral Sandpipers *C. melanotos* had the highest nesting densities. Monogamous and territorial species, in which both sexes incubate (Semipalmated and Stilt Sandpipers *Micropalama himantopus*, Dunlin *C. alpina*, Black-bellied *Pluvialis squatarola* and Lesser Golden Plovers *P. dominica*), showed high site and mate fidelity with return rates of 30-69% from one year to the next and mate fidelity greater than 68%. Species which were promiscuous and opportunistic and in which a single sex incubates (Pectoral Sandpipers, Red *Phalaropus fulicarius* and Red-necked Phalaropes *P. lobatus*) showed low site fidelity (return rates 4-17%). We had no returns of Buff-breasted Sandpipers *Tryngites subruficollis* or Long-billed Dowitchers.

Among the site-faithful species, males generally had greater site tenacity than females but intact pairs had greater site tenacity than either males or females that returned with a new mate. Mean distances moved between nest sites from one year to the next was less than our estimate of territory radius for the territorial species indicating that most birds returned to the same territories. All shorebirds except the plovers and Red-necked Phalaropes were observed to re-use nest cups from previous years but the highest rates of re-use were found for Semipalmated Sandpipers (17%), Stilt Sandpipers (15%), and Dunlin (10%).

Hatching success was high (80% for all shorebirds, 1989-1992) compared to other North Slope studies. On average, Semipalmated and Pectoral Sandpiper broods moved a gradually increasing distance from their nest site during each day after hatch but there was considerable variability. Some broods remained in the vicinity of the nest site throughout the brood-rearing period while others moved as far as 800 m in 7 days from hatch. Stilt Sandpiper and Dunlin broods tended to move farther and faster than Semipalmated and Pectoral Sandpiper broods and never remained in the vicinity of the nest site for more than 1 day.

Shorebird brood movements were generally towards lake-basin complex wetlands or along lake shores. In 1992, most Semipalmated Sandpipers broods hatched between 25 June - 2 July, while Pectoral Sandpiper hatching was less synchronous with hatching dates from 28 June to 19 July. Male Semipalmated Sandpipers generally stayed with the brood longer than females. Maximum brood attendance observed was 18 days for male Semipalmated Sandpipers, 10 days for females and 21 days for female Pectoral Sandpipers.

BROOD REARING AND CHICK BEHAVIOR IN KILLDEER *Charadrius vociferus* AND PIPING PLOVERS *C. melodus*

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Studies on parental care in shorebirds have focused on the behavior of adults during the egg phase of breeding. Research on the behavior of young shorebirds and their relationship to parental care is rare because of the logistical problems associated with following highly mobile family groups. This study focused on the behavior of adults and their young in two shorebird species with precocial, nidifugous young. I compared the brood-rearing behavior of wild Killdeer *Charadrius vociferus* and Piping Plover *Charadrius melodus* families in remote undisturbed sites in northern Michigan.

Observations were made on eight families of each species from hatching to fledging and included both parental and chick behaviors. All observations were made during daylight hours. Piping Plovers hatched more eggs (hatching success = 85.4% vs. 54.4% and fledged more young (fledging success = 37.1% vs. 26.5% per breeding attempt than Killdeer.

Chick mortality was highest within the first few days of hatching. Killdeer led their broods over longer distances and used more brood-rearing habitats than Piping Plovers which remained on sandy beaches within 100 m along lakeshores. Brood-rearing behavior of parent birds were similar for both species with both sexes sharing in brooding and attending duties. However, differences were found between the antipredator displays given by the adults which included injury feigning, false brooding, crouched runs, approach and attack, and alarm calls. Killdeer gave higher intensity antipredator displays and directed them most frequently toward mammalian predators while Piping Plovers had a more varied repertoire directed toward avian predators. Antipredator displays were most often given by non-attending parents while attending parents stayed close to the chicks and led them away from potential predators.

Both species defended their young from conspecifics and other species of shorebirds that approached within 15 meters. Attending parents of both species maintained close distances (<3 m) to their broods during the first week after hatch but Piping Plovers stayed closer to their chicks (<6 m) than Killdeer (<8 m) after one week. Distances between attending adults and their broods were maintained through parental vigilance and brood-gathering vocalizations.

