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Lesley Joan Evans Ogden[1], *Keith A. Hobson*[2], *David B. Lank*[3], *and* *Shabtai Bittman*[4]

ABSTRACT. Although shorebirds spending the winter in temperate areas frequently use estuarine and supratidal (upland) feeding habitats, the relative contribution of each habitat to individual diets has not been directly quantified. We quantified the proportional use that *Calidris alpina pacifica* (Dunlin) made of estuarine vs. terrestrial farmland resources on the Fraser River Delta, British Columbia, using stable isotope analysis (δ13C, δ15N) of blood from 268 Dunlin over four winters, 1997 through 2000. We tested for individual, age, sex, morphological, seasonal, and weather-related differences in dietary sources. Based on single- (δ13C) and dual-isotope mixing models, the agricultural habitat contributed approximately 38%

hivers), le reste provenant de la zone intertidale. Toutefois, d'importantes variations ont été notées entre individus, la proportion d'alimentation en milieu agricole représentant de 1 % à 95 % de leur diète. Chez les jeunes oiseaux, l'apport alimentaire terrestre (43 %) était beaucoup plus élevé que chez les adultes (35 %). Nous avons estimé que chez 6 % des adultes et 13 % des juvéniles obtenaient au moins 75 % de leur régime alimentaire de source terrestre. Les données isotopiques n'ont révélé aucune corrélation entre le sexe et la taille corporelle générale et la proportion du régime alimentaire provenant de source terrestre. L'utilisation de l'habitat agricole par le Bécasseau variable a culminé au début de janvier. Les adultes ont obtenu une plus grande proportion de leur apport alimentaire en milieu terrestre pendant les périodes plus froides avec de fortes précipitations, tandis que cette relation n'était pas observée chez les juvéniles. Les variations saisonnières en matière d'utilisation des habitats agricoles suggèrent qu'ils sont utilisés plus intensivement durant les périodes de stress énergétique. Les zones agricoles terrestres semblent avoir une importance constante comme habitat pour les juvéniles, tandis qu'elles représentent des lieux d'alimentation alternatifs pour les adultes et fournissent un apport alimentaire d'urgence lorsque les conditions météorologiques sont extrêmes. La perte ou la réduction des habitats agricoles adjacents aux estuaires pourraient avoir un effet négatif sur la condition des oiseaux limicoles, les juvéniles étant touchés de façon disproportionnée.

Key Words: *carbon-13, nitrogen-15, shorebirds, non-breeding ecology, supratidal habitat use, Calidris alpina pacifica, diet*

INTRODUCTION

Conservation of increasingly threatened coastal habitats has been identified as a key strategy for stemming the population declines currently seen in many species of North American shorebirds (Brown et al. 2001, Donaldson et al. 2001). In shorebirds, most adult mortality takes place during migration or on the wintering grounds, and, given their

