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ENVIRONMENTAL AND HABITAT CORRELATES OF PASTURE USE BY NONBREEDING SHOREBIRDS[1]

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Abstract. Throughout coastal regions of the world, pasturelands often augment important and declining intertidal foraging habitats for nonbreeding shorebirds (Suborder Charadrii). Little is known, however, about factors influencing bird use of pastures. Hence, we examined the spatial distribution of shorebirds in coastal pastures near Humboldt Bay, California from October 1991–May 1992 and correlated spatial distribution patterns with environmental and habitat variables. Shorebirds used pastures in a nonrandom (clumped) fashion. Pasture use varied seasonally for Killdeer (*Charadrius vociferus*), Marbled Godwit (*Limosa fedoa*), and Common Snipe (*Gallinago gallinago*); Dunlin (*Calidris alpina*) and Black-bellied Plover (*Pluvialis squatarola*) use increased when it rained, and Dunlin, Black-bellied Plover, and Killdeer use increased nearer the time of a new moon. At the level of the individual pasture, the likelihood of encountering most species (5 of 6) increased as vegetation height decreased. The likelihood of pasture use by Dunlin and Killdeer increased when shorebirds used pastures the previous week. Extensive, nonrandom use of coastal pastures by nonbreeding shorebirds indicates that conservation planning for shorebirds should consider habitat characteristics. In the vicinity of Humboldt Bay and other coastal bays, use of pastures by shorebirds can be increased by practices that provide short vegetation. Although shorebird use did not correlate with use of pastures by cattle, grazing by livestock is probably the means by which to achieve habitat characteristics attractive to shorebirds while maintaining compatible human uses on private lands. Regular use of some pastures by shorebirds indicates that site faithfulness may be important and that "traditional" sites need to be identified and protected.

Key words: shorebirds, Charadrii, pastures, spatial distribution, logistic regression, bird-habitat relationships, vegetation height.

INTRODUCTION

The value of coastal pastures to nonbreeding waterbirds is well known (Townshend 1981, Goss-Custard and Durell 1983, Colwell and Dodd 1995), especially in areas where intertidal habitats have been mostly "reclaimed" by humans. In coastal areas, loss of important intertidal foraging habitats has been partially offset by agricultural land use practices, which provide habitats for waterbirds, especially shorebirds (suborder Charadrii). Although the importance of pasturelands to nonbreeding shorebirds is widely recognized, little is known about environmental and habitat features associated with shorebird distributions in these habitats. Several studies have demonstrated that nonbreeding shorebirds frequent short-vegetation pastures (Fuller and Youngman 1979, Milson et al. 1985, Colwell and Dodd 1995), presumably because prey are easier to capture and/or predator vigilance is facilitated by short vegetation. It also has been suggested that some waterbirds associate with livestock because of foraging benefits (Thompson et al. 1982, Colwell and Dodd 1995). For some waterbirds, pasture use has been shown to increase when standing water is present (Colwell and Dodd 1995). However, less is known about environmental conditions and habitat characteristics associated with pasture use by shorebirds.

Elsewhere, we showed that a waterbird community numerically dominated by shorebirds had greater species richness and densities of most species in grazed pastures with short vegetation (Colwell and Dodd 1995). However, waterbird species did not respond uniformly to short vegetation. Here, we expand our analysis of variables influencing shorebird use of pastures to encompass environmental conditions prevailing at the time of use, as well as habitat characteristics of pastures themselves. Our objectives are to: (1) examine the spatial distribution of shorebirds within coastal pastures of northern California adjacent to important nonbreeding habitats (Colwell 1994), and (2) eval-