No differences were found between the percentage of time Killdeer and Piping Plover chicks spent brooding, feeding, resting, or preening. Chicks of both species spent over 80% of their time feeding (>12 pecks/minute) after the age of one week. Neither Killdeer nor Piping Plover chicks fed as frequently (<75%; <6 pecks/minute) during the first week after hatch because of the proportion of time they spent brooding.

None of the chicks were observed being brooded after age 14-days. Piping Plover chicks maintained closer distances to each other (<3 m) than Killdeer (<5 m) after the age of one week. All chicks responded to their parent's alarm calls and antipredator behaviors and not to predators, other shorebirds, or conspecifics.

In conclusion, both Killdeer and Piping Plover chicks were dependent on their parents for thermoregulation and protection from predators. In addition, recognition of potential predators appeared to be learned from parental responses. Adult plovers showed discriminatory abilities in the recognition of predators and responded differently according to predator type. Observed differences in parental care between Killdeer and Piping Plovers may have resulted from differences in brood rearing habitats and predation pressure and not from chick behaviors.

THE EFFECTS OF CHANGING PREY DENSITIES ON FORAGING RED-NECKED PHALAROPES *Phalaropus lobatus*: THE FUNCTIONAL SIGNIFICANCE OF SEXUAL SIZE DIMORPHISM IN A CHANGING ENVIRONMENT

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The idea that prey densities affect the feeding behavior of birds underlies many approaches in ecology. It is routinely inferred, for example, that changes in prey densities at degraded wetlands have negative effects on migratory bird populations. Yet, to date, there are few direct measures of the effects of changes in prey densities on the feeding performance of birds. The possibility that these potential effects act differently upon the feeding performances of the sexes within a sexually dimorphic species is virtually always ignored despite the widespread assumption that morphological differentiation strongly implies some form of niche partitioning.

This gap in our understanding of the consequences of sexual size dimorphism is perhaps even more serious in cases where the evolution of size dimorphism is thought to have been the result of selection on life history traits unrelated to feeding, such as competition for mates.

Laboratory experiments with captive Red-necked Phalaropes *Phalaropus lobatus* demonstrated that the feeding performance of this sexually size-dimorphic polyandrous species varied in a complex manner with changes in prey densities and individual-level effects on feeding rates and efficiency. Individuals used in this study spanned a four-fold range in mean feeding rates and varied in their responses to different prey densities. In particular, some individuals reached an upper limit in feeding rate where further increases in prey densities did not result in increased feeding rates. Further, this limit was reached at prey densities far exceeding those available, on average, to phalaropes feeding in the field.

Phalaropes employ surface tension transport of prey and analyses of this feeding mechanism and the bill morphology of this species indicate that the source of variation in feeding performance is likely to be due to bill-size effects on prey transport times. Thus, sexual size dimorphism may impose morphology-mediated limits on the feeding performance of large-billed individuals (primarily females) and may have important consequences in environments where the sexes are not diet partitioning because prey diversity is low and prey are patchy and ephemeral. Since surface-tension prey transport may be widespread among shorebirds, these conclusions may apply to a wide variety of species.

THE WESTERN HEMISPHERE SHOREBIRD RESERVED NETWORK: BUILDING ON ACHIEVEMENTS IN SHOREBIRD CONSERVATION

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The Western Hemisphere Shorebird Reserve Network (WHSRN), a program of Wetlands for the Americas (WA), is a voluntary collaboration of private and government organizations that works to identify and conserve critical staging sites for shorebirds. Habitat protection is fostered through voluntary commitments to long-term management to benefit shorebirds and other wetland dependent species. Since its inception in 1985, WHSRN has been highly successful in co-ordinating public and private landowners throughout the Americas. To date, 21 major shorebird staging areas in 7 countries have been incorporated into the Network. By promoting international recognition of these reserves, WHSRN has assisted landowners in generating the support and resources needed to conserve the sites for migratory shorebirds.

WHSRN's initial focus was, by necessity, the identification of major shorebird staging areas. To help accomplish this, workshops were held to train Latin American biologists in census and banding techniques. These workshops were highly successful in that the participants formed local shorebird

groups in six countries that continue to conduct shorebird research, train new biologists, and promote wetland conservation. There are now therefore many Latin American biologists working in shorebird research and conservation.