METHODS

Study area

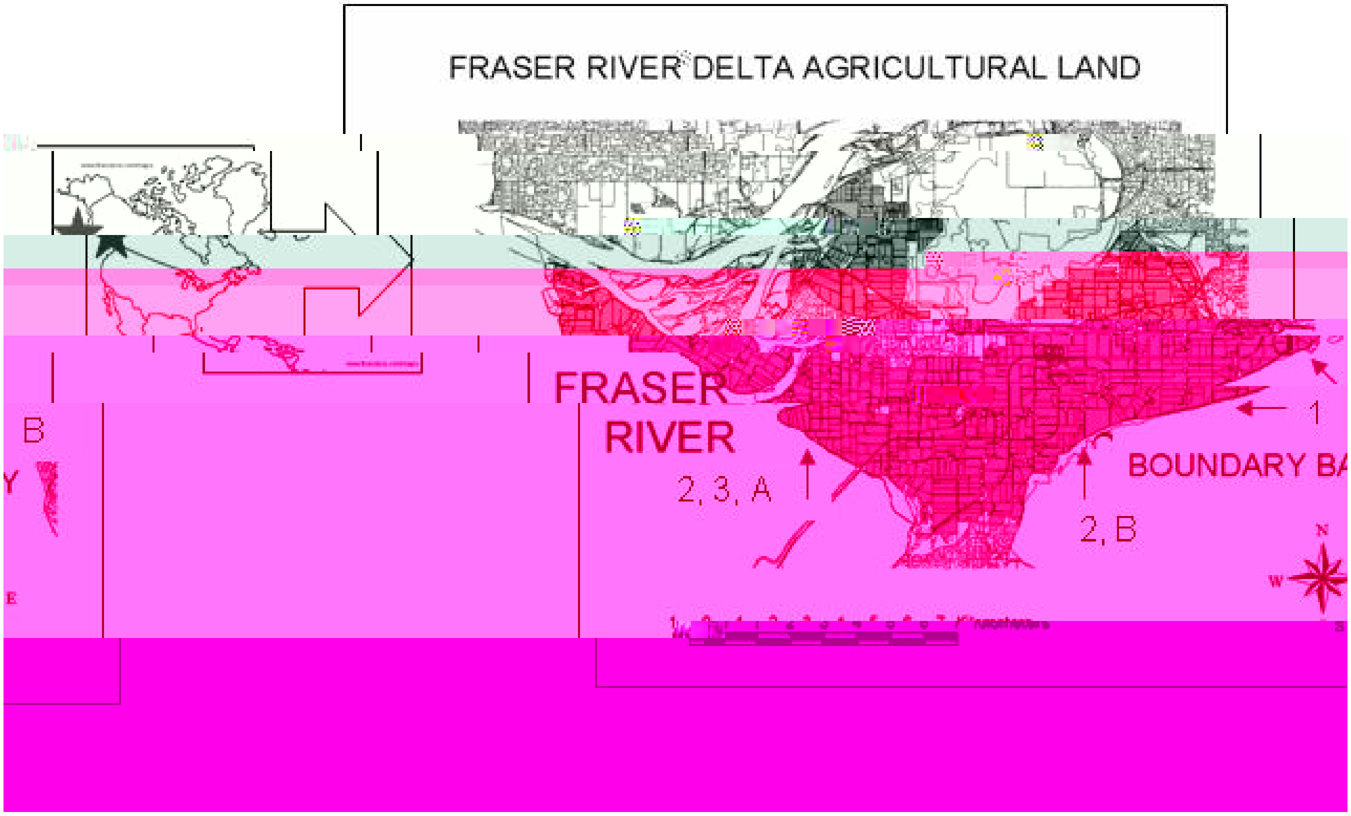
As seen in Fig. 1, the intertidal flats of the Fraser Delta (49°10'N, 123°05'W), the largest estuary on Canada's west coast, provide habitat for internationally significant numbers of migrating and overwintering shorebirds, waterfowl, and raptors (Butler and Campbell 1987). Dunlin are the most numerous shorebird species overwintering in the delta, with an average winter population size of 30,000 (Butler 1994). Dunlin begin to arrive in the delta as early as July, but most of them arrive at the beginning of October (Evans Ogden 2002) and are thereafter highly site-faithful residents until their departure in April (Shepherd 2001). The delta consists of approximately 257 km^2 of intertidal flat adjacent to approximately 127 km^2 of land farmed since the late 1800s, when natural salt marshes were diked and converted to agricultural use. Farmland consists of a mosaic of fields, including bare earth with or without crop stubble; cover crops such as winter wheat; perennial grasses; winter vegetable crops such as cabbage; and berry crops. The delta has a semidiurnal mixed tidal regime, and tide levels in part drive the timing of use of estuarine vs. adjacent agricultural habitats. The terrestrial habitat is used particularly during high tides, which in winter can inundate the entire surface area of intertidal flat. However, a radio telemetry study recently elucidated extensive nocturnal foraging activity in fields during winter (Shepherd and Lank 2004), when tides are significantly lower than during the day, thus suggesting that abiotic and/or biotic factors other than tidal variation are also involved.

