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RH: Human disturbance of nonbreeding sanderlings

Title: **Effects of human disturbance on nonbreeding sanderlings at Assateague Island National Seashore**

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Abstract:

Key words: *Calidris alba*, sanderlings, human disturbance, behavior, energetics, nonbreeding, time budget, recreation, Maryland

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INTRODUCTION

The literature contains scattered but increasingly more common references of the impact of human disturbance on avifauna, including raptors (*e.g.*, Stalmaster and Newman 1978, Knight and Knight 1984, Levenson and Kroplin 1984, Fraser *et al.* 1985, Knight and Skagen 1986, Buehler *et al.* 1991, Fernandez and Azkona 1993), waterfowl (*e.g.*, Morton *et al.* 1989b, Dahlgren and Korschgen 1992, Ward *et al.* 1994), seabirds (*e.g.*, Anderson and Keith 1980, Hand 1980, Burger 1981, Pierce and Simons 1986, Anderson 1988), colonial waterbirds (Grubb 1978, Kaiser and Fritzell 1984, Erwin 1989, Bratton 1990, Klein 1993), and other avifauna (*e.g.*, Wunz 1971, Watson 1988, Frederick and Collopy 1989, Yalden and Yalden 1989, Mabie *et al.* 1989, Burger and Gochfeld 1991, Kenney and Knight 1992, Pfister *et al.* 1992). Several annotated bibliographies also have focused on the effects of general types or sources of disturbance on wildlife: noise (Fletcher *et al.* 1971, Dufour 1980), nonconsumptive outdoor recreation (Boyle and Samson 1983), aircraft noise and sonic booms (Gladwin *et al.* 1988), and recreational boating (York 1994). Knight and Gutzwiller (1995) edited an anthology of writings on researching and managing wildlife-recreationist interactions.

The most cited avian response to disturbance is flight and its consequences. Flying is an energetically costly behavior; estimates range from 9 to15 times basal metabolic rate (BMR)(King 1974). Additionally, increased time in flight may increase susceptibility to accidental death (Blokpoel and Hatch 1976), predation, or being shot (Bartelt 1987). Birds also must cease whatever other behavior they were engaged in prior to flushing, which may include courtship, nesting, brooding, or foraging activities with consequences not only for themselves but often for their clutch or brood.

In the most proximate sense, disturbance increases maintenance costs by increasing energy expenditure and decreasing energy intake. Morton (1992) suggested that birds can ultimately respond to disturbance-induced costs by increasing energy intake, habituating, and/or dispersing. Increased energy intake compensates for increased maintenance costs, habituation effectively reduces elevated maintenance costs, and dispersal avoids disturbance. These responses are not mutually exclusive; for example, Owens (1977) observed that brant avoided heavily disturbed feeding sites in early winter but used all such areas later as food stocks became depleted elsewhere. Failure to respond adequately with one or more of these three strategies will likely result in impaired fitness (*e.g.*, reduced body mass or fat reserves) of individuals or reduced populations.

Shorebirds clearly have mechanisms that allow them to adjust their rate of energy intake. Several possible foraging constraints could be relaxed to increase net rate of foraging intake. There are clearly numerous foraging methods (Baker and Baker 1973) some of which show higher capture rates but generally at the expense of higher locomotion costs. Shorebirds can select among microhabitats (Baker and Baker 1973) and among prey patches within microhabitats (Dugan 1982). They can alter search patterns (Pienkowski 1983), forage in flocks (Myers *et al.* 1979, Thompson 1983), defend territories (Goss-Custard 1970, Myers *et al.* 1979), vary prey size selectivity (Bengston and Svensson 1968, Goss-Custard 1977a, Myers *et al.* 1980), switch prey (Connors *et al.* 1981), forage at night (Dugan 1981, Pienkowski 1983), vary diurnal foraging time (Swennen *et al.* 1989), vary search and handling times (Thompson 1983, Swennen *et al.* 1989), adjust giving-up and waiting times (Pienkowski 1983), vary scan time for predators and kleptoparasites (Barnard and Thompson 1985), and perhaps modify search space geometry (Pienkowski 1983). Although not discussed here, shorebirds also may draw on body reserves (Dugan *et al.* 1981, Swann and Etheridge 1989, but see Davidson 1982) to supplement foraging that does not fully compensate for disturbance costs. Compensatory foraging options, therefore, may include changes in search pattern, prey selectivity, time allocation, and nutrient reserves.