Thanks to the efforts of many biologists throughout the Americas, most staging areas supporting large concentrations of shorebirds (over 100,000 shorebirds annually) have been identified or probably will be identified within the next few years. WHSRN will work to incorporate all such ideas that are not yet a part of the network and have an interest in joining. Beyond simply adding additional sites though, WHSRN must work to develop strategies to strengthen and build upon the Network concept. To use trulye the program as a means to promote the conservation of all shorebird species, a survey of species coverage of WHSRN sites needs to be undertaken. In the case of species that do not concentrate in extremely large numbers, different conservation strategies need to be developed.

WHSRN has already initiated a special registry program for the Piping Plover *Charadrius melodus*. This registry provides recognition and support to landowners working to protect Piping Plovers and their habitats. Additional registries will be created (where practical) for other species of special concern, as defined by a survey of shorebird biologists. In addition, as institutional capabilities are increased, WHSRN will recognize Regional Reserves (those supporting between 20,000 and 100,000 shorebirds per year, or 5-15% of a species flyway population). Although WHSRN does not currently have the resources to incorporate these many smaller staging areas, it does recognize the critical role they play often in a cumulative nature (as in the prairie pothole region of North America) and as alternative staging sites.

WHSRN will also continue to work to strengthen its current network of reserves. WHSRN will assist North American sites in shorebird management, habitat acquisition, and public education. At South American sites, WHSRN will promote management planning, the establishment of protected areas and public education programs. In addition, scientific and educational "twinnings" of reserves supporting large numbers of the same species and populations of shorebirds will be facilitated. A conference will be held to provide sites with information on shorebird biology and management, an opportunity to exchange information and expertise, and a forum to voice needs, offer suggestions and analyze the first eight years.

In South America, shorebird habitat will benefit from WHSRN's outgrowth formation of Wetlands for the Americas. WA will undertake an inventory and status report of South American wetlands as well as promoting wetland conservation legislation, national wetland management strategies and the development of sustainable use plans for key wetland areas. These activities should have a positive effect on the conservation of shorebird habitats in South America.

In North America, WHSRN is working to enhance wetland habitats by promoting management strategies to benefit shorebirds and other waterbirds. Using the *Shorebird Management Manual* (Helmers 1992) as a base, WHSRN is conducting regional workshops for refuge mangers and private landowners.

The WHSRN program has accomplished much in its few short years of existence. To build upon these accomplishments, the program must continually evolve to better meet the needs of shorebird populations. It is hoped that, through a continued partnership with managers, landowners, and researchers, successful strategies can be developed and implemented.

THE ESTIMATION OF LIPIDS IN MIGRATING SANDPIPERS

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Current techniques to estimate lean mass and lipid levels in birds involve the derivation of predictive equations that relate morphological measurements and, more recently, total body electrical conductivity (TOBEC) indices to known lean and lipid masses. Using cross-validation techniques, we evaluated the accuracy of several published and newly-generated inter- and intraspecific predictive equations to estimate lean and lipid mass. To do so, we used laboratory determinations of lipid content in 22 Semipalmated Sandpipers *Calidris pusilla* and 22 White-rumped Sandpipers *C. fuscicollis* collected in central Kansas during spring migration.

Lipids were extracted using a modified Soxhlet apparatus. We also tested ideas in Morton *et al.* (1991), which states that current statistical approaches to TOBEC methodology misrepresent the precision in estimating body fat. Three previously-published interspecific equations using TOBEC indices predicted lean mass of our sample of birds with a range of 8-28% error.

To derive fat estimates from equations relating lean mass to TOBEC indices, lean mass is generally subtracted from total body mass. The three published equations used in this manner were not useful in predicting fat levels, averaging 53-155% in error rates. Cross-validation tests of a new equation that related lean mass and TOBEC indices of our two species revealed an average of 4.6% error in predicting lean mass. Subsequent subtraction to estimate fat yielded a 23.2% error in estimating fat.

Using stepwise multiple regression, we generated intraspecific equations to estimate lipid mass directly from body mass, morphological measurements and TOBEC indices. This form of equation, unlike the previous commonly-used form, allows for the calculation of prediction intervals for lipids. Body masses and morphological measurements alone explained a substantial portion of the variation (ca. 90%) in the fat masses of both species. The addition of TOBEC indices to these equations improved the predictive model more for the smaller Semipalmated Sandpiper than for the larger White-rumped Sandpiper. TOBEC indices explained an additional 7.8% and 2.6% of the variation in fat mass and reduced the minimum breadth of prediction intervals of 0.95 g (32%) and 0.39 g (13%) for Semipalmated and White-rumped Sandpipers, respectively.

