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MARINE AND AGRICULTURAL HABITAT PREFERENCES OF DUNLIN WINTERING IN BRITISH COLUMBIA

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Abstract: We examined winter habitat preferences of individual dunlin (*Calidris alpina*) in the Fraser River delta, British Columbia, Canada, adjacent to agricultural land near an area of dense and increasing human settlement. We used radiotelemetry and compositional analysis to quantify and describe dunlin habitat selection at 2 scales (regional and local) throughout the 24-hr day and daily tidal cycles. We tested for differences between sex and age classes, and among birds captured at different sites. Patterns of habitat preference differed between sexes and among dunlin from different sites in the delta, but we detected no difference between age classes. We ranked habitat types in order of dunlin preference and tested for significant differences among habitat ranks. Dunlin showed a significant preference for tidally influenced marine habitats at both scales and throughout the study area. However, most individuals (>80%) also used terrestrial habitats, usually during high tide and primarily at night. The role of terrestrial habitats in the ecology of Fraser River delta dunlin previously had been underestimated because these habitats are used far more at night than during the day. Regionally, soil-based agricultural crops ranked above other terrestrial habitats, and pasture was the only terrestrial habitat that was ranked highly and preferred at both scales. Pasture vegetation tends to be short, and pasture fields in the Fraser River delta are fertilized heavily and naturally with cattle manure. We recommend that managers promote the maintenance of a mosaic of soil-based agricultural crops—with a particular emphasis on naturally fertilized pastures—for dunlin and other shorebirds wintering in the Fraser delta. Terrestrial habitat fragmentation also should be kept to a minimum, as dunlin preferred large fields, likely in response to predation risk.

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Mobile animals typically move among habitats to pursue different activities at different times. The most accurate means of modeling population-level responses to changes in habitat conditions may involve incorporating the behavioral variation among individuals and classes of individuals (Sutherland and Gosling 2000). Sex-related differences in habitat selection commonly are attributed to sexually dimorphic feeding specializations or to differences in competitive abilities, often related to body size (Smith and Evans 1973, Desrochers 1989, Marra 2000, McLoughlin et al. 2002). Age-related differences in habitat selection have been attributed to competitive exclusion by dominant adults, differences in experience, and/or developmental constraints (Orians 1969, Goss-Custard et al. 1982, Marchetti and Price 1989, Lind and Welsh 1994).

Animals also may use different criteria when selecting habitat at different temporal or geographical scales (Morris 1987, Beyer and Haufler 1994, Pedlar et al. 1997, Saab 1999). Home ranges may be chosen based on food availability, while use patterns within ranges may be influenced by predation risk or the availability of other resources such as nest sites (Orians and Wittenberger 1991, McLoughlin et al. 2002). Foraging efficiency and predation regimes may differ by day or night (Robert and McNeil 1989, McNeil et al. 1992, Thibault and McNeil 1994, Sitters 2000). Since all these mechanisms can produce differential impact of habitat changes on components of populations and/or at different times, understanding the behavioral basis of habitat selection for individuals will improve our ability to manage and conserve species in the face of habitat loss, alteration, and fragmentation.

Habitat availability changes continuously for many invertebrates, fish, and shorebirds that use tidally influenced environments. Intertidal habitats may be available for only a short time each tide cycle, and may be completely unavailable during other times (e.g., high tides for birds, low tides for fish). Animals may utilize alternative habitats to meet daily energetic requirements or for safety. Migratory shorebirds (Scolopadidae and Charadriidae) wintering in coastal wetlands at temperate latitudes often use alternative forag-

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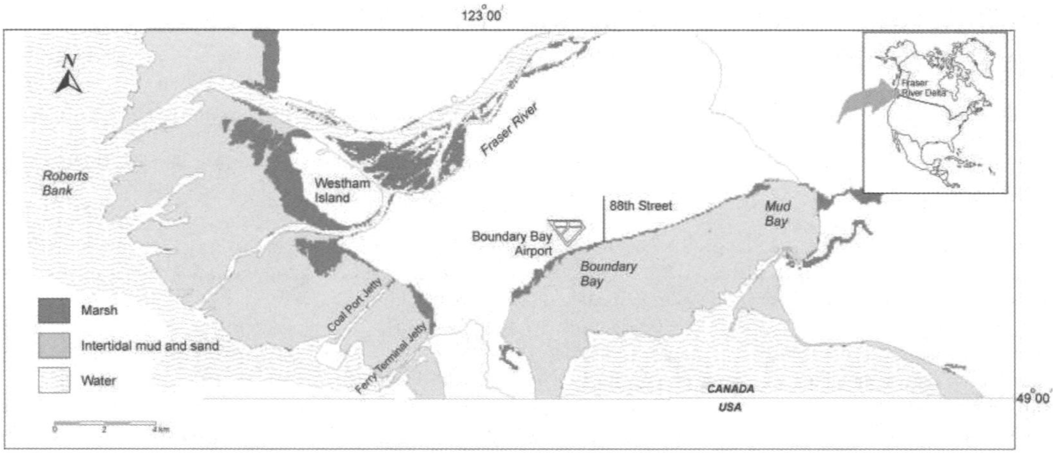

Fig. 1. Our study area in the Fraser River delta, British Columbia, Canada.

ing habitats during high tide (Velasquez and Hockey 1991, Warnock and Takekawa 1995, Weber and Haig 1996, Dann 1999), and may use different diurnal and nocturnal foraging habitats (Robert et al. 1989, Mouritsen 1994, Dodd and Colwell 1998).