We chose to study the responses of nonbreeding sanderlings (*Calidris alba*) to human

disturbance. Data from the International Shorebird Survey indicate that North American populations of sanderlings monotonically decreased 80% between 1972 - 1983 (Howe *et al.* 1989). Myers (1989) suggested that the widespread use of pesticides in South America, and continued loss and degradation of coastal habitats are two pervasive factors that could account for declining populations. Anthropogenic disturbance of sanderlings during the nonbreeding season, when sanderlings are away from the remote high arctic, may constitute a serious form of habitat degradation. Recent studies on the east coast of North America have shown that anthopogenic disturbance can displace sanderlings from their staging areas (Pfister *et al.* 1992) and reduce time spent foraging on their wintering areas (Burger and Gochfeld 1991).

The nonbreeding season of sanderlings is 10 months, with the actual winter residence usually 4 - 8 month within a single 10-km sector of coastline. Sanderlings distribute themselves during the nonbreeding season from New Jersey (40°N) on the east coast to Washington (50°N) on the west coast and south to Tierra del Fuego (55°S); the mean nonbreeding latitude is 5°S (Myers 1981). Sanderlings feed in the swash zone during the winter and migration, primarily on species of molecrab (*Emerita* sp.). In areas where tidal flats are available, sanderlings forage on outer beaches at high and mid-level tides, switching to protected sandflats as the tide recedes (Connors *et al.* 1981).

We studied the effects of anthropogenic disturbance on free-ranging sanderling populations at Assateague Island during two winters. This 60-km island, off the Atlantic coasts of Maryland and Virginia (38°15' N), was designated as part of the International Shorebird Reserve in 1990. It is an important resting and feeding site during the southward migration in the late summer and early fall, and a small population persists throughout the winter. However, the island also is used by relatively high numbers of humans who are visiting or recreating at the Assateague Island National Seashore (AINS). Human and sanderling visitation patterns at AINS are similar and the potential for conflicting use of the beach is high. In this paper, we specifically address three questions: Does disturbance affect sanderling occurrence on the beach? Does disturbance affect sanderling density on the beach? Does disturbance affect sanderling behavior while on the beach? We hypothesized that variation in food availability would mediate their responses. This is most easily tested during the winter months when energy balance may be more critical for nonbreeding sanderling (Maron and Myers 1985).

Study area

The Maryland portion of Assateague Island consists of two public lands and a few scattered private inholdings. The National Park Service (NPS) administers the 3,200-ha AINS and the Maryland Department of Natural Resources administers the 275-ha Assateague State Park (Figure 1). The Verrazano Bridge spans the estuarine waters of Sinepuxent and Chincoteague Bays, which separate AINS and Assateague State Park from the mainland. Tides occur semidiurnally at 12.4-h intervals and daily tidal fluctuations on the ocean side range from 0.8 - 1.9 m in Jan (National Park Service 1982). NPS began operating a continuously-recording weather station on AINS in Nov 1991; precipitation, air temperature, wind speed, relative humidity, and barometric pressure are integrated at 1-h intervals.

AINS is an ideal site for studying human disturbance. During winter, only pedestrians (no dogs or vehicles) are allowed on 9.5 km of beach on the north end (AN), and land access is restricted to entry from the south. Consequently, the frequency of disturbance diminishes rapidly the further north one goes on AN. The south end (AS) of AINS consists of 2.9 km of beach on which pedestrians and dogs are permitted (pedestrian zone), and 19.3 km of beach on which pedestrians, dogs, and ORVs are permitted (ORV zone). Thirteen boardwalks provide access over the primary dune to the pedestrian zone from a paved road and bicycle path, parking lots for 500+ vehicles, campsites for 86 single units, and group campsites for 125 people, all of which are immediately adjacent to the beach. The ORV zone is accessed from a sand road that runs behind the primary dune with 15 marked access points, the first of which is

immediately south of the pedestrian zone. The number of ORVs is limited to 145 at any given time, and the vehicles are regulated by a one-off/one-on system if the number exceeds 145. AN and AS are separated by 3.2 km of beach that is part of Assateague State Park.

