

The impact of human disturbance on shorebirds at a migration staging area

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Human disturbance was investigated as a factor that might limit the capacity of a staging area to support migrating shorebirds. Long-term census data were used to test the hypothesis that human disturbance at an important coastal migration staging area has a negative impact on shorebird movement patterns because of (1) displacement of shorebirds from preferred resting areas within the study area; and (2) abandonment of the study area. Results revealed that four of seven species showed one or more types of movement in response to disturbance. The impact of disturbance was greater on species using the heavily distributed front side of the beach. The abundance of impacted species may be reduced by 50% at high disturbance levels. Abundance of front-beach species, such as red knot Calidris canutus and short-billed dowitcher Limnodromus griseus, declined between 1972 and 1989 more than back-beach species, such as blackbellied plover Pluvialis squatarola and semipalmated plover Charadrius semipalmatus; red knot and short-billed dowitcher declined more at Plymouth Beach than at two comparable, but less disturbed, coastal staging areas and more than the overall eastern North American population. Disturbance is implicated as a potential factor in long-term declines in shorebird abundance at Plymouth Beach. The impacts of disturbance could be reduced or perhaps eliminated by closing one or more small portions of the front beach as refuge resting areas during migration.

INTRODUCTION

Shorebirds are one of the most highly migratory groups of animals known to science. The migration strategies of many species include a series of visits to staging areas between wintering and breeding areas, where they feed intensively to acquire

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fat needed for long-distance, non-stop flights to their next staging area, frequently thousands of kilometers away (Morrison, 1984; Senner & Howe, 1984). The concentration of shorebirds during migration raises a concern that populations of some species are highly vulnerable if the well-being of strategic staging areas is compromised. This concern was recently heightened by the finding that some populations of nearctic shorebirds may have declined dramatically since the 1970s (Howe *et al.*, 1989). The causes of these declines are unknown, but potential factors include loss or degradation of habitat in wintering and staging areas due to development, human disturbance, pesticide use, water pollution, and oil spills (Senner & Howe, 1984; Myers, 1988). In order to enact conservation measures for shorebirds, information is needed on factors that may affect the capacity of staging areas to support migrating shorebirds. This study assesses how human disturbance impacts migrating shorebirds at an important coastal staging area.

Although the impact of human disturbance on breeding shorebirds has been documented (Senner & Howe, 1984; Flemming et al., 1988), few studies have evaluated how the impact of human disturbance may affect non-breeding shorebirds. In one study, shorebirds were the most sensitive group of coastal birds in immediate behavioral reaction to disturbance (Burger, 1981). Interspecific differences among shorebirds in sensitivity to disturbance have also been shown (Furness, 1973a). Human disturbance has been associated with a lower frequency of occurrence in (Burger, 1981), and abandonment of (Furness, 1973b; Mitchell et al., 1989), preferred resting or feeding areas by non-breeding shorebirds. In this study, we used long-term census data to relate abundance and distribution of resting shorebirds to disturbance levels at the time of censusing. This method of assessing the impact of disturbance has been termed 'indirect', as opposed to 'direct' methods that rely on behavioral observation (Burger, 1981). We test the hypothesis that human disturbance is associated with movement of shorebirds at a high-tide resting area, either (1) through changes in shorebird resting site selection; or (2) through reduced overall shorebird abundance. The hypotheses are not mutually exclusive. In addition, we explore the hypothesis that longterm abundance declines may be associated with human disturbance.

STUDY AREA

The study site, Plymouth Beach (42° 00' N, 70° 40' W), a 5-km long sand spit extending into Plymouth Bay (Fig. 1), is one of the northernmost of a series of barrier beaches running along the Atlantic coast of the United States between Florida and Cape Cod Bay. The east side faces Cape Cod Bay and is an open, sandy beach subject to high wave-energy, especially during the winter. The west side is sheltered from strong wave action and is typical of a low-energy beach, with extensive development of tidal flats, mussel beds, and some salt marsh. A 4070-ha bay, of which 45.7% is exposed

at low tide (Iwanowicz et al., 1974), is sheltered behind Plymouth and nearby Duxbury Beaches (Fig. 1). Data from the International Shorebird Survey (ISS) show that the large concentrations of shorebirds at Plymouth Beach make the site one of conservation importance (Harrington et al., 1989). Abundance of most shorebird species at Plymouth Beach during fall migration peaks during late July and early August, coinciding with the peak period of human recreational use of the beach. Passage of adult shorebirds at Plymouth Beach is generally followed by the passage of juveniles, as at most North American staging areas during fall migration (Morrison, 1984); however, the periods of juvenile and adult migration may overlap (Manomet Bird Observatory (MBO), unpublished data).