Shorebirds and other coastal species have been subject to substantial habitat alteration since the arrival of European settlers in North America. More than 75% of wetlands in the Canadian Maritime Provinces and 50% of coastal wetlands in the contiguous United States have been lost or altered, primarily by agriculture and urban/suburban development (National Wetlands Working Group 1988, Bildstein et al. 1991, National Oceanic and Atmospheric Administration 2001). Coastal counties house approximately 53% of the U.S. population, and population growth in these areas exceeds the national average (Culliton 1998). Loss of coastal wetlands has been cited as a contributing factor in the population declines of shorebird species in North America, and habitat conservation and restoration have been identified as the primary means of stabilizing shorebird populations (Donaldson et al. 2001, Brown et al. 2001).

The state of North American wetlands is particularly important to the Pacific Coast subspecies of dunlin (*C. a. pacifica*), a calidrid sandpiper dependent on wetlands throughout much of its life cycle. Dunlin have been listed as a species of concern in the United States because of population declines attributed to coastal wetland habitat loss (Warnock and Gill 1996, Brown et al. 2001). The *pacifica* subspecies of dunlin breed in Alaska and are common winter residents from southern British Columbia to Mexico (Warnock and Gill 1996). The Fraser River delta in British Columbia, Canada, is the northernmost site in North America to support a large population throughout the winter, supporting 30,000–60,000 birds (Butler and Campbell 1987, Warnock and Gill 1996). The numbers of wintering dunlin in the delta have remained stable over the last 40 years, despite the delta's proximity to the rapidly growing city of Vancouver (Butler and Vermeer 1994, Shepherd 2001*a*). Although this is an area of dense and increasing human settlement, some land immediately adjacent to the delta has been placed in a land reserve for agricultural use, and some have suggested that dunlin use of this habitat helps maintain the Fraser River delta population (Butler 1999, Shepherd 2001*b*). To make better management decisions and influence land-use practices in the region to maintain habitat for dunlin, we require knowledge of dunlin habitat use and habitat-selection patterns.

We used radiotelemetry to examine habitat preferences of individual dunlin of known sex and, when possible, known age, that were trapped at 3 different sites in the Fraser River delta. We examined habitat preferences across tidal cycles, throughout the 24-hr day, and at both regional and local scales. We used the data on habitat preferences to make management recommendations for dunlin and other shorebirds in the Fraser River delta.

STUDY AREA

We conducted our study in the Fraser River delta (49°05′N, 123°12′W) in southwestern British Columbia (Fig. 1). The Fraser River delta is the largest wetland on Canada's Pacific coast and supports the country's highest densities of waterbirds, raptors, and shorebirds in winter (Butler and Campbell 1987). It is a key stopover site for many species of migrant birds flying between breeding habitat in Canada, Alaska, and Russia and wintering habitat in the southern United States and Central and South America. Over 2 million shorebirds use the delta annually, including internationally important populations of dunlin and western sandpipers (*C. mauri*; Butler and Vermeer 1994; R. W. Butler, Canadian Wildlife Service, personal communication).

Our study area included marine intertidal and marsh habitats on Roberts' Bank, in Boundary Bay, and in Mud Bay, and agricultural, urban, and other terrestrial habitats separated from the marine habitats by a system of dikes (Fig. 1). Two jetties, a ferry terminal, and a coal port facility extend from the shoreline to beyond the low water mark on Roberts' Bank, and have altered water flow and sediment movement characteristics in the area (McLaren and Ren 1995). Intertidal sediments range from fine mud to sand, with finer sediments occurring in areas of river outflow (Sewell 1996). The tidal regime is such that the intertidal zone on Roberts' Bank is submerged approximately 1 hr before and exposed approximately 1 hr later than the intertidal zone in Boundary Bay and Mud Bay.

Capture and Marking

We caught dunlin in mist nets at night at 3 sites during the winter of 1995–1996. We fitted 47 birds with 1.45-g radiotransmitters (model BD-2G; Holohil Systems Ltd., Carp, Ontario, Canada). Between 20 and 23 December 1995, we radiomarked 25 dunlin in Mud Bay. Between 17 and 23 February 1996, we radiomarked 12 dunlin in western Boundary Bay and 10 on Westham Island, which is situated on Roberts' Bank (Fig. 1). We banded each bird and took the following measurements: mass, unflattened wing chord, tarsus length, and culmen length (from the tip to the margin between mandible and feathers at the center of the upper mandible). Dunlin are sexually dimorphic, with females generally larger than males (Page 1974). We used a maximum likelihood model to determine sex using culmen length data (Shepherd et al. 2001). We radiomarked 23 males, 22 females, and 2 dunlin of unknown sex, with a 91.5% probability of correctly assigning sex. Juveniles usually can be distinguished from adults by the presence of buffy-edged inner median coverts until about mid-winter (Page 1974, Paulson 1993). We therefore aged dunlin captured at Mud Bay in December using this technique and recorded 13 adults and 11 juveniles.

Radiotelemetry

We tested radio signal ranges and detected signals from a distance of at least 4 km in the open marine habitat and at least 650 m in terrestrial habitat (although signals generally were detected from at least 1 km in terrestrial habitat). We tested radio location accuracy by comparing actual (using a Global Positioning System [GPS] unit) and estimated (using radiotelemetry) locations of 3 radiotransmitters in marine and terrestrial habitats within our study area. The mean linear distance between the actual and estimated locations of the 3 test radios was 71 m (SE = 20). We used this measure of telemetry error to quantify the potential for bias in our habitat preference analyses. We detected radiotransmitters up to 38 days after deployment.

We began data collection after dunlin had had a 3-day, post-attachment adjustment period. We used a dual-Yagi (5-element) peak/null van mast telemetry system (Warnock and Takekawa 1995) to locate birds from 61 fixed stations set along the raised dikes separating the marine and terrestrial habitats and along roads within the terrestrial habitat. We took 2 compass bearings on each radiomarked dunlin from consecutive telemetry stations and minimized the time between bearings ($\bar{x}$ = 6.4 min, SE = 0.1). During daytime high tides, when dunlin flocks were close to the dike and radio signals were particularly strong, we visually pinpointed discrete flocks containing radiomarked individuals whenever possible. We took rough bearings on the signal(s) from 2 points adjacent to the flock and obtained locations using the odometer in our vehicle to measure the distance between the discrete flock containing the radiomarked individual(s) and the nearest telemetry station. This methodology minimized location error due to the collection of bearings directed toward each other (parallel bearings).