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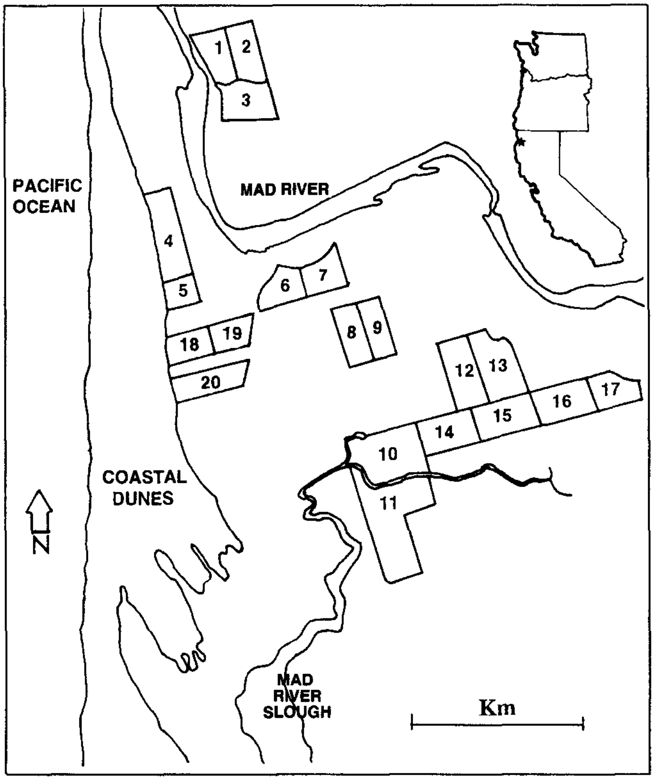

FIGURE 1. Location of 20 pasture plots within the larger study area in northern California.

uate the relative contributions of variables explaining nonrandom shorebird distributions. We include in our analysis variables representing site faithfulness of birds to pastures in order to understand whether or not birds use pastures consistently, at least over short periods of time. Finally, we discuss conservation implications of our findings, focusing on bird-habitat relationships that can be manipulated.

METHODS

STUDY AREA

We studied shorebirds in coastal pastures located between the Mad River Slough of Humboldt Bay and the Mad River estuary in northern California (40°5′ N, 124°0′ W; Fig. 1). Much of this area was coastal salt marsh, but humans converted intertidal habitats to pastures nearly a century ago (Haynes 1986); these pastures are currently grazed year-round by cattle (*Bos taurus*). Within the larger study area defined by Figure 1, we examined shorebird use of 20 pastures varying in size from 2.3–13.6 ha. We selected these study plots because cooperative landowners permitted access for research; hence, the study plots are not a random sample and may not be representative of local pasture habitats. Colwell and Dodd (1995) provide a complete description of the area.

BIRD SURVEYS

Each week from 1 October 1991 to 1 May 1992, we collected data on shorebird distribution within pastures in two ways. First, during weekly surveys (see below), we recorded opportunistically the location (± 100 m) and number of shorebirds observed on the ground. Second, on each of the 20 pasture plots we surveyed shorebirds weekly by scan sampling (Altmann 1974) during daylight hours, beginning surveys within 2 hours of mean high tide for Humboldt Bay. Compared with intertidal habitats (Colwell 1993, 1994), pastures appear to be supplemental feeding sites used by shorebirds during high tides (Hoff 1979), especially during winter. We used 8.5 × 44 mm binoculars and a 22× spotting scope to survey each pasture from the same location 1 m outside a perimeter fence, although on some occasions we surveyed at greater distances if we thought birds would be frightened by our presence. Surveys lasted the time required to scan pastures and record data on species, their abundances, and behaviors (not presented in this article). After each survey, we walked a zig-zag path through each pasture to flush unseen birds (0.7% of all bird detections), which may have been hidden by vegetation.

HABITAT AND ENVIRONMENTAL MEASUREMENTS

We analyzed variables potentially influencing shorebird use of pastures at two levels—environmental and habitat (pasture) characteristics (see below). At both levels of analysis, variables varied temporally and spatially in a similar manner.

Environmental variables. Prior to each survey, we recorded the following environmental variables: (1) maximum height of high tide coincident with the survey based on National Oceanic and Atmospheric Administration (NOAA) data (Tidelogs 1991, 1992), (2) time of day (sunrise–10:00; 10:01–14:00; 14:01–sunset), (3) week of the study (1 October = week 1, 27 April = week 29), (4) moon phase (new, quarter, half, three quarters, full; ignoring waxing and waning conditions) based on NOAA data (Tidelogs 1991, 1992), (5) wind speed estimated in km hr^{-1}, (6) wind direction measured in compass bearing, (7) temperature (°C), and (8) whether or not it rained. Finally, we recorded the amount of precipitation in the 24-hr period preceding the survey date based on data collected approximately 2 km south of the study area (B. Alden, pers. comm.).