Public use of the Maryland portion of AINS averaged 714,800 visitors annually from 1988 - 1992. Visitation tends to peak in July or August, with numbers exceeding 100,000 during either month (Figure 2). Even in January, which is usually the month of least visitation, visitors averaged 9,563 (SE = 1,341.8) from 1988 - 1993. A public use suggested that 11.3% of trips to AINS originate during November - March (Wright and Van Horne 1991). Of these visitors, 64% participated in recreational walking, 48% participated in wildlife photography, 12% participated in saltwater fishing, and 6% used ORVs (Table 1). These are common recreational activities observed on the beach during winter.

Temporal use of AINS by sanderlings has a bimodal distribution, with a vernal migration pulse in April - May and a larger autumn pulse in July - August (Figure 3). Biweekly beach surveys conducted by NPS personnel show that sanderling populations in November - March varied from 30 - 2700 during 1987 - 1992. Minimum counts during January, usually the month when sanderling populations are lowest, averaged 397 (SE = 128.8) from 1987 - 1993. Dunlins (*Calidris alpinus*) and black-bellied plovers (*Pluvialis squatarola*) also winter on AINS, but are less abundant and tend to be found on bayside tidal flats.

METHODS

Plots

Sanderling density and behavior, human activity, and prey availability were quantified on 200-m plots during Nov 1991 - Apr 1992 and Oct 1992 - Mar 1993. Sample plot distribution was stratified over location (AN, AS) and time of day (<1000, ≥1000 - <1400, ≥1400), and randomly allocated using 161-m (0.1 mile) segments on AINS beach. Plot boundaries were marked with PVC conduit. Beach slope was categorized as gentle, steep, or edge during both years; however, a clinometer was used to measure slope angle during the second year. Beach surface was categorized as smooth or undulate. Distances from the water line to the crests of both berm and primary dune (if present and < 100 m) were measured. Wind direction, wind speed, and ambient air temperature were recorded. Cloud cover was categorized in 25% increments.

Scan sampling methodology (Altmann 1974) was used to estimate time budgets of wintering sanderlings. Six scans, each ≥10 min apart, were recorded with a microcassette recorder; the first scan was initiated 15 min after marking the plot boundaries. Behavioral categories included peck/probe, glean, search-walk, search-run, search-pause, rest, maintenance, alert, stand, walk, run, fly, and aggression. Gleaning involved substrates other than sand; *e.g.*, debris and horseshoe crabs (*Limulus polyphemus*). Flying was recorded only if the event involved individuals leaving or landing upon the plot; consequently, total flight time was underestimated by scan sampling. Numbers of other avian species, pedestrians ≤10 m and >10 m from the water, equestrians, dogs, parked vehicles, moving vehicles, and aircraft ≤150 m AGL also were recorded during each scan. Total disturbances per plot was the sum of vehicles, pedestrians (including anglers and swimmers within 10 m of shore), equestrians, and dogs.

At the end of the sixth scan, prey availability in the plot was assessed with 101-mm diameter core samples (80 cm^2) to a depth of 4 cm (Loegering 1992). Five core samples were collected at 50-m intervals from within the swash zone, transferred to plastic bottles, fixed in 10% formalin, and dyed with Rose Bengal. Bottled samples were agitated and the elutriate was decanted through fine-mesh cheese cloth. Soft-bodied macroinvertebrates (≥1 mm) were

picked from the cloth and the remaining sand precipitate was sieved for bivalves. All organisms were preserved in ethanol, and subsequently classified as amphipods (Order Amphipoda), polychaetes (Class Polychaeta), coquina clams (*Donax variabilis*), and 3 size classes of mole crabs (≤10 mm, >10 mm - ≤20 mm, >20 mm; *Emerita talpoida*). Total invertebrates per plot was the sum of *Emerita*, *Donax*, polychaetes, and amphipods.