Shorebirds feed on the tidal flats behind the barrier beaches and move to high-tide resting areas on Plymouth Beach and Duxbury Beach (3-5 km from Plymouth Beach). The intertidal flats behind Plymouth Beach are the muddiest in the estuary and receive the most intense shorebird use. Most shorebirds resting here apparently follow the same



Fig. 1. The study area: ---, Intertidal flats exposed at low tide. (Adapted from a diagram originally published as Fig. 1 in Schneider, D. C. & Harrington, B. A. (1981). Timing of shorebird migration in relation to prey depletion. Auk, 98, 801-11.)

Species	Mean peak" abundance 1972–1975	Mean peak" abundance 1986–1989	Resting-site selection
Black-bellied plover Pluvalis squatarola	738	474	Back-beach
Semipalmated plover Charadrius semipalmatus	380	455	Back-beach
Ruddy turnstone Arenaria interpres	160	61	Back-beach
Sanderling Calidris alba	1 200	327	Front-beach
Semipalmated sandpiper Calidris pusilla	5912	1844	Front-beach
Red knot Calidris canutus	295	57	Front-beach
Short-billed dowitcher Limnodromus griseus	299	34	Front-beach

Table 1. Abundance of shorebird species in first and last four years of the study at Plymouth Beach, Plymouth, Massachusetts (1972-1989)

⁴Mean of highest annual census counts.

cycle day and night, since they are not present at lower tides at night. Night feeding is widespread among shorebirds (Burger, 1984; Robert *et al.*, 1989). Observation of individually color-marked shorebirds has shown that local movement occurs between Plymouth and Duxbury Beaches but that most individuals show fidelity to a particular hightide resting area (MBO, unpublished data).

The seven most abundant shorebird species at Plymouth Beach during southbound migration, July through September (Table 1), all breed in the North American arctic and subarctic regions and winter primarily in Central and South America, although some species have populations that winter along the United States Atlantic and Gulf coasts (Hayman et al., 1986). No shorebirds winter at Plymouth Beach, except as vagrants. At Plymouth Beach there is a division among species in resting site selection. Black-bellied plover Pluvialis squatarola, semipalmated plover Charadrius semipalmatus, and ruddy turnstone Arenaria interpres occur in greatest numbers along the marshy edges of the back side of the beach; semipalmated sandpiper Calidris pusilla, sanderling C. alba, red knot C. canutus, and short-billed dowitcher Limnodromus griseus occur in larger numbers along the open tip and front side of the beach. The former species will be referred to as 'back-beach' species and the latter as 'front-beach' species. The back-beach species include two plover species that often prefer to feed in muddy habitats (MBO, unpublished data), which occur along the low-energy back side of Plymouth Beach. Thus, the selection of roosting habitat may be correlated with foraging strategy. Back-beach species also tend to have later migration schedules and peak abundance of adults generally occurs after the peak period of human disturbance (MBO, unpublished data).

Beach access for recreation beyond the first kilometer of Plymouth beach is generally restricted to four-wheel-drive vehicles because of the distance from the nearest paved road. Summer recreational activities center on sandy sections of the outer beach (Fig. 1). The back beach is little used for recreation except as an alternative access route to the tip of the beach along a narrow trail. The tip of the beach is used primarily for fishing and at times remains relatively undisturbed even when the outer beach is crowded. The number of vehicles allowed on the beach was not limited prior to 1988, at which time restrictions were applied only under conditions of unusually high tides. Numbers of vehicles on the beach during fall shorebird migration ranged from none, at times such as early in the morning and during bad weather, to more than 1000 on peak use days, such as holidays and warm, sunny weekend days. The number of vehicles on peak visitation days increased over the course of the study, generally ranging from 75-200 in the 1970s to 200-600 in the 1980s.