Bird capture and sampling

Two hundred and eighty-six Dunlin were captured between October and April over the winters of 1997–1998 through 1999–2000, and in November 2000, using mistnets and a floating clap net (L. J. Evans Ogden, *unpublished data*) placed around the Fraser Delta (Fig. 1). In 1997–1998, birds were captured at night in agricultural fields adjacent to the coastal intertidal flats. However, low densities of Dunlin in these fields resulted in low capture success and a small sample size, and in 1998–1999, birds were captured in fields and at two locations on the intertidal flats of Boundary Bay (49° 00’N, 123°0 ’W) and Brunswick Point, (49°03’N, 123° 01’W). In 1999–2000, all birds were captured on the intertidal flats at Brunswick Point. Birds were captured within 3 h of high tide, usually on an ebbing tide, during the hours of darkness, which varied seasonally between 1600 and 0800 PST. We did not conduct a full season of sampling in 2000–2001, but include here Dunlin captured on two dates in November 2000 for which blood samples were taken prior to an experimental study of these individuals in captivity (Evans Ogden et al. 2004).

We measured length of culmen, tarsus, and wing chord; aged birds as juvenile, i.e., in their first year of life, or adult using plumage characteristics (Warnock and Gill 1996); determined mass; and extracted a 300-µL blood sample from the brachial vein of each bird. A sufficient volume of blood for isotope analysis was obtained from 268 of the 286 captured birds. Culmen length was measured from bill tip to the margin between the mandible and feathers at the center of the upper mandible. Tarsus was measured from between the second toe to the tarsal-tibia joint, with the leg held so that the tarsus was perpendicular to the tibia. Wing chord was measured as the flattened length of the longest primary feather. We used whole blood, which provided an indication of diet source integrated over a time window of at least 21 ± 1 d or two half lives, based on laboratory studies of captive Dunlin to determine turnover times of ^{13}C and ^{15}N (Evans Ogden et al. 2004). To ensure that all Dunlin would have isotopic signatures indicative of their winter diet and retain no residual signature from their summer breeding grounds, Dunlin captured prior to 24 November were excluded from our analyses.

Fig. 1. Agricultural lands in the Fraser River Delta (gray shading). Arrows indicate locations of Dunlin capture and invertebrate sampling. Numbers indicate year of sampling for Dunlin commencing 1997–1998. Letters indicate type of invertebrates sampled: A = terrestrial invertebrates, B = estuarine invertebrates.



This method is ideally suited to this study, because it provides time-integrated insights into winter diet and because many Dunlin prey are soft-bodied organisms (e.g., Warnock and Gill 1996) that are quickly digested and therefore difficult or impossible to detect in dissected stomachs or feces (e.g., Duffy and Jackson 1986). Some previous studies using this technique have raised concerns regarding the metabolic routing of nutrients, in that isotope analysis of tissues provides relatively good

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Fig. 2. Isotopic values (mean ± SD $\delta^{15}N$ and $\delta^{13}C$) for Dunlin whole blood (all years combined, *n* = 268), estuarine invertebrates (*n* = 21 samples), and terrestrial invertebrates (*n* = 16 samples). End points illustrated here are raw values and are not corrected by known fractionation factors. Samples of scoter (*n* = 5) and American robin (*n* = 5) are muscle tissue.

Table 1. Isotopic values for estuarine and terrestrial invertebrate samples of Dunlin prey species.

Location	Species sampled	*N*	$\delta^{15}N$(‰)Mean SD		$\delta^{13}C$ (‰)Mean SD	
Estuarine	Clam (*Macoma* sp., *Mya* sp.)	4†	9.75	(2.73)	-17.21	(3.53)
	Snails (*Bittium* sp.)	8	9.90	(1.50)	-11.00	(1.67)
	Polychaete annelids	9‡	12.38	(0.79)	-15.19	(1.88)
	Total	21	10.94	(1.95)	-13.98	(3.25)
Terrestrial	Earthworm (*L-umbricusolychaete an-*					

Table 2. Proportions of Dunlin diet from terrestrial and estuarine sources as calculated with the two-isotope and single-isotope mixing models.