We collected location data day and night during standardized tracking sessions within 3 hr before and after high and low tides. We also sampled activity budgets throughout the 24-hr day and across tide stages (discussed in Shepherd 2001*b*), which included the collection of location data, as described above, approximately every 2 hr.

We located Mud Bay dunlin during 42 tracking sessions, and every 2 hr during 67 hr of activity sampling, covering all but 2 days from 26 December 1995 to 26 January 1996. We located Westham Island and Boundary Bay dunlin during 45 tracking sessions, and every 2 hr during 64 hr of activity sampling, on all but 6 days from 21 February 1996 to 28 March 1996.

We used only 1 location per bird per session in the analyses. We considered the locations to be statistically independent since tidal action altered habitat availability between subsequent sessions (high and low tides) and the time between tracking sessions was sufficient for dunlin to fly to any point in the Fraser River delta. Dunlin are a flocking species; however, flock membership in the Fraser River delta did not appear to be fixed. Flocks routinely broke apart and coalesced into different formations throughout a tidal cycle, and individuals spread out and foraged across the mudflat at low tide. Sixty-six percent of all high-tide dunlin locations were of radiomarked individuals in flocks that did not contain any other marked birds. Of the remaining high-tide locations, the median number of dunlin detected in flocks with other radiomarked birds was 2, even though group size at capture was 3, 6, and 8 (all other radiomarked dunlin used in the analyses were captured singly). We used a program compatible with Arcview Geographical Information Systems (GIS; Environmental Systems Research Institute 1996) to triangulate the bearings and obtain Universal Transverse Mercator (UTM) coordinates for each individual radiomarked dunlin located on each tracking session (McCullough 1996).

Statistical Analyses

We considered statistical test results to be significant at $P < 0.05$, except for interaction terms, which we considered significant at $P < 0.10$ since significance tests for interaction terms have lower power than those for main effects (Littell et al. 1991). The results we reported of 2-way analyses of variance (ANOVA) or multivariate analyses of variance (MANOVA) were those of the reduced models in cases where the interaction term was not significant, and we reported least-squares means taking the other factor into account.

Home-range Estimates

We estimated fixed kernel 95% utilization distributions (UDs) to represent home ranges of radiomarked individual dunlin in the Fraser River delta because this method provides the least biased estimate of home range (Worton 1995, Seaman et al. 1999). The home range is therefore the area within which an individual dunlin has a 95% probability of being located. We made the home-range estimates using the Arcview GIS and Spatial Analyst programs and the Animal Movement Analysis Extension (Hooge and Eichenlaub 1997). We used least-squares cross validation as the smoothing parameter.

We calculated UDs for each dunlin with ≥15 radio locations (n = 31 birds). To determine whether our sample sizes of locations—which were limited due to the short battery life of the small transmitters—created any biases in our home range and/or core area estimates due to "unusual erratic wanderings" (sensu Brown 1975), we performed a series of 3 tests. We used ANOVAs to compare home ranges and/or core areas estimated using the smallest (<20) and largest (>30) numbers of locations with those of the remaining birds. In addition, we used correlation analysis to determine (1) whether fixed-kernel home ranges and/or core areas varied with sample size and (2) whether the 95, 75, 50, and 30% UDs were proportionate. Thirty of the original 31 Dunlin remained in the data set once the sample size tests were completed.

We included locations collected during activity budget sampling (1 per tide stage) in the estimates where the locations did not overlap temporally with locations collected on standardized tracking sessions. We compared home-range sizes including and excluding activity locations separately by banding site using ANOVA and found no differences ($F_{1,>10} < 0.8$, $P > 0.31$ for all sites).

Home-range Comparisons

We used 2-way ANOVAs and Bonferroni adjusted multiple t-tests on log-transformed data to compare home-range sizes among categories of dunlin. We tested for differences between sexes, among sites, and, within the Mud Bay site, between sexes and age classes.

Habitat Categories

We constructed a habitat map for our study area using data from the following digital maps: British Columbia Ministry of Environment, Lands, and Parks 1988 Terrain Resource Information Management (TRIM) maps (1:20,000); Canadian Wildlife Service 1989 Inventory of the Wetlands of the Fraser Lowland; Agriculture and Agri-Food Canada 1996 Inventory of Fraser Valley Agricultural Practices; and orthophotos taken by the Canadian Wildlife Service in 1995 (Fig. 2). We identified 2 marine habitat categories within