METHODS

Field data collection

Censuses of shorebirds at Plymouth Beach were made by staff and interns at the MBO in July, August, and September from 1972 to 1989. Shorebird counts were made using binoculars and spotting scopes by one to five observers traveling along the beach in a vehicle following a standard route. Both the front and back beaches are open with little vegetation to obscure roosting flocks, which are usually clearly visible; thus, systematic error caused by missing large flocks (Rappoldt *et al.*, 1985) is unlikely. Censuses were timed to begin within an hour of high tide and usually were completed in 1.5-3 h. Many different observers participated over the 18-year period; however, B. A. Harrington supervised the censuses and trained observers for the duration of the study. We assume that observer variations are random over the course of our study and will not affect the results.

Counts of vehicles on the beach were made during most censuses from 1973 to 1989 as an index of recreational use of the beach. Although the most serious disturbance was probably caused by pedestrians and unleashed dogs, the vehicle count provided an index of disturbance that was easier to obtain. Beginning in 1979, shorebird and vehicle counts were separated into 15 zones on the beach to incorporate resting-site selection into the data. For the present study, shorebird counts have been categorized by consolidating these zones into three, corresponding to the front beach, back beach, and tip of beach. Shorebird counts from 45 censuses between 1975 and 1978 were also divided into these three zones on the basis of information in original field notes.

A disturbance study was not the primary censusing goal, which varied from year to year with ongoing research. The frequency of censuses during southbound shorebird migration varied from several times a week to less than once a week. Census effort was usually greatest in late July and August, when most shorebird species were at their migration peaks. The census schedule throughout the 1980s was usually adjusted to avoid occasions when high beach traffic volume was expected, because disturbance might interfere with data gathering. It is our assumption that any shorebird responses we detected at low to moderate levels of disturbance during those years would be even more apparent at higher disturbance levels.

Data screening

We have screened our census data to address two main problems: (1) some of the censuses were not statistically independent with respect to total species counts; and (2) shorebird abundance varied in relation to migration phenology. In Appendix 1 we show how we addressed these problems by (1) manipulating the data set to reduce the problem of lack of independence; and (2) developing a procedure to limit the census data for each species to its peak migration period. The number of total censuses and those falling within the peak migration period of each species is shown in Table 2. In treating the lack of independence, we developed a modified data set in which censuses were combined, reducing the number of censuses by about 25%.

For analysis of movement within the study area, censuses with vehicle count by zone were used

Year	Total censuses ^a	Black-bellied plover	Red knot	Ruddy turnstone	Sanderling	Short-billed dowitcher	Semipalmated plover	Semipalmated sandpiper
1989	9	5	3*	1	2	3*	3	1
1988	12	5	6*	7	6	4	6	6
1987	15	5	5*	5	6	5*	6	5
1986	25	7	2	3	6	12*	5	7
1985	28	9	16	11	13	7	6	14
1984	22	9	8	8	9	6	8	8
1983	14	5	3	4	5	3*	3	5
1982	22	10	2	1	2	5*	2	2
1981	9	2	4	2*	3	6*	4	3
1980	28	11	9	8	11	8	9	7
1979	12	4	5	4	5	6	5	5
1978	8	7	5	5	5	7	6	5
1977	30	13	12*	10	14	12	12	11
1976	33	13	16*	14	14	15	13	14
1975	29	15	17	17	17	7	12	12
1974	18	14	1	9	11	9	9	9
1973	31	14	1	10	12	10	7	14
1972	33	6	11	6	9	14	14	8
Totals	378	154	126	125	150	139	130	136

Table 2. Number of total censuses and of censuses within species-specific migration window peaks (see Appendix 1)

"Vehicle counts were recorded by zone for censuses after 1979; between 1973 and 1979 counts were not recorded by zone, but vehicle counts for front-beach, back-beach, and tip-of-beach zones were obtained for 45 censuses (1975–1978) on the basis of original field notes; censuses done in 1972 have no vehicle counts. *, median count <10. (1979-1989; 45 from 1975-1978). Counts for a species of less than 20 were eliminated from the analysis, since such low abundance may not provide information about resting-site selection. The species most affected by this restriction were short-billed dowitcher, for which 35 of 65 available censuses were excluded from this part of the analysis, and red knot, for which 41 of 71 were excluded. Both species began to disappear from Plymouth Beach in the 1980s. Statistical independence was not an issue in testing the hypothesis that disturbance is associated with shorebird distribution, because daily variation in the location of resting flocks was apparent at Plymouth Beach, so the original census data were used. For the analysis of movement outside the study area, the manipulated data set of censuses in species specific migration peaks were used (1973-1989). Data for a year in which the annual median count of a species was less than 10 (Table 2) were excluded, because with such low counts any relationship between human activity and abundance would be obscured. This procedure removed six years of data for shortbilled dowitcher, five for red knot, and one year for ruddy turnstone (Table 2). For determining abundance trends, we used all censuses (1972-1989).