Pasture characteristics. At the start of a survey, we tallied the number of cattle using a pasture. To assess the importance of shorebird site faithfulness to pasture use, we also noted whether or not shorebirds had used a pasture the previous week. After each bird survey, we quantified vegetation height, water depth, and soil penetrability at 10 random locations within each pasture. We measured vegetation height and water depth to the nearest cm by dropping a sampling rod (3 mm diam.) vertically into the vegetation and recording maximum height at which vegetation and water contacted the rod (Colwell and Dodd 1995). We gauged the degree to which

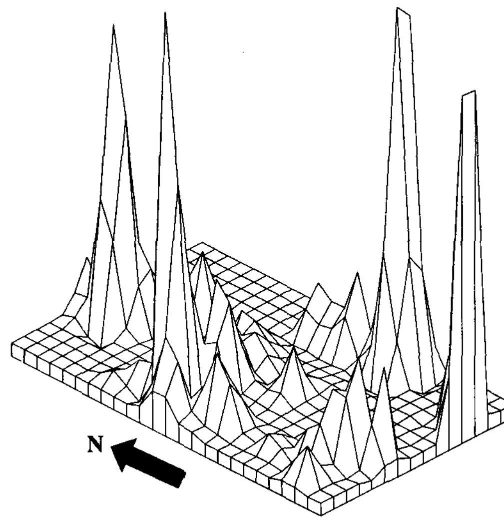

FIGURE 2. Perspective plot showing spatial variation in shorebird distribution across the larger study area. Grid cells are approximately 150 × 150 m. Data represent summed observations for the 1 October 1991 to 1 May 1992 study period.

birds could penetrate the soil with their bills using a device similar to that described by Myers et al. (1980; see Colwell and Dodd 1995 for details). We summarized habitat data by calculating means of 10 random samples from each pasture visit, yielding a single data point for each pasture per week.

DATA SUMMARY AND ANALYSIS

We examined the spatial distribution of shorebirds in two ways. First, we collated shorebird locations (x, y coordinates) for the entire study period and graphically portrayed the distribution (Fig. 2) using geostatistical methods (Rossi et al. 1992). Second, we summarized the average (± SD) density, as well as the prevalence (proportion of observations; n = 29 weeks) of shorebirds in each pasture (Fig. 3).

We used logistic regression (Glantz and Slinker 1990, Trexler and Travis 1993) to examine correlates of shorebird use (presence or absence) of pastures because most (83%) surveys yielded no shorebirds, and multiple individuals tended to occur in pastures. We based analyses on 580 observations (20 pastures surveyed each of 29 weeks), although sample sizes for analyses of environmental (n = 571) and pasture (n = 560) correlates are smaller because of missing data points. Shorebirds move to pastures from inter-

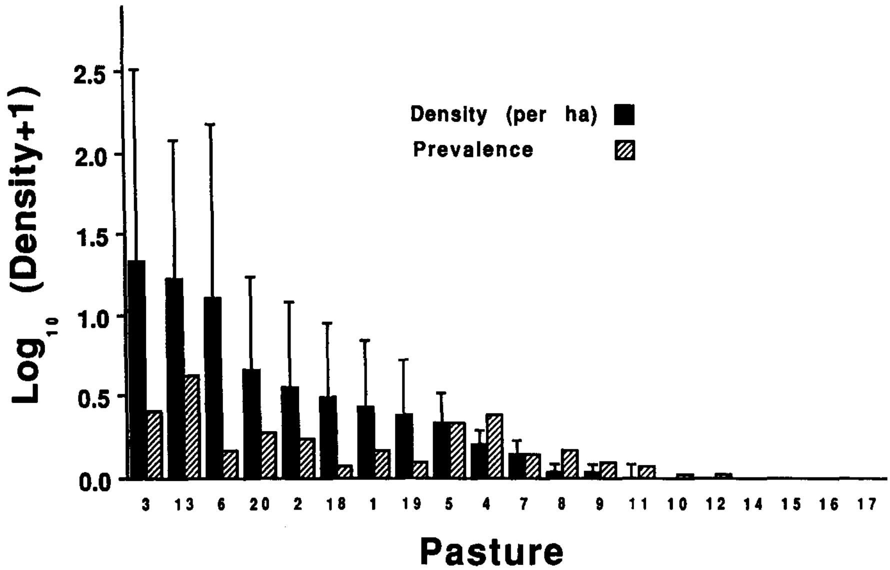

FIGURE 3. Average (± SD) shorebird density and prevalence (percent of 29 weekly observations in which shorebirds used pastures) for pasture plots. Prevalence scale (0.0–1.0) is embedded in the density scale; $n = 29$ for all data points. Pasture numbers correspond to Figure 1.

tidal habitats at least twice daily in response to rising (semi-diurnal) tides (Tidelogs 1991, 1992), hence we considered each survey of a pasture to represent an independent "choice" of habitat by birds. Additionally, to assure temporal independence of survey data collected at one week intervals, we screened the 29 weekly observations for each pasture using time series analysis (Hinze 1995), and found little evidence of autocorrelation (data available from senior author at mac3@axe.humboldt.edu).