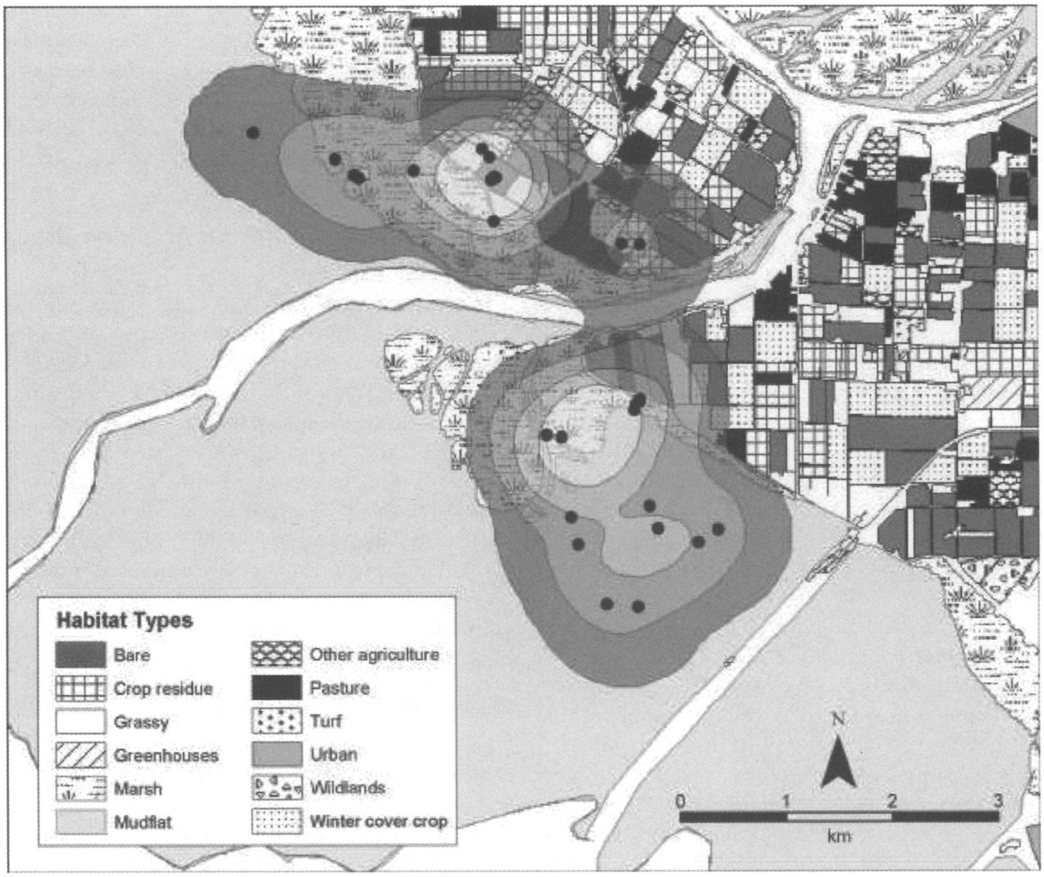

Fig. 2. The home range (darkest polygon), with point locations, of the Westham Island dunlin carrying radiotransmitter 6.059 layered over the habitat base map showing the categories used in the habitat preference analysis.

the study area: (1) mudflat, the unvegetated intertidal zone that was alternately exposed and inundated by the tide; and (2) marsh, the vegetated zone between the mudflat and the dikes that marked the boundary between marine and terrestrial habitats. We included small areas of terrestrial bog habitat within the marsh category.

We considered tide height and tidal amplitude to estimate the average amount of mudflat available during our study period. At mean low water (tide height = 0 m), our study area had 152.8 km^2 of exposed mudflat. At mean high water (no exposed mudflat) the predicted tide height was 4.51 m. Starting at mean low water and assuming a linear incline, approximately 10.2 km^2 of mudflat would have been submerged with each 0.3 m increase in tide height. The average predicted tide height during our tracking sessions was 3.08 m, so the total average amount of mudflat available to the dunlin in our study was 48.6 km^2. We compared predicted tide heights (from local tide charts) during our study to local tide gauge data collected by the Institute of Ocean Sciences (Sydney, British Columbia, Canada) and found the predicted heights to be accurate to ±0.1 m

Some dunlin in the Fraser River delta forage in terrestrial habitats, predominantly during high tide and particularly at night (Shepherd 2001*b*). We delineated 26 terrestrial habitat categories in our study area, which, for the initial analysis, we consolidated into the following 10: (1) bare, the nonvegetated, mud fields with some crop remains underground; (2) crop residue, the bare fields with above-ground crop remains; (3) pasture, the short grass fields generally grazed by cattle and fertilized naturally; (4) winter cover crop, including winter wheat, fall rye, spring barley, oats, annual rye grass, clover, and spring wheat planted to provide forage for waterfowl; (5) grassy/unknown, including grasslands, forage, weedy vegetation, uncultivated farmland, nonagricultural land such as lawns, and pieces of unclassified habitat; (6) wildlands, the tall grass fields with a few bushes and trees; (7) other agriculture, including nursery crops, fruit, berries, and some vegetables; (8) turf, the farms producing dense grass for lawns; (9) greenhouses, including large commercial operations; and (10) urban, including urban areas, Boundary Bay airport, and heavily wooded areas.

We layered the home ranges and radio locations of each dunlin over the habitat base map (Fig. 2) and examined habitat preferences at 2 scales. To quantify regional or second-order selection (Johnson 1980), we compared the proportions of habitats that fell within the individual dunlin's home range (used) to the proportions of habitats within the Fraser River delta study area (available). For the purposes of these analyses, we defined the study area as the proportions of habitats within a minimum convex polygon home range of all telemetry locations from all birds considered together. To quantify local or third-order selection (Johnson 1980), we compared the proportions of locations found within each habitat (used) to the proportions of habitats within each bird's home range (available).

The proportions of available terrestrial and marsh habitats differed among the 3 sites, and dunlin showed a high level of fidelity to the areas around these sites (Shepherd 2001*b*). We therefore tested to see whether dunlin selected habitats regionally if we restricted the definition of what was available. In this case, we determined habitat use from the mean proportion of radio locations within each habitat. We determined habitat availability from (1) the proportion of each habitat within our total study area, and (2) the proportion of each habitat within each site-specific study area (the minimum convex polygon sub-area around each bird's banding site).

Habitat Preference Analyses

We used compositional analysis (Aebischer et al. 1993) and MANOVA to determine whether dunlin exhibited habitat preferences and to test for differences among categories of individuals (i.e., sexes, ages, sites). When we found differences, we ranked the habitats in order of preference and determined which habitats were preferred over which other habitats. We ranked habitats in order of preference from 1 (most preferred) to 12 (least preferred). We then used *t*-tests to determine which habitat ranks differed significantly from each other ($P < 0.05$), and refer to them using the terms "preferred" or "avoided." To determine whether field size might also be a factor in the choice of terrestrial habitats by dunlin, we used a *t*-test to compare the size of fields that contained dunlin locations to the size of fields that did not.