Data analysis

To obtain a statistical test of the hypothesis that disturbance is correlated with displacement from roosting sites, we determined which of the three beach zones—front beach, back beach, and tip of beach—had the highest proportion of the total count for each species on each census. This zone was designated the 'preferred' zone. The data were then divided into two groups: censuses in which back beach was preferred and others. We then used a Wilcoxon Rank Sum test to determine whether censuses for which the back beach was the preferred resting site differed from the other sites in vehicle count.

To evaluate the hypothesis that overall abundance is associated with human disturbance, we tested for correlation between vehicle count and shorebird abundance. The total count for each species on the *i*th census in year *j*, x_{ij} , was normalized to a relative deviation from the annual mean count \bar{x}_j :

[normalized abundance]_{ij} = $(x_{ij} - \bar{x}_j)/\bar{x}_j$ (1)

to take into account the effect of temporal trends in shorebird abundance. Examination of the plots of normalized abundance versus vehicle count indicated that abundance may not be normally distributed with respect to disturbance, thus a nonparametric Spearman rank correlation was determined between the normalized abundance level and vehicle count.

Long-term trends were determined according to the following linear regression model (Geissler & Noon, 1981):

$$log [abundance index]_i = a + b_1 [year]_i + error$$
(2)

where abundance $index_i$ is the index of shorebird abundance in year_i. Because a linear regression model was used to determine temporal trends of shorebird abundance (Geissler & Noon, 1981), it was necessary to select a method of determining an annual index of abundance that would maintain the proper degrees of freedom in the regression model of one datum per year. We followed Howe *et al.* (1989) in using the mean of the highest three counts to reduce between-year variability caused by weather, local movement, or other factors, which may lower shorebird abundance on a given census but are not related to long-term trends.

A weighted regression was used, because the number of censuses per season varied from 1 to 17. By giving more weight to observations from years with more censuses, the higher probability of reflecting the true peak abundance level of that year is acknowledged. The weighting coefficient was not changed for years with more than eight censuses, because additional censuses provided redundant information with respect to peak abundance. The coefficient b_1 was transformed to an annual trend of percentage annual change (Holmes & Sherry, 1988), so that abundance trends could be compared with those from eastern North America determined by Howe *et al.* (1989).

We compared long-term trends in shorebird abundance at Plymouth Beach with those at two similar but disturbance-controlled staging areas and the overall population trends for eastern North America (Howe *et al.*, 1989). Monomoy National Wildlife Refuge (Monomoy NWR) is a barrier beach island approximately 60 km east of Plymouth Beach. E. Forsythe NWR, approximately 300 km south of Plymouth Beach, is part of a barrier beach system with extensive salt marsh development. Shorebirds were censused by International Shorebird Survey (ISS) cooperators (Morrison & Harrington, 1979) at high-tide resting areas at Monomoy NWR and at an artificial impoundment, a resting and feeding area, in the salt marsh at E. Forsythe. Both sites support a larger number of shorebirds during fall migration than Plymouth Beach (Harrington *et al.*, 1989) and are managed to prevent excessive human disturbance of wildlife. Howe *et al.* (1989) have calculated shorebird population trends for eastern North America based on census data from 33-63 coastal ISS sites. Abundance trends were determined for Monomoy NWR and E. Forsythe NWR using the same methods of analysis as for Plymouth Beach.

Throughout the analysis, seven separate statistical procedures were performed, one for each species of shorebird. In multiple related statistical tests, the probability of committing a type I error increases with each additional test (Miller, 1981). Formal methods of correcting for type I error level require adjusting the *p*-values for determining statistical significance (Miller, 1981). In this study this approach was not taken because the goal of the study was to test the hypothesis that human disturbance affects shorebird abundance and distribution; it is less important to make the correct decision about whether a given species is affected. We do note that at $\alpha = 0.05$ an average of 5% of the significant results are spurious.