The breadth of prediction intervals for models used to predict fat levels of individual birds must be considered when interpreting the lipid estimates.

REGIONAL MOVEMENT PATTERNS OF DUNLIN *Calidris alpina*: A RESPONSE TO RAIN?

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In recent years, much has been learned about the distribution and abundance of shorebirds in the Pacific Flyway. Nevertheless, seasonal movement patterns by shorebirds within the flyway remain poorly understood. Some shorebird species move regularly between coastal and interior sites often in response to inclement weather. It has long been speculated that Dunlin *Calidris alpina* wintering in coastal estuaries of central and northern California also move to inland sites to forage and roost.

Large mid-winter departures of 47% or more of the Dunlin at Bolinas Lagoon have occurred during 9 of 21 winters between 1971 and 1992. Analysis of 21 years of census counts at Bolinas Lagoon shows a strong negative correlation between early winter rainfall and early winter Dunlin numbers. However, length-of-stay data on color-banded Dunlin between 1984 and

1987 show that certain individual Dunlin consistently stay at Bolinas Lagoon from fall through to the next spring despite departures of large numbers in mid-season from Bolinas Lagoon.

In an attempt to document movements into the interior by coastal wintering Dunlin, a total of 75 Dunlin were dyed with picric acid at two sites, Bolinas Lagoon and Bodega Harbor, in the winter of 1991/1992. At Bolinas Lagoon, an additional 44 Dunlin were individually color-banded and 19 were fitted with radio transmitters. The first significant winter rainfall on the north-central coast of California in 1991 occurred in mid-December and Dunlin numbers at four coastal wetlands fell 44-84% between December 1991 and January 1992.

Regular, often daily, movements of up to 14 km between Bolinas Lagoon and San Francisco Bay were observed for both dyed and radio-tagged birds in January and February. Four radio-tagged and two dyed Dunlin were located in the Sacramento Valley up to 140 km from Bolinas. All four of the radio-tagged Dunlin located in the Sacramento Valley left the coast during, or soon after, a period of rainfall in the beginning of February.

We hypothesize that Dunlin in central California exhibit two overwintering strategies. One strategy is to migrate south and winter on the coast until it is time to migrate back to the breeding grounds. The second strategy is to begin wintering on the coast if little rainfall occurred that fall and move to the interior when winter storms create suitable habitat in the interior through flooding of seasonal wetlands, grasslands and agricultural fields. Mechanisms inducing movements to the interior are still unknown but rainfall appears to be one of them.

THE EFFECTS OF BAITWORM HARVESTING ON PREY POPULATIONS AND FEEDING BEHAVIOURS OF MIGRATING SHOREBIRDS

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The effects of baitworm harvesting activities on several species of invertebrate prey and on shorebirds foraging during a fall migratory stopover were investigated in the Bay of Fundy Hemispheric Shorebird Reserve in the Minas Basin, Nova Scotia.

The baitworm fishery is a multi-million dollar industry which has recently expanded into the Bay of Fundy Hemispheric Shorebird Reserve because of decreases in the baitworm harvests in New England and southern Nova Scotia. The bloodworm *Glyvera dibranchiata* is the principal baitworm harvested for commercial and sport fisheries and it is also an important food source for Black-bellied Plovers *Pluvialis squatarola* during southward migration. Harvesting activities also indirectly affect non-target invertebrate populations and the shorebirds that feed on them. Of particular interest is the Semipalmated Sandpiper *Calidris pusilla* and its amphipod prey *Corophium volutator* since more than 3/4 of the world population of this shorebird stops in the Bay of Fundy during southward migration.