We used stepwise forward logistic regression (Harrell 1986) to examine the relative importance of variables to pasture use by shorebirds, including only those variables explaining a significant ($P < 0.10$) amount of variation. We minimized spurious correlations with dependent variables by stopping model building when χ^2(Wald)-statistic for testing all variables jointly (residual χ^2) had a P-value exceeding 0.10 (Harrell 1986). We used the fraction of concordant pairs of observations, including one-half the number of tied pairs, to evaluate each logistic regression model, which is considered more reliable than a classification table for assessing the predictive ability of the model (Harrell 1986).

RESULTS

Within the larger study area, we recorded 28,099 shorebird sightings, 8,314 of which occurred on the 20 pasture plots. Of the latter sample, 95% of observations (ranked in order of decreasing density; Table 1) consisted of Dunlin (*Calidris alpina*; 54%), Black-bellied Plover (*Pluvialis squatarola*; 15%), Killdeer (*Charadrius vociferus*; 13%), Marbled Godwit (*Limosa fedoa*; 7%), Long-billed and Short-billed Dowitchers (*Limnodromus scolopaceus* and *L. griseus*, respectively; 6%), and Common Snipe (*Gallinago gallinago*; 2%). Species densities varied from 0.04–1.7 birds per ha. Most (78%) shorebirds observed in pastures foraged (Colwell and Dodd 1995).

Shorebirds occurred on 17% of surveys, but we encountered individual species on 1–8% of occasions (Table 1). Species' occurrences in pasture plots (prevalence) varied widely: Killdeer occurred in 55% of pastures, whereas dowitchers used 15% of pastures.

SPATIAL DISTRIBUTION OF SHOREBIRDS

Shorebirds varied greatly in their use of pastures. Over the entire study area, we recorded considerable variation in shorebird distribution (Fig. 2). On the four most heavily used areas, total counts exceeded 3,000 ($n = 3$) and 2,000 shorebirds ($n = 1$); many areas had little or no shorebird use. A nonrandom (clumped) spatial distribution was obtained for the 20 pastures as

TABLE 1. Results of stepwise forward logistic regression examining the relationship between pasture use by shorebird species and environmental and habitat variables.

Species (% use)[a]	Scale of analysis	Variables selected	Beta coefficient	SE	χ^2 (Wald) statistic	P	Concordant pairs
Killdeer (8)	Environmental	Week	−0.09	0.02	20.44	0.001	0.71
		Moon phase	−0.38	0.15	5.90	0.015	
	Pasture	Previous use	1.98	0.38	27.45	0.001	0.90
		Vegetation height	−0.33	0.08	22.38	0.001	
Dunlin (4)	Environmental	Rain during survey	1.37	0.49	7.78	0.005	0.58
		Moon phase	−0.53	0.25	4.61	0.032	
	Pasture	Previous use	1.38	0.49	8.02	0.005	0.82
		Vegetation height	−0.25	0.08	8.56	0.003	
Common Snipe (3)	Environmental	Week	−0.11	0.03	10.21	0.001	0.71
	Pasture	Vegetation height	−0.24	0.08	8.75	0.003	0.73
Black-bellied Plover (3)	Environmental	Rain during survey	1.77	0.56	9.90	0.002	0.66
		Moon phase	−0.88	0.32	7.47	0.006	
	Pasture	Vegetation height	−0.56	0.14	16.43	0.001	0.84
Marbled Godwit (2)	Environmental	Week	0.15	0.06	6.79	0.009	0.77
Dowitchers (1)	Pasture	Vegetation height	−0.33	0.16	4.11	0.04	0.80

[a] The percentage of surveys (n = 580) in which we observed the species using pastures.

well (Fig. 3). Shorebird densities ranged from 0–20.9 birds per ha and shorebirds occurred on 0–62% of surveys.

We detected similar distributions of bird observations for the larger study area and pasture plots (Kolmogorov-Smirnov test, $D = 0.16$, $P > 0.05$); most observations (67% of study area and 83% of pasture plots) yielded no shorebirds. In those cases in which shorebirds occurred, 75% of observations within the larger study area had > 10 birds, whereas 47% of pasture plot observations had > 10 birds.