RESULTS

The hypothesis that human disturbance causes front-beach species to change resting-site selection was supported by the Wilcoxon test, which showed that the disturbance level affected the frequency with which semipalmated sandpipers, sanderlings and ruddy turnstones preferred the back beach (p = 0.01; p < 0.01; p = 0.04) (Table 3). Sanderlings show a change in the pattern of distri-

 Table 3. Wilcoxon Rank Sum test (normal approximation) for relationship between shorebird resting-site preference^a and vehicle count. Censuses available for this analysis were from the years 1979 to 1989 and from 45 censuses between 1975 and 1978 (see Methods section)

Species ^{<i>b</i>}	Back- prefe	beach rence	Z	р ^с	
	Yes	No			
Black-bellied plover	77	10	-0.52	0.52	
Semipalmated plover	65	8	-0.44	0.66	
Ruddy turnstone	61	12	-2.01	0.04	
Sanderling	28	66	+2.86	<0.01	
Semipalmated sandpiper	38	44	+2.55	0.01	
Red knot	21	9	-0.20	0.84	
Short-billed dowitcher	16	14	-0.87	0.38	

^{*a*}Yes = highest count in back beach; no = highest count in front beach or tip of beach.

^b Back-beach species above, front-beach species below, broken line.

^cNull hypothesis: preference for back beach is not associated with vehicle count.

bution on the beach with disturbance level (Fig. 2). At low disturbance levels (vehicle count <20), on average more than 50% of the census total was from the front beach; however, at high disturbance levels (vehicle count >100), this percentage dropped to 11%. The semipalmated sandpiper showed a similar pattern in response to disturbance. In contrast, back-beach species such as the black-bellied plover did not show a large change in resting-site selection between disturbance levels (Fig. 3). Although ruddy turnstones showed a relationship between frequency of selection of the back beach and disturbance level, they preferred the back beach at all disturbance levels.



Fig. 2. Mean proportion of total count on censuses of low (1), medium (2), and high (3) disturbance levels for three zones of Plymouth Beach. Sanderling is a front-beach and black-bellied plover a back-beach species.



Fig. 3. Normalized abundance plotted against vehicle counts (a) normal scale, (b) \log_{10} scale with Cleveland smoothing plot/ k = 0.5 (Cleveland, 1979). Sample sizes are given in Table 4.

Table 4. Spearman rank correlation between normalized shorebird abundance and number of vehicles, Plymouth Beach (1973– 1989)

Species"	N ^b	R	p
Black-bellied plover	82	+0.013	0.43
Semipalmated plover	80	-0.13	0.32
Ruddy turnstone	79	-0.22	0.11
Sanderling	104	-0.34	<0.001
Semipalmated sandpiper	96	-0.094	0.22
Red knot	59	-0.28	0.04c
Short-billed dowitcher	60	-0.24	0.01

"Back-beach species above, front-beach species below, broken line.

^hNumber of census counts used in the analysis.

^c Interpretation of test statistic for red knot is uncertain because procedure used to simulate statistical independence changed significance of the result (see Discussion).

We analyzed movement outside the study area using both sets of the census data before and after it was modified to address the potential lack of statistical independence, and found similar results (Appendix 1). We present the statistical results of the data for which independence was simulated, which have nearly identical but slightly higher p-values than the original census data in cases of significant results. The hypothesis that human disturbance causes reduced shorebird abundance was supported by a negative correlation between vehicle counts and shorebird abundance for two of the four front-beach species at $\alpha = 0.05$ (Table 4). The red knot showed a negative correlation (p =0.04); however, in contrast to short-billed dowitcher and sanderling, which showed greater significance,

the correlation was not significant (p = 0.19) with the original census data. The difference presumably occurs because combining censuses reduces the high variation in the abundance of the red knot at times of low disturbance levels which seems to occur because of long-distance foraging flights (MBO, unpublished data). Because we have no basis for determining the correct interpretation of the *p*-values, we do not evaluate the hypothesis based on the statistical result for the red knot.