Randomization Models for Analyses Using Individual Dunlin

Samples often did not meet the assumption of normality, so we used bootstrap and randomization models to test the robustness of the MANOVA and ANOVA results. For tests to determine whether dunlin selected habitats nonrandomly, we performed bootstrap tests with replacement on the *F*-statistic results of the MANOVAs and estimated the 95% confidence intervals of the bootstrap distributions (1,000 bootstrap samples). We reported the 95% confidence intervals of *F*-statistics and their associated *P*-values. For comparisons between groups, we tested our hypotheses by randomizing the *F*-statistics.

Measurement of Bias Due to Telemetry Error

Using Arview, we created circular buffers with radii equal to the mean linear distance between the actual and estimated locations of the 3 test radiotransmitters around each individual telemetry location for which we did not have visual confirmation. Buffer circles were therefore 142 m in diameter. Using the same methodology employed to calculate the proportion of each habitat type within each home range, we calculated the proportion of each habitat type within the buffer circles associated with each point location. Overall, 11.0% of point locations had buffers that incorporated >1 habitat type (i.e., the buffer encompassed habitat types other than the habitat associated with the given point). Broken down by macrohabitat, 5.4% of marsh and mudflat point locations and 28.8% of soil-based agricultural locations had buffers that encompassed >1 habitat type and therefore exhibited the potential for bias due to telemetry error.

To determine whether bias might be a factor in our habitat preference analyses, we calculated (for buffers encompassing >1 habitat type) the mean proportion of the buffers occurring in the same habitat type as that of the point location. On average, 75.2% of the area covered by marine buffers and 72.6% of the area covered by terrestrial buffers were in the same habitat type as that of the point location. Less than 2% of marine buffers fell into

Table 1. Proportions of unconsolidated habitats available to dunlin, mean proportions of unconsolidated habitats within dunlin home ranges, and rank order (1 to 12) of unconsolidated habitats within dunlin home ranges (regional selection) in our Fraser River delta study area, British Columbia, Canada. Ranks that share a letter are not statistically different from each other ($P > 0.05$).

Habitat type	Available	Home range	Rank[a]
Mudflat	0.280	0.576	1 - A
Marsh	0.083	0.100	2 - B
Crop residue	0.048	0.039	3 - B
Pasture	0.089	0.073	4 - BC
Bare	0.083	0.050	5 - CD
Winter cover	0.035	0.018	6 - DE
Grassy/unknown	0.250	0.115	7 - E
Wildlands	0.030	0.011	8 - F
Other agriculture	0.007	0.004	9 - FG
Greenhouses	0.003	0.001	10 - H
Urban	0.089	0.013	11 - GHI
Turf	0.003	0	12 - I

[a] Ranks numbered 1 (most preferred) through 7 are selected relative to ranks 8 through 12, which are avoided.

the terrestrial zone, and 0.5% of terrestrial buffers fell into the marine zone. In the marine macrohabitat, 26.3% of the buffer areas around marsh point locations fell into mudflat habitat, and 23.4% of the buffer areas around mudflat locations fell into marsh habitat, so we did not find evidence for bias in marine habitat preferences.

The terrestrial zone was consolidated into 6 habitat types, so for buffers that encompassed >1 terrestrial habitat, we calculated the mean proportions of the buffers that fell within each of the other 5 habitats. Of the 27.4% of the terrestrial buffer circles that encompassed >1 habitat, on average 7.6% fell within crop residue habitat, 6.5% within grassy/unknown habitat, 4.8% within pasture habitat, 4.3% within winter cover crop habitat, 2.5% within residual habitat, 1.2% within bare habitat, and 0.5% within marsh habitat. We used a chi-square test to determine how these values compared to equal values across terrestrial habitat types, and we found no significant difference among the habitat types ($\chi^2_5 = 6.4$, $P = 0.27$). In addition, nearly a third (28.6%) of the agricultural locations with buffers that incorporated >1 habitat type were attributed to a single individual. We feel confident in asserting that no evidence suggests bias in our results due to telemetry error.

RESULTS

Home-range Estimates

Seventeen of the 30 dunlin in the home-range sample were present in our study area every day of radiotracking; 9 more were missing on 1 day only. Overall, the average dunlin was absent from 18.3 ± 2.5% of tracking sessions.

Dunlin home-range size differed by banding site ($F_{2,24} = 14.1$, $P < 0.001$), with Boundary Bay dunlin using larger areas (52.6 ± 4.6 km^2 [mean ± SE]) than either Mud Bay (23.9 ± 3.5 km^2) or Westham Island dunlin (19.0 ± 5.6 km^2). We found a marginally significant difference in mean home-range size between the sexes ($F_{1,24} = 4.3$, $P = 0.05$), with males having smaller home ranges (28.6 ± 3.9 km^2 [mean ± SE]) than females (35.0 ± 3.4 km^2). Juvenile mean home-range size (24.1 ± 2.2 km^2) did not differ from that of adults (23.6 ± 2.9 km^2; $F_{1,11} = 0.4$, $P = 0.55$).

Regional Habitat Preferences

Regional habitat use by dunlin was nonrandom ($\lambda = 0.009$, $F_{11,19} = 182.4$; 95% CI of *F*-statistic [bootstrap sample] = 174.5 to 7,450.6; $P < 0.001$). Dunlin avoided 5 of the terrestrial habitats (wildlands, other agriculture, greenhouses, urban, turf; Table 1), so we consolidated them under the title "residual" for remaining analyses. Regional habitat use was still nonrandom once the residual habitats had been consolidated ($\lambda = 0.03$, $F_{7,23} = 93.9$; 95% CI of *F*-statistic [bootstrap sample] = 76.5 to 341.9; $P < 0.001$). Mudflat made up 58% of the mean home range (Table 2) and was preferred by dunlin over all habitats (Table 3). The remaining habitats each made up <13% of the mean home range. Marsh, crop residue, and pasture were ranked second, third, and fourth, respectively, and were preferred over winter cover, grassy/unknown, and residual habitats. The mean size of fields containing dunlin radio locations (0.12 ± 0.8 km^2 [mean ± SE], $n = 64$) was larger than the mean size of fields available in the study area (0.08 ± 0.3 km^2, $n = 739$; $t_{801} = -5.6$, $P < 0.001$).