Invertebrates were collected along six 100 m-long transects set throughout the study mudflat, 50 m of which were in overturned sediments (experimental) and 50 m in undisturbed sediments (control). Analysis of variance was used to compare experimental and control samples. The mean densities of *G. dibranchiata* were lower in the experimental sample ($25.3/m^2$) than the control sample ($29.0/m^2$) but these differences were not statistically significant. In relation to previous years, harvesters reported a considerable decrease in their catch in 1992. No statistically significant density differences were found for non-target polychaete or nemertine worms. The mean density of *C. volutator* was lower for the control sample ($335.0/m^2$) than the experimental sample ($545.4/m^2$) reflecting the amphipod's preference for loose sediment, but this difference was also not statistically significant. Invertebrate densities were extremely low in relation to data collected in previous years ($4085/m^2$ in 1990). Hence, further sampling will be undertaken in 1993 to determine whether this decrease in amphipod density was a result of baitworm harvesting.

Black-bellied Plover diet and feeding behaviour in overturned vs. undisturbed sediment was examined using focal animal sampling. Prey species and size, probe and peck rates, probe success, capture rates, and other behaviour were recorded. A multivariate analysis of variance was performed to see whether there was a difference between overturned and undisturbed sediments in the area of highest exploitation by harvesters and formerly of highest exploitation by plovers. A significant difference was found at the 5% level. Individual analyses of variance performed on each variate showed that the capture rates of plovers feeding in undisturbed sediment were three times greater than those of plovers feeding in overturned sediment ($p=0.001$) and probe success for plovers in undisturbed sediment was more than twice that of plovers feeding in overturned sediment ($p=0.01$). Since polychaete worms are the primary source of food for Black-bellied Plovers on southward migration through Minas Basin, this difference may be sufficient to affect the birds' ability to deposit enough fat for the transoceanic flight to their wintering grounds.

Faeces from focal plovers were collected and examined for remains of the prey species to relate to the observed diet. Remains of all prey species seen being consumed were found in the faecal samples.

Four 625 m^2 plots containing known proportions of overturned and undisturbed sediment were censused in order to determine the numbers of sandpipers (primarily Semipalmated, but also some Least *Calidris minutilla* and White-rumped *C. fuscicollis*) feeding in each sediment type. A chi-square test was performed to see whether the observed patterns of use differed significantly from the expected random pattern and no significant difference was found. These sandpipers are tactile foragers and are known to follow the receding tide line in search of crawling amphipods.

My preliminary results indicate that should disturbance be a factor in foraging-habitat selection, it is overcome in this case by the limited available space along the receding tide line. Peck, capture and success rates for sandpipers in overturned vs. undisturbed sediments will be investigated in 1993 to see whether harvesting activities affect sandpiper foraging efficiency.

MOVEMENT PATTERNS OF WESTERN SANDPIPERS *Calidris mauri* DURING WINTER AND SPRING IN SOUTH SAN FRANCISCO BAY, CALIFORNIA

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Traditional color-banding studies provide information on general movement patterns of shorebird populations. However, problems inherent to this method, including the extensive effort required to resight marked shorebirds in large areas or at night, often result in incomplete distributional data. I used radio telemetry to determine the specific movement patterns and habitat use of a population of Western Sandpipers *Calidris mauri* in south San Francisco Bay (SFB) during the winter and spring of 1991-1992.

Although degradation and loss of over 90% of the historical wetland habitat has occurred, SFB supports one of the highest populations of shorebirds in North America. Midwinter numbers of Western Sandpipers, the most abundant species in SFB, are estimated to be about 150,000 birds, increasing to 500,000 during spring migration. Despite the importance of SFB for sandpipers, little research has been conducted on their ecology. This study presents the first data on home range and habitat use of Western Sandpipers in SFB.

Western Sandpipers were capture during high tide in mist nets erected in three salt pond sites located about five km apart. A total sample of 110 Western Sandpipers were radio-marked: 60 during winter (November - February) and 50 during spring (April - May). Transmitters (Holohil Systems 1 g, 26-38 days, 3-4 km range) were attached using a marine epoxy specially developed for attachment to birds. Location data were collected using trucks with dual Yagi antenna systems (null-peak) supplemented by aerial surveys. The position of birds was recorded daily during each high and low tide cycle. Telemetry data were compiled in a geographic information system (ARCINFO).

Radio-marked Western Sandpipers were successfully tracked for up to five weeks during winter (51) and spring (46). The sandpipers exhibited high site fidelity; none of the marked birds were located outside of the south SFB region despite extensive aerial surveys. Radio-marked birds had similar habitat use patterns during early winter, late winter, and spring. Salt pond habitats were used 58% of the time, mudflats 27% and semi-vegetated marsh 10%. Less than 5% of use was in upland non-marine habitat.