The regression model of shorebird annual abundance index on year (eqn 2) showed that at Plymouth Beach, the five front-beach species suffered greater declines in abundance than the three backbeach species (Table 5). The short-billed dowitcher and red knot at Plymouth showed the strongest negative abundance trends of any species at any site, including the pooled Atlantic coastal sites (the trend for sanderling at E. Forsythe NWR is discounted because of the low average count). The trend at Plymouth for the short-billed dowitcher was 180% greater than the next largest trend at the other two sites; the trend for the red knot was 65% greater.

DISCUSSION

Movement of shorebirds in response to disturbance

Of the seven shorebird species in the analysis, four showed movement in response to disturbance, either by shifting roosting-site selection or leaving Plymouth Beach. The semipalmated sandpiper did

 Table 5. Abundance trends (mean percentage annual change) of seven shorebird species at Plymouth Beach, Monomoy NWR,

 E. Forsythe NWR, and eastern North American coastal sites

Species ^a	Plymouth Beach (1972–1989)		Monomoy NWR (1974–1989)		E Forsythe NWR (1974–1989)		Eastern N America (1972–1983) ^b	
	Trend	Mean high count	Trend	Mean high count	Trend	Mean high count	Trend	Number of sites
Black-bellied plover		(546)	-0·2	(1684)	-5.6	(662)	5.4*	(55)
Ruddy turnstone	+1.2 -5.5*	(116)	-3.9 -3.9	(150)	+12.7 -1.7*	(51)		(47)
Sanderling Semipalmated sandpiper Short-billed dowitcher Red knot	9.2*** 6.8*** 16.5*** 15.7***	(822) (3 897) (121) (257)	6·6* 8·0*** 0·6 9·5*	(1 940) (2 690) (1 766) (1 000)	$ \begin{array}{r} -19.0* \\ +6.5 \\ -5.9 \\ -1.5 \end{array} $	(86) (4238) (2853) (149)		(52) (63) (59) (33)

Significance levels for eastern North America were determined by Howe *et al.* (1989); other significance levels are from coefficient b_1 in the regression model (eqn 2). Significance levels: * = p < 0.10 ** = p < 0.05 *** = p < 0.01.

^aBack-beach species above, front-beach species below, broken line.

^bSource: Howe et al. (1989).

not show a significant correlation between abundance and disturbance, but examination of the data shows that of 14 censuses with vehicle counts of greater than 100, 13 had abundance counts below the annual mean (Fig. 3). If more censuses had been made with vehicle counts greater than 100, it is likely that the semipalmated sandpiper would also have shown a negative correlation between abundance and vehicle count.

In Fig. 3 it is possible to estimate the reduction in shorebird abundance from low to high disturbance levels by measuring the reduction in abundance along the smoothing curve. For the sanderling and short-billed dowitcher, the reduction is around 50% ($[1\cdot 2 - 0\cdot 6]/1\cdot 2$). Examination of Fig. 3 also suggests that shorebird species have different threshold responses to disturbance. The sanderling seems to show a steady response to all levels of disturbance; the short-billed dowitcher seems to be very sensitive to a level of disturbance between 10 and 40 vehicles, at which point its abundance sharply declines; the semipalmated sandpiper may show a response at high disturbance levels.

Our results, however, probably do not indicate the true severity or pervasiveness of the impact of human disturbance on migrating shorebirds, due to limitations of the data. That our data did not show a change in resting-site selection for the other front-beach species, red knot and short-billed dowitcher, we attribute to two factors: (1) fewer censuses were available for these species because of elimination of low counts; (2) these species often responded to disturbance by immediately abandoning the beach. That movement due to leaving Plymouth Beach by the red knot was not convincingly established by statistical procedures is probably a result of the high variation in abundance shown by this species. Since in the 1980s red knots and short-billed dowitchers began to disappear from the study area, the data became insufficient to show the true relation between abundance and disturbance. The severity of the impact of human disturbance on the red knot and short-billed dowitchers is probably most evident in their long-term decline in abundance.