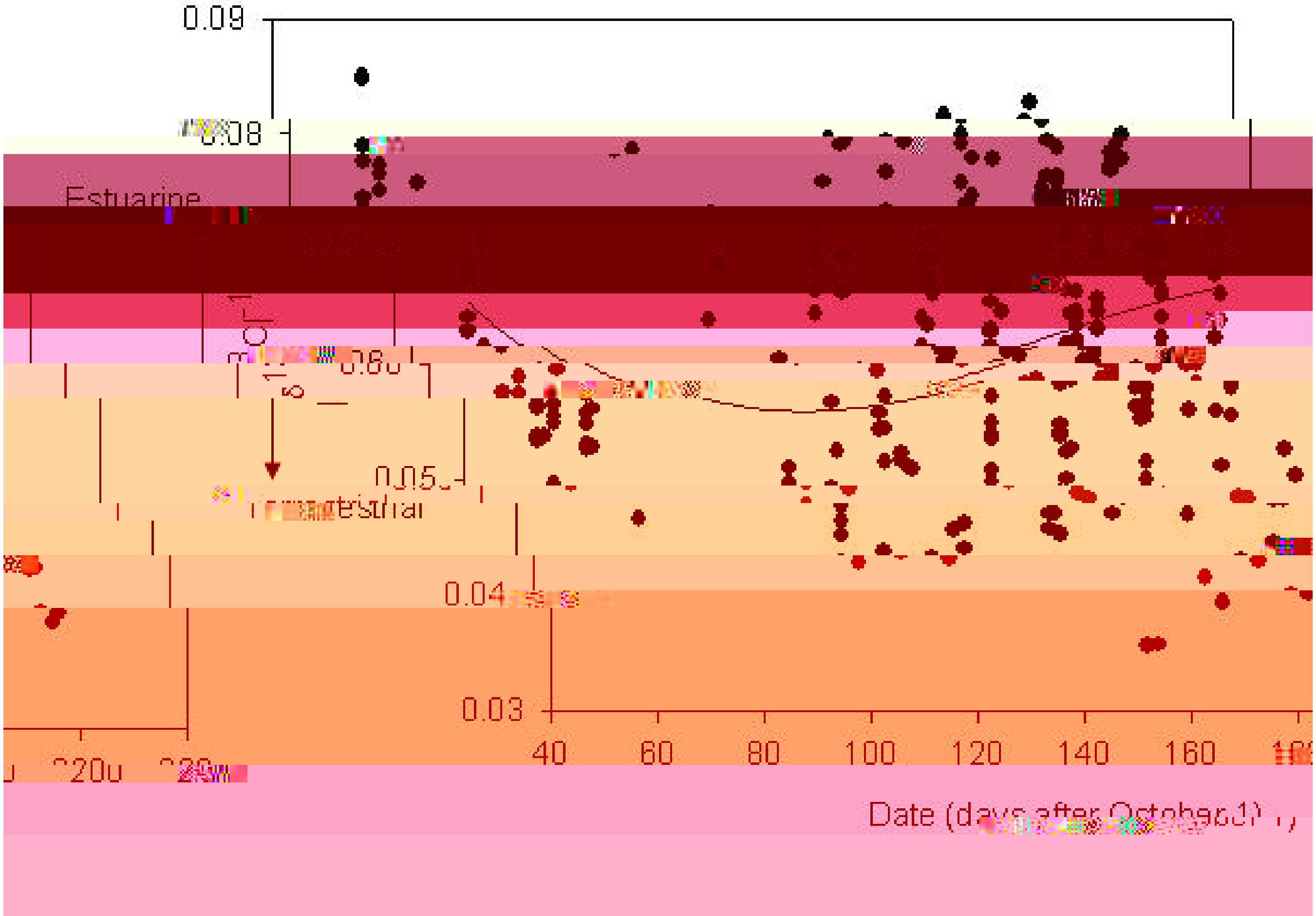
Year and capture site	Sample size	Mean $\delta^{13}C$ value (‰)	Mean $\delta^{15}N$ value (‰)	Terrestrial % of diet†	95% Confidence intervals†	Terrestrial % of diet‡	Standard deviation‡	Minimum terrestrial % of diet‡	Maximum terrestrial % of diet‡
2000-2001 BP shore	31	-15.32	12.32	0.28	0.17–0.40	0.30	2.38	0.01	0.69
1999-2000 BP shore	181	-16.30	11.85	0.36	0.26–0.46	0.37	0.23	0.06	0.95
1998-1999 BB shore	8	-19.02	12.56	0.59	0.42–0.77	0.54	0.20	0.28	0.89
1998-1999 BB field	25	-16.94	13.70	0.41	0.32–0.50	0.38	0.10	0.23	0.68
1998-1999 BP field	11	-18.05	11.78	0.51	0.42–0.60	0.50	0.16	0.10	0.78
1997-1998 BB field	12	-19.67§	12.62	0.64	0.51–0.77	0.58	0.17	0.35	0.87
Average 1997-2000	268	-16.54	12.13	0.38	0.29–0.47	0.38	0.22	0.01	0.95