Regional habitat selection differed between sex categories (Table 4). Both sexes preferred mudflat to all the other habitat categories, and both sexes also had crop residue followed by pasture in the top 4 ranks (Table 3). However, we found a higher proportion of marsh habitat in the female (13%) than in the male (7%) home ranges, with females ranking marsh second and males ranking it fourth. Females also were more selective than males, preferring the habitats ranked 2 and 3 (marsh and crop residue) to those ranked 5 through 7 (bare, winter cover, grassy/unknown), and avoiding the residual habitat in relation to all habitats. Males showed no preferences among habitats ranked 2 through

Table 2. Proportions of habitats available to dunlin, mean proportions of habitats within dunlin home ranges, and mean proportions of dunlin radio locations found in each habitat in our Fraser River delta study area, British Columbia, Canada. Sample sizes (number of dunlin) in parentheses.

	Mudflat	Marsh	Bare	Crop residue	Grassy/ unknown	Pasture	Winter cover	Residual
Available:								
Total study area	0.28	0.08	0.08	0.05	0.25	0.09	0.04	0.13
Westham Island		0.38	0.12	0.15	0.18	0.07	0.07	0.03
Boundary Bay		0.07	0.14	0.06	0.35	0.14	0.04	0.20
Mud Bay		0.07	0.07	0.06	0.43	0.18	0.04	0.16
Home ranges:								
Overall (30)	0.58	0.10	0.05	0.04	0.12	0.07	0.02	0.03
Male (13)	0.59	0.07	0.06	0.04	0.12	0.08	0.02	0.03
Female (15)	0.55	0.13	0.05	0.04	0.12	0.07	0.02	0.03
Westham Island (6)	0.45	0.30	0.06	0.04	0.09	0.03	0.03	0.01
Boundary Bay (8)	0.55	0.07	0.06	0.02	0.15	0.06	0.01	0.08
Mud Bay (16)	0.63	0.04	0.04	0.05	0.11	0.10	0.02	0.01
Radio locations:								
Overall (30)	0.72	0.14	0.03	0.01	0.02	0.07	0.01	0.01
Westham Island (6)	0.40	0.51	0.05	0.01	0.01	0.02	0	0.01
Boundary Bay (8)	0.69	0.09	0.06	0.03	0.04	0.06	0.02	0.02
Mud Bay (16)	0.85	0.03	0	0.01	0.02	0.09	0	0.01

6, preferring them only to the residual habitat. We found no age effect on regional habitat preferences when tested with sex ($\lambda = 0.27$, $F_{7,5} = 1.9$, $P = 0.22$).

Regional habitat selection also differed among the 3 banding sites (Table 4). Mudflat made up 45% of the mean home range at Westham Island, 55% at Boundary Bay, and 63% at Mud Bay (Table 2). Mudflat was ranked first and preferred over all other habitats at Boundary Bay and Mud Bay but was ranked second at Westham Island, where it was less preferred than marsh but more preferred than any of the terrestrial habitats (Table 3). Marsh was ranked first at Westham Island (30% of the mean home range), second at Boundary Bay (7%), and sixth at Mud Bay (4%). Crop residue, which was ranked third at Westham Island and Mud Bay (4 and 5% of the mean home range, respectively), was ranked seventh at Boundary Bay (2%). Pasture was ranked second at Mud Bay (10% of the mean home range), third at Boundary Bay (6%), and only seventh at Westham Island (3%).

We used an alternate test of regional habitat selection within restricted site-specific study areas to determine whether regional selection simply may have arisen as a result of differences in habitat availability among sites. Regional habitat use determined by radio locations was nonrandom

Table 3. Rank order (1 to 12) of habitats within dunlin home ranges as determined from dunlin radio locations in the Fraser River delta, British Columbia, Canada. Sample sizes (number of dunlin) are in parentheses. Ranks that share a letter are not statistically different from each other ($P > 0.05$).

	Mudflat	Marsh	Bare	Crop residue	Grassy/ unknown	Pasture	Winter cover	Residual
Available:	1	5	6	7	2	4	8	3
Home ranges:								
Overall (30)	1 - A	2 - B	5 - CD	3 - B	7 - E	4 - BC	6 - DE	8 - F
Male (13)	1 - A	4 - BC	5 - BC	2 - B	6 - BC	3 - BC	7 - CD	8 - D
Female (15)	1 - A	2 - B	5 - CD	3 - B	7 - D	4 - BC	6 - CD	8 - E
Westham Island (6)	2 - B	1 - A	5 - C	3 - C	6 - D	7 - D	4 - C	8 - E
Boundary Bay (8)	1 - A	2 - BC	4 - BC	7 - C	5 - BC	3 - BC	8 - C	6 - BC
Mud Bay (16)	1 - A	6 - D	5 - D	3 - C	7 - D	2 - B	4 - D	8 - E
Radio locations:								
Overall (30)	1 - A	2 - B	8 - D	6 - CD	4 - CD	3 - BC	7 - D	5 - CD
Westham Island (6)	2 - B	1 - A	3 - BC	6 - C	7 - C	5 - C	8 - C	4 - C
Boundary Bay (8)	1 - A	2 - AB	5 - BC	7 - BC	3 - BC	6 - BC	4 - BC	8 - C
Mud Bay (16)	1 - A	3 - BC	8 - E	6 - CDE	5 - CD	2 - B	7 - DE	4 - BC

Table 4. Results of multivariate analysis of variance randomizations testing for regional and local habitat selection among sex and site categories of dunlin in the Fraser River delta, British Columbia, Canada. Regional selection was determined from the proportions of habitats within the home range, and availability from the proportions of habitats within the entire study area. Local selection was determined from the mean proportion of radio locations within each habitat, and availability from the proportion of each habitat within each home range.