CORRELATES OF PASTURE USE

Environmental variables. Pasture use by shorebirds correlated with three environmental variables (Table 1): (1) rain during a survey, (2) phase of moon, and (3) week of study. Dunlin and Black-bellied Plovers were more likely to use pastures when it rained during a survey. The likelihood of pasture use by Dunlin, Black-bellied Plover, and Killdeer increased nearer in time to the new moon. From October to May, pasture use decreased by Killdeer and Common Snipe, but Marbled Godwit use increased.

Pasture characteristics. Two characteristics of pastures contributed significantly to pasture use by shorebirds (Table 1). For five of six species (not Marbled Godwit), use varied inversely with vegetation height. All shorebird observations occurred in pastures with vegetation less than 20 cm; 93% occurred in pastures with vegetation less than 15 cm, and 82% occurred in pastures where vegetation was less than 10 cm. Finally, the likelihood of pasture use by Dunlin and Killdeer increased when shorebirds used a pasture the previous week.

DISCUSSION

The nonrandom distribution of shorebirds in coastal pasturelands of northern California (see also Colwell and Dodd 1995) appears to be influenced by a small number of variables operating at several spatial and temporal scales. These variables parallel the series of choices proposed in hierarchical models of avian habitat selection (Svardson 1949, Hildén 1965, Wiens 1985) in which an individual's choice of habitats is influenced by geographical position and habitat configurations, modified by interspecific interactions and site fidelity.

Elsewhere, we reported that landscape effects were relatively unimportant with none of the five shorebird species showing a preference ($P > 0.15$; stepwise regression of average species' densities) for pastures near the bay, estuary, and beaches (Colwell and Dodd 1995), which are the main foraging areas for most shorebirds (Colwell 1994). Movements of shorebirds from intertidal areas into pastures prompted by rising tides can be observed almost daily (Colwell, unpubl. data). However, the conclusion that landscape position does not influence pasture use by shorebirds is tempered by the restricted spatial distribution of pastures we sampled—all pastures were within approximately 3 km of intertidal habitats. In the vicinity of Humboldt Bay, however, some pastures lie at distances greater than 5 km from intertidal areas. We strongly suspect that inclusion of pastures more distant from intertidal areas than the 20 plots we studied would have yielded pronounced landscape effects.

Three environmental variables (week of the study period, moon phase, and rain at the time of a survey) correlated with pasture use by shorebirds. Three species varied seasonally in their use of pastures but patterns differed among species. From October to May, pasture use by Killdeer and Common Snipe decreased, whereas Marbled Godwit use increased. Seasonal changes in pasture use (White and Harris 1966, Hoff 1979, Colwell and Dodd 1995) are probably associated with migration phenology (Hoff 1979), as well as variation in profitability of foraging in intertidal and pasture habitats (Townshend 1981, Colwell, unpubl. data).

Pasture use correlated inversely with moon phase for three species: Dunlin, Black-bellied Plover, and Killdeer occurrence increased at times nearer the new moon. Our results, based on diurnal observations, are similar to those reported by Milsom (1984) who showed Lapwings (*Vanellus vanellus*) foraged more during daylight hours when more time elapsed to the next full moon. The diurnal relationship between moon phase and pasture use differs from studies of nocturnal foraging in intertidal habitats where shorebird occurrence correlates positively with moon phase (Robert et al. 1989, Swennen 1990, Zwarts et al. 1990). Shorebirds may forage more on nights nearer the full moon because prey are more active and/or more visible compared with nights of low illumination (Pienkowski et al. 1984). The inverse relationship between diurnal pasture use and moon phase may arise owing to related changes in the availability of prey in pastures and/or intertidal habitats.

Precipitation has been shown to influence pasture use by a variety of waterbirds (Reed et al. 1977, Hirst and Easthope 1981), but mostly through its effects on habitat characteristics, especially standing water. In intertidal habitats, precipitation reduces prey availability (Goss-Custard 1984, Pienkowski et al. 1984), but it may increase prey availability in pastures. For example, Curlews (*Numenius arquata*) used pastures adjacent to the Tees estuary in England when cold temperatures and winter rains reduced access of birds to polychaete prey intertidally and increased the availability of earthworms as prey in pastures (Townshend 1981).