†Single-isotope ($\delta^{13}C$) model.
‡Dual-isotope model.
§Significantly different (*P*P

Seasonal patterns

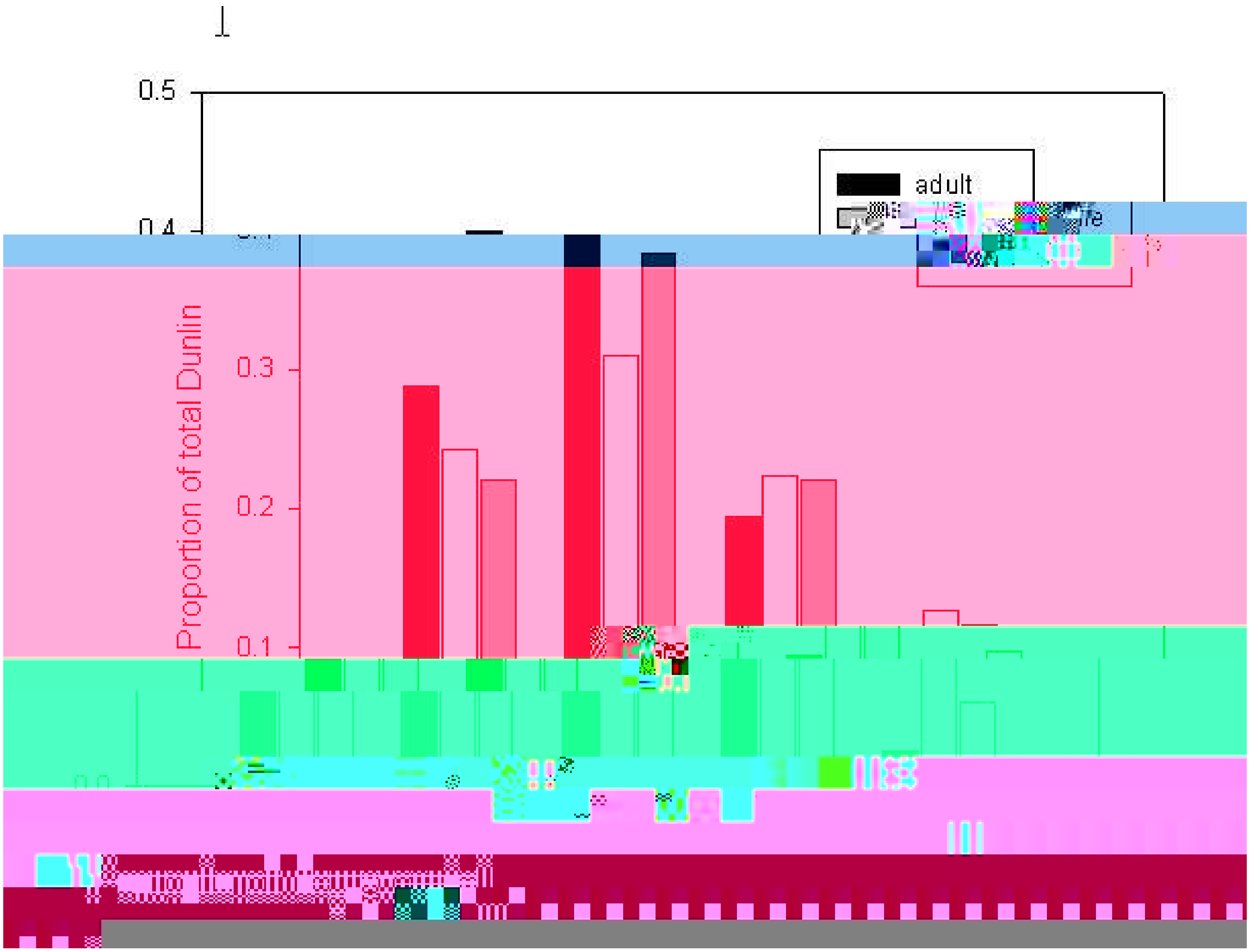
Although terrestrial habitat was a dietary contributor throughout the winter, the proportion of Dunlin diet from fields shifted seasonally. Field contribution to diet rose during autumn, peaked in early winter, and declined through the remainder of the season (Fig. 3). Although statistically significant, the r^2 value was low (0.09), and thus the