Scale	Group	λ	*F*	df	*P*-value full model	*P*-value reduced model
Regional:	Sex	0.40	3.4	7, 16	0.11	0.01
	Site	0.03	11.4	14, 32	<0.001	<0.001
	Interaction	0.31	1.8	14, 32	0.16	
Local:	Sex	0.81	0.5	7, 16	0.80	0.51
	Site	0.19	3.0	14, 32	0.006	0.002
	Interaction	0.30	1.9	14, 32	0.08	

whether we used our entire study area (λ = 0.05, $F_{7,23}$ = 64.4; 95% CI of *F*-statistic [bootstrap sample] = 43.2 to 5,006.1; P < 0.001) or site-specific availability designations (λ = 0.05, $F_{6,24}$ = 74.0; 95% CI of *F*-statistic [bootstrap sample] = 52.0 to 1,359.8; P < 0.001).

Local Habitat Preferences

Local habitat use by dunlin was nonrandom (λ = 0.07, $F_{7,23}$ = 45.5; 95% CI of *F*-statistic [bootstrap sample] = 29.8 to 467.2; P < 0.001). Seventy-two percent of the locations were recorded on mudflat (Table 2), which was preferred over all of the other habitats (Table 3). Marsh, which was ranked second with 14% of the locations, was preferred over all of the terrestrial habitats except pasture, which was ranked third with 7% of locations. The remaining terrestrial habitats each held 3% of the locations or fewer, and were used interchangeably by dunlin.

We found a significant interaction between sex and site in habitat selection (Table 4) due to differences among the groups in the selection of terrestrial habitats. We found no consistent pattern of differences between the sexes among sites, and sex itself was not a statistically significant factor either before or after removal of the interaction term from the model. We will not discuss these patterns here, except to say that they highlight variability in the ranking of terrestrial habitats. We found no effect of age on local habitat preferences when tested with sex (λ = 0.29, $F_{7,5}$ = 1.7, P = 0.26).

Local habitat selection differed among the 3 banding sites (Table 4). Mudflat made up 40% of the locations at Westham Island, 69% at Boundary Bay, and 85% at Mud Bay (Table 2). Mudflat was ranked first at Mud Bay, where it was preferred over all other habitats (Table 3). It was also ranked first at Boundary Bay, but it was not preferred over marsh, which was ranked second and made up 9% of locations. Mudflat and marsh together were preferred over all of the terrestrial habitats (Table 3). Mudflat was ranked second at Westham Island, where it was less preferred than marsh (51% of locations) but more preferred than any of the terrestrial habitats except bare field, which ranked third. Bare field was the only terrestrial habitat that was preferred in relation to the others at Westham Island. At Boundary Bay, residual was ranked last, but no preferences were shown among the remaining terrestrial habitats. Pasture was ranked second at Mud Bay (9% of locations) and did not differ from marsh (which was ranked third with 3% of locations), but was preferred over grassy/unknown, crop residue, winter cover, and bare habitats.

DISCUSSION

Overall Habitat Preferences

Dunlin in the Fraser River delta showed a significant preference for marine habitats at both regional and local scales. However, most individuals (>80%) also used terrestrial habitats (Table 2), usually during high tide and primarily at night. Dunlin use of the terrestrial habitats previously had been underestimated because these habitats are used far more at night than during the day. Patterns of preference for these habitats differed somewhat between sexes and among dunlin from different sites in the delta, but we detected no differences between age classes.

Intertidal mudflat habitat ranked first and was preferred over all other habitats, both regionally and locally (Table 3). Mudflats in the Fraser River delta support high densities of invertebrate shorebird prey (Shepherd 2001*b*, McEwan and Farr 1986, Baldwin and Lovvorn 1994). More than 65% of the average dunlin's daily winter foraging time (15.7 hr) was spent in marine habitat, primarily mudflat (Shepherd 2001*b*), and marine food items made up approximately 70% of their diet (Evans-Ogden 2002). In a related study of the same dunlin population, Shepherd (2001*b*) found that invertebrate prey density accounted for differences in space-use patterns. Marine home-range size decreased as marine invertebrate prey density within the home range increased, with prey density accounting for 63% of the variance in range size (Shepherd 2001*b*).

Mudflat habitat also likely has the lowest diurnal risk of predation of all habitats in the Fraser River delta. Open mudflats offer the best visual horizon for observing the approach of avian predators (Whitfield 1985), and early warning of an attack has been shown to decrease a shorebird's likelihood of mortality (Page and Whitacre 1975, Cresswell 1996, Hötker 2000). Peregrine falcons (*Falco peregrinus*) hunting dunlin in the Fraser River delta were successful on 33% of 15 surprise attacks and only 8% of 287 aerial chases (Dekker 1998, 1999).

Marsh was ranked second at both regional and local scales, although it was not preferred over pasture or crop residue habitats. Marshes provide a refuge for dunlin when mudflats are inundated at high tide. Marshes generally are farther from falcon roost sites and have fewer landscape features obstructing lines of sight than the more fragmented terrestrial habitats bounded by trees, hedgerows, and fence posts (Hötker 2000). Although marsh habitat generally may be safer than terrestrial habitat, marsh vegetation can be dense and tall, and the substrate less suitable for foraging. Individual dunlin may choose terrestrial habitats over marsh at times when they perceive themselves to be at increased risk of starvation—times when the benefits to be accrued from additional foraging opportunities outweigh the increased risk of predation (Lima 1986, Lima and Dill 1989).