Abundance trends

The fact that long-term declines in abundance at Plymouth of the four front-beach species were greater than the three back-beach species implicates disturbance as a possible cause of the declines. This implication is further supported

by the result that two front-beach species at Plymouth suffered greater declines at Plymouth than they did over the same period at two major, disturbance-limited staging areas in the same region, and greater declines than in eastern North America (1972-1983). Preliminary results with more recent ISS data show that no shorebird species is showing a significant decline (1972-1989) in eastern North America that was not apparent in the earlier data (Marshall Howe, pers. comm.). Another indication that disturbance has contributed to the declines of red knot and shortbilled dowitcher is that peak numbers of red knot and short-billed dowitcher juveniles passing through Plymouth Beach, after the period of intense human disturbance, now exceed the peak number of adults; in contrast during the early years of this study the ratio of juveniles to adults was much lower (MBO, unpublished data). If the declines of red knot and short-billed dowitcher were caused by habitat alterations or other environmental change, the juvenile abundance would probably have shown similarly sharp declines. Our behavioral observations of red knot and short-billed dowitcher during censuses indicated that these species frequently left Plymouth Beach when disturbed. Other studies (Furness, 1973a; Mitchell et al., 1989) have indicated that, among shorebirds, the red knot is particularly sensitive to human disturbance.

Consequences of reduced abundance

The results indicate that front-beach species are more severely affected by disturbance at Plymouth than back-beach species. Front-beach species are exposed to more direct human disturbance because recreational activities are concentrated on the front side of the beach. Front-beach species also tend to have earlier migration windows than back-beach species, which tend to peak in mid-late August when recreational use of the beach is less intense. Two back-beach species, black-bellied plover and semipalmated plover, were found in large numbers on the front side of the beach before 1975 (B. A. Harrington, personal observation), but since 1975 few large counts of these species have been reported on the front beach. Thus these species could have adjusted their resting-site selection to avoid disturbance.

Although intense human disturbance occurs only at irregular intervals at Plymouth Beach, the longterm declines of red knot and short-billed dowitcher

abundance indicate that the disturbance may be sufficient to lower the capacity of Plymouth Beach as a resting area for shorebirds in the staging area. Shorebirds displaced from Plymouth Beach may find refuge in undisturbed areas on Duxbury Beach. Irregular censuses at Duxbury over the period 1972-1989 indicate that sanderling, red knot, and short-billed dowitcher have not suffered large declines, and that sanderling may have increased in abundance (ISS database 1972-89, Manomet, MA, USA, unpublished data (see also Morrison & Harrington, 1979)). Counts at Duxbury show that it has not absorbed the reductions in shorebird abundance at Plymouth Beach during the study. Flight range formulas for shorebirds based on the metabolic cost of flight (Castro & Myers, 1989) indicate that the energetic cost of switching from Plymouth to Duxbury, while continuing to commute to the same tidal flats, would be inconsequential. However, the high frequency at which shorebirds select resting sites in close proximity to feeding areas (ISS database 1972-89, Manomet, MA, USA, unpublished data (see also Morrison & Harrington, 1979)) argues for the biological importance of this proximity. Proximity of the resting area to the feeding area could, for example, increase feeding efficiency by maximizing feeding time through the ability to detect when intertidal feeding areas become available as the tide falls. Regardless of whether shorebirds from Plymouth are able to utilize relatively protected areas such as Duxbury, we suggest that many other staging areas do not have suitable alternative resting sites and that alternative staging areas are limited (e.g. Myers et al., 1987; Harrington et al., 1989).

Management implications

The negative relationship between abundance of short-billed dowitcher and sanderling and disturbance occurs at disturbance levels of less than 50 vehicles. This level of disturbance represents at most 10 vehicles per linear km of beach—a very low level of disturbance compared to typical recreational use in the 1980s. Severely reducing access to Plymouth Beach would provide needed protection of resting areas, but at an unacceptable cost to recreational users of the town-managed beach. Alternative strategies are available. Based on historical patterns of shorebird use of the beach, we believe the best alternative would be to close off one or more small portions of the front or tip of

the beach to provide protected resting zones during migration. An indication that this measure would be successful is that in the past de facto resting sites have existed, where shorebirds could avoid disturbance without leaving the beach. As late as 1973, a large area of recently deposited sand between a pair of breakwaters at the very tip of the beach was inaccessible to vehicles and was relatively free of human disturbance. MBO observers reported that on some days of high disturbance virtually the entire Plymouth Beach shorebird assemblage could be found in this spot. In 1975 and 1976 an area of dunes just south of the tip also acted as a refuge, but a revegetation program soon made the dunes unacceptable to the birds as a roosting site.