Fig. 3. Cubic regression fit for date versus predicted relative contribution of terrestrial diet for all Dunlin sampled over four winters. The predictive equation is: $y = 0.1070 - 0.0012x + 0.0000084x^2 + 0.000000018x^3$, $r^2 = 0.091$, $P = < 0.0001$. The Y-axis represents a transformation of $\delta^{13}C$ data ($|\delta^{13}C|^{-1}$) and is an index of relative use of each ecosystem (estuarine versus terrestrial) in Dunlin diet. [See Erratum]



bills feed disproportionately more in terrestrial habitat. In least and western sandpipers *Calidris minutilla* and *C. mauri*, the ability to evade predators via escape flight differs by sex because of sex-related differences in wing shape and wing-loading (Burns and Ydenberg 2002). Females, who are larger, have enhanced escape performance compared with males. If female Dunlin possess a similar superiority in escape performance, we predicted a male-biased predation risk in the terrestrial habitat producing a sex bias toward females. However, our data did not support this prediction. Previous shorebird studies that have looked for sex differences in winter field use have found a male bias (Townshend 1981, Warnock et al. 1995). An additional study of a sample of Dunlin killed by strychnine-poisoned grain in fields of the Central Valley of California indirectly suggested that males feed disproportionately in fields (Warnock and Schwarzbach 1995).

Fig. 4. Frequency distribution of percentage of diet derived from fields for all Dunlin (1997–2000) and by age class (1998–2000). Frequencies represent the proportion of individuals from within that age class. Proportion of diet terrestrial based on two-isotope model calculations.