Repeated locations for individuals indicated exclusive use of areas as small as 1 km^2. There was little difference in sites chosen for night versus day feeding and roosting areas. Western Sandpipers foraged at night on a regular basis but, during night low tides, there were more birds remaining in roosting areas as compared with day low tide locations. Males were the first to leave SFB in spring for the breeding grounds in Alaska. Over 80% (30) of sandpipers marked during spring in SFB were relocated in British Columbia or Alaska.

Western Sandpipers wintering in SFB appear to be segregated into smaller populations with strong site fidelity to local areas. Losses of feeding or roosting habitat could be critical for these local subpopulations which may also suffer increased bioaccumulation of contaminants in polluted sites. Salt ponds, an important habitat for the songbirds, are recognized as an important roosting habitat but may also represent an important foraging habitat as bird use of salt ponds occurred during low as well as high tides.

TEST OF A MODEL PREDICTING SHOREBIRD DISTRIBUTION AND ABUNDANCE IN SOUTH CAROLINA COASTAL SOFT-SEDIMENTS

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Past shorebird studies identified four factors critical in determining the distributions and abundances of shorebirds in marine soft-sediments during the non-breeding season. These include prey abundance and its effect on shorebird distribution, prey size on the basis of the tendency of shorebirds to gather where prey is largest, shorebird abundance and its effect on prey, and prey unavailability to shorebirds because of high water depths or difficulty in penetrating a hard substrate.

No study has integrated these factors into a conceptual model predicting shorebird and prey distributions and abundances. In fact, there is no unifying principle describing predator-prey relationships in marine soft-sediments. The goals of this study are to propose and test a predictive model of shorebird and prey abundances.

The model hypothesizes that if water depths and soil penetrability do not preclude shorebirds from foraging, prey supply (abundance, size, quality) and shorebird abundance are related in a feedback loop. Shorebirds are most abundant in areas of potentially highest prey supply yet at high shorebird densities, prey supply is limited by shorebirds. The model further hypothesizes that in the absence of shorebirds, prey supply is determined by physical and chemical factors that influence the detrital community. Thus, physical and chemical factors may indirectly affect the densities of foraging shorebirds.

Parts of the model regarding water depths and the shorebird-prey feedback loop were tested in preliminary experiments. Work was conducted in brackish impoundments and intertidal areas at the Yawkey Wildlife Center, Georgetown, South Carolina. In 1991, shorebird numbers and water depths were recorded twice a week from February through May in 10 x 10 m plots. Numbers and the identities of prey (mainly polychaete worms and insect larvae) were recorded monthly from core samples taken in each plot. In 1992, shorebird exclosures and cage controls were placed in plots (30 x 30 m) open to shorebirds. The numbers of shorebirds in each plot were recorded twice weekly. Core samples were taken from exclosures, plots, and cage controls initially, and after three and eight weeks.

Results show narrow distributions of water depths used by shorebirds corresponding to levels no greater than "belly deep". Mean depths were: American Avocets *Recurvirostra americana*, 8 cm, s.d.=9, n=61; Dowitchers *Limnodromus* spp., 5 cm, s.d.=4, n=404; peep *Calidris* spp., 1 cm, s.d.=2, n=1168. In 1991, no relationship was found between shorebird and prey abundances until May when mean shorebird densities were high (2.4 shorebirds/100 m^2). At that time, there was a positive relationship between shorebird and prey abundances ($p=0.005$, $r^2=0.12$, $n=65$). In the 1992 shorebird exclosure study, there was a positive relationship between the numbers of shorebirds inside the plots and prey abundances within exclosures at a marginally significant level ($r^2=0.566$, $n=5$, $p=0.084$) in May when mean bird densities were high (1.8 shorebirds/100m^2). The shorebird-prey relationship was much weaker in April ($r^2=0.081$, $n=24$, $p=0.175$) when mean shorebird densities were low (0.32 shorebirds/100 m^2).

Results are consistent with the model. Further tests are planned for 1993. The model may have broader applications to other species assemblages with three trophic-levels in shallow soft-sediments. Findings are also relevant for those who manage impoundments for shorebirds. Water depths should be kept at levels no greater than shorebird belly depths and practices that encourage invertebrate colonization should be employed.