We found similar patterns in coastal northern California. Both seasonal and daily use of pastures by shorebirds correlated with precipitation. With winter rains, shorebird use of pastures increased in association with decreased availability of prey in intertidal habitats (Carrin 1973, Colwell 1993) and increased prey availability in pastures (Colwell, unpubl. data). Moreover, pasture use by Dunlins and Black-bellied Plovers increased when it was raining, but not in association with the amount of rain in the day prior to a survey. Precipitation presumably influences pasture use by either increasing the availability of prey in pastures and/or decreasing prey availability in intertidal habitats (Evans 1976, Townshend 1981).

Regression models consistently identified vegetation height as being strongly associated with pasture use by shorebirds—short vegetation increased the likelihood of pasture use. For all shorebirds (except Marbled Godwits), pasture use increased significantly as vegetation height decreased. These results corroborate findings based on coarse-scale analyses of pasture characteristics averaged over the 29-week study period (Colwell and Dodd 1995). We suspect that pastures with short vegetation are used by shorebirds because prey availability is greater in less structured vegetation (Eiserer 1980), and/or detection of predators is enhanced in open habitats (Colwell and Dodd 1995). The second of these two nonmutually exclusive explanations is probably most applicable to small shorebirds, which are more affected by vegetation height than larger species. At a given vegetation height (i.e., 10 cm), smaller birds would have their vision obstructed by vegetation to a greater extent than larger birds. Interestingly, the one exception to the vegetation height-pasture use relationship is the largest species, Marbled Godwit.

Our analyses indicate that pasture use by two of the most abundant species—Dunlin and Killdeer—correlated strongly with previous pasture use. These results, together with the clumped spatial distribution of shorebirds (Fig. 2) and observations of similar numbers of a species using the same pasture repeatedly (Colwell, unpubl. data), suggest that pasture use by shorebirds is "traditional," at least over short periods of time. Furthermore, we often observed shorebirds leaving intertidal habitats and repeatedly moving into the same pastures. Similar patterns of localized and predictable shorebird distributions in grasslands of southern England led Fuller and Youngman (1979) to suggest that Golden Plovers (*Pluvialis apricaria*) exhibit strong site fidelity over periods of several years.

Elsewhere, we examined bird use of these same 20 pastures based on an analysis of a more diverse waterbird community including waterfowl, wading birds, gulls and shorebirds (Colwell and Dodd 1995). Results presented here offer broad support for conclusions of our earlier paper, especially the strong inverse relationship between vegetation height and shorebird use of pastures.

CONSERVATION IMPLICATIONS

Like other large bays and estuaries along the Pacific coast of North America, Humboldt Bay is considered critical habitat for migrating and wintering shorebirds (Senner and Howe 1984, Colwell 1994). Pastures adjacent to many of these intertidal areas provide foraging habitat for waterbirds (Colwell and Dodd 1995), especially during the nonbreeding season when intertidal prey abundance declines (Carrin 1973, Colwell 1993) and energetic demands of over-wintering increase at temperate latitudes (Evans 1976). Nevertheless, the value and importance of these habitats to nonbreeding waterbirds remains largely unknown.

Nonrandom use of coastal pastures by nonbreeding shorebirds and bird-habitat relationships provide the basis for conservation action involving local, regional and national agencies working with private landowners adjacent to intertidal habitats. At Humboldt Bay, the conservation value of pastures for shorebirds varies spatially, and the effectiveness of habitat manipulations to benefit shorebirds and other waterbirds may vary across the landscape. But, landscape effects require further study. We suspect that in other coastal areas of the world with important shorebird wintering habitats and adjacent pasturelands a cursory knowledge of spatial movements of shorebirds may enhance local conservation efforts. Our analyses indicate that some shorebird species use pastures consistently (at least over short periods of time), suggesting site-faithfulness is an important conservation consideration. "Traditional" use of pastures indicates the need to identify and protect these habitats.

Finally, the strong relationship between vegetation height and shorebird use of pastures provides useful information to integrate shorebird conservation with management of lands to benefit livestock and dairy interests. However, given the narrow taxonomic focus of this paper, we do not necessarily wholeheartedly endorse grazing as a land use practice fully compatible with other conservation interests (e.g., raptors, wading birds). On the other hand, we wish to emphasize the conservation value of land use practices associated with dairy and livestock industries in coastal habitats. We argue that these practices are infinitely more desirable than other land use options (e.g., housing development) that cause greater, irrevocable damage to natural and seminatural landscapes.

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