The rapid increase in the number of off-road vehicles (Primack, 1980) and a general population increase in coastal areas are likely to increase recreational use of traditional shorebird staging areas. This study has indicated that human disturbance displaces shorebirds from traditional resting areas, thereby reducing the utility of impacted areas to migrating shorebird populations. The management need for protecting coastal nesting birds, such as terns (e.g. Sterna spp.) and the piping plover Charadrius melodus, is obvious. However, we believe that disturbance effects on transient or non-breeding shorebirds may have been overlooked by resource managers, in part because migrating populations visit staging areas only briefly, and in part because the impact of disturbance may not be obvious. Yet conservation measures are well justified for migrating shorebirds, since the number of migrating individuals may exceed the number of breeding individuals in the same location by many orders of magnitude, and some locations may be crucial refueling areas in the bottlenecks along temperate migration paths.

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APPENDIX 1

PROCEDURES FOR DETERMINING PEAK MIGRATION PERIODS AND REDUCING PROBLEMS OF LACK OF INDEPENDENCE IN SHOREBIRD CENSUS DATA

To reduce variation in shorebird counts caused by seasonal fluctuation, the analysis was limited to counts occurring during species-specific migration peaks. Since some species showed between-year variation in migration timing, an annual beginning date for the migration peak was determined by a fixed formula: the first count that was at least 40% of the mean of the three highest counts. The interval of peak migration for each year commenced at the beginning date and was the number of days of the long-term average migration peak, which was visually determined from the plot of all years of data (counts plotted as percentage of the mean of the highest three counts for each year) as the interval between dates corresponding to 40% of the highest three counts, both before and after average peak migration. In determining the longterm peaks, we ignored later secondary peaks caused by juvenile passage. For most species this procedure resulted in a peak migration period near the 21-day fixed period used by Howe et al. (1989) for reducing variation in shorebird counts.

In some years of low censusing effort, the beginning date determined may have been well past the actual onset of peak migration; with such a 'late' beginning date, some censuses in the long-term interval of peak migration might include low counts of lingering adults or counts in which the abundance would be affected by late-arriving juveniles. To prevent such inappropriate censuses from being included, the species-specific migration peak for each year was always terminated at the end date used to determine the long-term peak interval. In some cases, the peak abundance of a species was particularly late (e.g. red knot 1973–74), possibly because mostly juveniles used the staging area, and most of the early censuses were not included in the migration peak because of the end-date cutoff.

Censuses were sometimes conducted on consecutive days or within a few days for investigations of migration phenology. For this reason some groups of censuses may not have been statistically independent with respect to shorebird abundance. This problem was especially acute in 1972-1974 when at times almost daily censuses were conducted. Thus, we developed a procedure to simulate independence in the data set for the purpose of statistical analysis. We made the assumption that censuses made at least four days apart (i.e. five-day interval) were statistically independent for our analysis because a considerable turnover of the resident shorebird population would occur. The basis for this assumption was: (1) the mean lengthof-stay for semipalmated sandpipers at Plymouth Beach is approximately eight days (M. L. Kasprzyk,

pers. comm.; see also Dunn et al., 1988) and limited data for other shorebird species indicated similar length of stay (MBO, unpublished data); (2) an interval greater than four days represents a period over which significant migratory departures and arrivals will likely occur because of favorable weather conditions (Lank, 1983). Within a fourday interval, we assumed that censuses were not independent unless a large difference in disturbance level occurred because, according to our hypothesis, shorebird abundance is affected by disturbance level. To reduce the effect of the lack of independence, we combined any censuses occurring within a four-day period with similar disturbance levels and used the mean of the shorebird and vehicle counts to represent a single census.

To provide a criterion for combining censuses, disturbance was categorized into three levels: 0–19; 20–99; >100. By following the above criteria, the total number of census counts was reduced by approximately 20% after all the appropriate counts were combined. Most of the combined censuses were from the low-disturbance category. To investigate the sensitivity of the statistical results to the procedure we used to simulate independence, the analysis was done both with the manipulated data set and with the original census data. The results of statistical tests were the same ($\alpha = 0.05$) with the exception of one species, for which the difference occurred for reasons not related to statistical independence (see Discussion).