For some of the dunlin wintering in the Fraser River delta, at the northern end of their core winter range, access to nearby terrestrial habitats may be required for them to meet their energy needs (Davidson and Evans 1986). On average, >60% of the time dunlin spent in terrestrial habitats was spent foraging (Shepherd 2001*b*), and terrestrial food items made up approximately 30% of the average dunlin's diet (Evans-Ogden 2002). Several other studies have asserted that alternative high-tide foraging habitats, in particular soil-based agricultural fields, are crucial to support populations of wintering shorebirds (Rottenborn 1996, Butler 1999, Dann 1999, Masero and Perez-Hurtado 2001). Lovvorn and Baldwin (1996) found that intertidal habitats with adjacent farmland supported between 75 and 94% of 4 waterfowl species wintering in the Puget Sound region, and that few sites without adjacent farmland supported significant populations. Predicted mortality rates of oystercatchers (*Haematopus ostralegus*) wintering in Britain, in an environment similar to that of the Fraser River delta, increased significantly when upshore and field foraging areas were removed from the model (Stillman et al. 2000).

Under regional selection, the soil-based agricultural crops (bare, crop residue, pasture, winter cover) were ranked above the other 2 terrestrial habitats (grassy/unknown and residual, which included greenhouses), both of which were less preferred than all but winter cover. Pasture was the only terrestrial habitat that was ranked high and preferred at both scales. Pastures in the Fraser River delta are fertilized heavily and naturally with cattle manure, and likely support higher densities of terrestrial invertebrates compared to crop fields (Fratello et al. 1989). Pasture vegetation also tends to be short, and densities of dunlin using pastures in California correlated negatively with vegetation height (Colwell and Dodd 1995, Long and Ralph 2001).

Within the terrestrial zone, dunlin preferred pasture, but they also selected a mosaic of other soil-based agricultural crops. The ability of dunlin to make use of several different habitat types does not imply that they are not dependent on a given habitat (Myers et al. 1979). In the Fraser River delta, each agricultural habitat may contain the resources to satisfy different nutritional requirements, and may also offer different trade-offs between energy intake, energy expenditure, and predation risk. Dunlin may select among agricultural habitats based on their body's internal state at a given moment and may prefer a range of different habitats through time.

The patterns of dunlin terrestrial habitat selection in our study may have been influenced by factors other than ground cover. The mean size of fields used by dunlin was 50% larger than the mean size of available fields, perhaps because larger fields provide more open space and therefore allow for greater advance warning of an approaching predator. The selection of terrestrial habitats also may have been influenced by factors such as standing water levels and proximity to roads, as well as by the history of land use in each habitat block. For example, a bare field that previously had been fallow and recently had been plowed under might be more attractive than one that had been intensely cultivated in recent years. Future studies will hopefully address these issues and determine whether any of these factors significantly influence dunlin habitat preferences.

Sex-specific Habitat Preferences

Male and female dunlin differed in their regional habitat preferences. Females were more selective in their choice of habitats, exhibiting more statistically significant preferences between habitat ranks. Females also had more marsh habitat in their home ranges than males, perhaps because females were more likely to be located in marine than in terrestrial habitats (Shepherd 2001*b*, Shepherd et al. 2001).

Site-specific Habitat Preferences

Both regional and local habitat selection differed among dunlin from different sites within our study area. Boundary Bay and Mud Bay dunlin preferred mudflat to all other habitats, but Westham Island birds ranked mudflat second to marsh (Table 3). Regionally, the Westham Island dunlins' preference for marsh over mudflat can be explained in part by the greater proportion of marsh habitat at Westham Island compared to the other 2 sites (Table 2, Fig. 1), and because the available proportion of marsh (against which use was measured) was calculated over our entire study area. Similarly, the low regional ranking of marsh habitat by Mud Bay dunlin likely was due to low availability. Locally, the Westham Island dunlins' preference for marsh over mudflat may be due to tide-related differences in habitat availability. The tidal regime in the Fraser River delta is such that the mudflat habitat on Roberts' bank (the Westham Island area) is submerged approximately 1 to 2 hr longer than the mudflat habitat in Boundary and Mud Bays.

We found considerable variation in the site-specific ranking of terrestrial habitats both among sites and between scales, and many of the habitats that ranked high were not significantly preferred over those ranked low. This is consistent with our hypothesis that dunlin selected a mosaic of soil-based agricultural crops, however, the observed variation possibly was due in part to our fairly small sample of dunlin ($n = 30$), especially when broken down by site ($n = 6$, 8, and 16). In addition, we examined 8 habitat categories, some of which were available in small proportions (Table 2).

MANAGEMENT IMPLICATIONS

Although agriculture often is detrimental to native flora and fauna, many coastal areas already have been altered for agricultural use, and soil-based agricultural habitats are among those that can be considered suitable for dunlin and other wintering shorebirds. We recommend that managers promote the maintenance of a mosaic of soil-based agricultural crops, with a particular emphasis on naturally fertilized pastures, in the Fraser River delta and similar coastal ecosystems. Maintaining diversity in agro-ecosystems may be the key to maintaining diverse and stable populations of wintering birds, as well as other taxa (Vandermeer and Perfecto 1997). The stability of the Fraser River delta dunlin population may be related to the availability of a mosaic of soil-based agricultural crops adjacent to dunlin's preferred mudflat habitats.

We also recommend that field fragmentation be kept to a minimum since dunlin preferred larger fields, likely in response to predation risk. Industrial greenhouse operations recently have proliferated in the Fraser River delta, from 101 ha (1.4% of the soil-based agricultural land) to 154 ha (2.1%) in <2 years (City of Ladner, Corporation of Delta, unpublished data). Large-scale greenhouses are permitted under a British Columbia provincial government Agricultural Land Reserve policy that governs these areas; however, these greenhouses eliminate habitat previously available to wildlife and fragment remaining habitat. These data have been provided to policy makers responsible for land use planning in the area and hopefully will be considered.

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