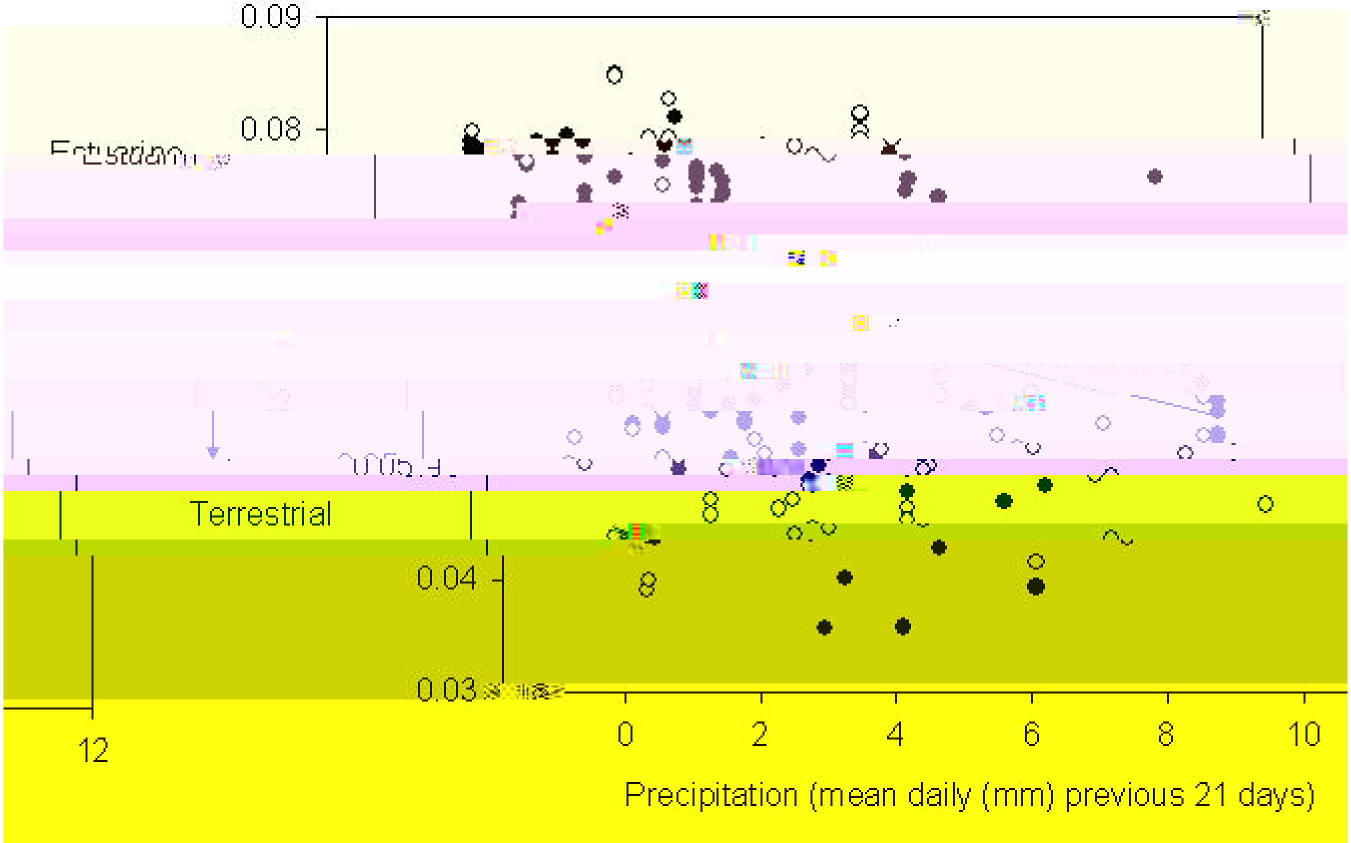


Age differences

The most common interpretation of field feeding by shorebirds has been that birds mainly feed in terrestrial habitat when they cannot meet their energy requirements solely from intertidal flat feeding (Goss-Custard 1969, Heppleston 1971). We found age differences in habitat use, with juveniles deriving an average of approximately 43.2 ± 24% of their diet from terrestrial habitat, as compared with 34.5 ± 20% for adults, throughout the winter. This suggests differential starvation-predation risk trade-offs with respect to age classes. In several shorebird species, juveniles appear to be less efficient foragers than adults (Groves 1978, Goss-Custard and Le V. dit Durell 1987, Marchetti and

Fig. 5. Relative use of fields (as represented by transformed $\delta^{13}C$ values) and mean minimum temperature for previous 21-d period, separated by age class, adults represented by black filled circles, juveniles by open circles. The Y-axis represents a transformation of $\delta^{13}C$ data ($|\delta^{13}C|^{-1}$) and is an index of relative use of each ecosystem (estuarine versus terrestrial) in Dunlin diet. The linear regression line of significantly increasing field use with declining temperature is shown in black for adults. The trend line shown for juveniles (dotted line) is for comparison only and is not significant. [See Erratum]

Fig. 6. Relative use of fields (as represented by transformed δ^{13}C values) and mean total precipitation for previous 21-d period, separated by age class, adults represented by black filled circles, juveniles by open circles. The Y-axis represents a transformation of δ^{13}C data ($|\delta^{13}C|^{-1}$) and is an index of relative use of each ecosystem (estuarine versus terrestrial) in Dunlin diet. ASY refers to after-second-year birds, and SY to second-year birds. The linear regression line of significantly increasing field use with increasing precipitation is shown in black for adults. The dotted line shown for juveniles is for comparison only and is not significant. [See Erratum]



Cresswell (1994) determined that juvenile Redshank foraged in habitat that maximized their prey intake rate at the expense of increased predation risk as a result of their higher risk of starvation in comparison with adults. Dierschke (1998) determined that, during migratory stopover, juvenile Dunlin fed in habitats that were more profitable in terms of food resources, but of higher risk of predation, whereas adults chose safer habitats. Similary, Warnock (1990) found that juvenile Dunlin fed disproportionately more than adults in riskier habitats. We did not quantify prey abundance, availability, or profitability in either estuarine or terrestrial habitats, but suspect that juveniles are forced to feed in a riskier habitat because they need to spend longer feeding each day than adults do to balance their energy budgets, thus requiring increased use of fields when intertidal foraging habitat is unavailable. Our findings suggest that, in the absence of fields, juvenile survivorship at this site might decline at a faster rate than that of adults.

Effects of weather

In our study area, juveniles regularly used terrestrial habitat, but adults used terrestrial habitat to a greater extent during colder periods, when their energy demands and the risk of mud flats and fields freezing over were higher. Increased adult use of fields during periods of greater precipitation may be related to the availability of prey, which probably decreases on the intertidal flat while concurrently increasing in fields (Gerstenberg 1979, Heitmeyer et al. 1989, Warnock 1994, Colwell and Dodd 1997). Increased use of fields during winter rains has been reported previously for Dunlin in California (Warnock et al. 1995). Increased field use may also result from an overall increase in time spent feeding during rain (Kelly and Weathers 2002). In Scotland, Heppleston (1971) determined that, under severe weather conditions, juvenile oystercatchers (*Haematopus ostralegus occidentalis*), feeding at slightly lower rates than adults, were unable to compensate for the food deficit incurred, resulting in higher mortality. Our data suggest that the terrestrial habitat provides an important buffer against starvation for adult Dunlin, especially during periods of extreme weather. With models of global climate change predicting increasingly severe weather extremes such as exceptionally low temperatures and more frequent intense precipitation events (Easterling et al. 2000), terrestrial habitats adjacent to estuaries may become increasingly important for wintering shorebird populations.

CONCLUSION

Given its close proximity to Vancouver, one of the fastest growing cities in North America, the Fraser Delta will almost certainly face increasing development pressure on it terrestrial landscape in coming decades. Loss of farmland as a result of the expansion of greenhouse agriculture and urban development may adversely affect the fitness of nonbreeding Dunlin, particularly juveniles. Models developed for Oystercatchers in the UK predict that shorebirds in estuaries lacking adjacent agricultural fields have a higher winter mortality rate than do those in estuaries with fields (Stillman et al. 2001). The Fraser Delta is, in fact, the northernmost site in which significant numbers (> 10,000) of Dunlin overwinter (Butler and Campbell 1987), and adjacent farmland may be contributing substantially to the estuary’s ability to support su,m-253.8(su,mp5174.53.8nmiat3.8(su,1l)t [( )1-93(Fn)o4.8(n93ict)8(n93iK

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