Plot-sampling protocol required that 200-m boundaries be established at the start of an observation period. Because sanderlings were sometimes already present on the plot, we chose to wait 15 min before initiating the first scan, regardless of the presence or absence of sanderlings. Sanderling occurrence during this setup period and their flush response (none, some, all) were recorded. We also recorded the occurrence of sanderlings on the plot at any time during the observation period, regardless of whether they were detected during scan sampling. The observation period was the total time spent on a plot, from setup through core sampling.

Sanderlings in flight were observed between scans of plots. Date, time, location, wind speed, direction, flock size, and direction of flight were recorded. Flock was defined as any group with ≥ 1 sanderlings. Wind direction was categorized as north or south. Data collected during October and November were pooled because of small sample sizes. For contingency analyses, the frequency of flocks was weighted by flock size. For parametric analyses, flock size was log-tranformed.

In addition to human activities that were scored during scans, we recorded total numbers of pedestrians, dogs, vehicles, and aircraft that entered the plot during the observation period. Parties that remained on the plot during the entire observation period or those that left but never returned to the plot were counted once; parties that passed through the plot but returned during the observation period were counted a second time. This total count of discrete activities during a known period was used to derive a rate of disturbance.

Local times were converted to time from sunrise (38° N) and time from nearest peak high tide (corrected for Sandy Hook, NJ; NOAA 1991, 1992, 1993). For categorical analyses, day was divided into early (< 3.5 h postsunrise), mid (3.5 - 7 h postsunrise), and late (≥ 7 h postsunrise) trimesters. Tidal stage was categorized as low (≤ 4.5 h prepeak or ≥ 4.5 h postpeak), flood (1.5 - 4.5 h prepeak), high (± 1.5 h peak), and ebb (1.5 - 4.5 h postpeak). Density and rate data were expressed as continuous, binomial, or ordinal variables (Table 12). The natural logarithmic transformation was applied to all density and rate data to stabilize the variance and reduce skewness (Sokal and Rohlf 1981:419); back-transformed data were expressed as geometric means. Behavioral proportions were normalized with the angular transformation (Sokal and Rohlf 1981:427).

Logistic regression was used to assess the influence of human activities on sanderling occurrence after controlling for other temporal and spatial variables. We used stepwise model selection method of PROC LOGISTIC (SAS 1987), with the level of variable entry and stay set at $p = 0.30$ and $p = 0.05$, respectively. We used analysis of covariance (ANCOVA) to determine the effect of human activities on sanderling density. We used multivariate analysis of variance (MANOVA) to determine the effect of disturbance occurrence on behaviors.

Intentional disturbance

Thresholds for agitation, ambulation, and flight responses to disturbance were determined by intentionally exposing sanderlings to anthropogenic activities. Sanderlings were approached in a vehicle (16 kph) or on foot (4.8 kph) within 0 m and 20 m of the swash zone; whether the approach was above or below the berm was recorded. As the birds were approached, weighted flagging was dropped on the beach when agitation, ambulation, and/or flight was first detected. Agitation included any signs of vigilant behavior and wing- or leg-stretching. Flushed

sanderlings were timed with a stop watch to determine time in flight. Distances between flagging(s) and the point at which sanderlings were first observed and/or flushed were subsequently measured with a tape to determine threshold distances. We tested associations between response and disturbance type, and response and distance from water with 2 x 2 contingency analyses (n = 88, df = 1). T-tests were used to test for differences between mean agitation, ambulation, and flush distances averaged by disturbance type.

Time and energy budget estimation

The numbers of sanderlings scored in each behavior (*i.e.*, subtotals) were summed over the six scans of each plot. The proportional time spent in each behavior was determined by dividing each subtotal by the total number of sanderlings observed during the six scans. Behavioral time budgets were subsequently constructed by taking a weighted (by sanderling count) average of plot values.

Time budgets were converted to energy budgets by weighting each behavioral category by an appropriate multiple of basal metabolic rate (BMR). BMR was estimated as 2.1889 $kJ \cdot h^{-1}$ using a mean body mass of 55 g (n = 24; see Chapter 2), an oxygen consumption value of 1.98 $ml \cdot g^{-1} \cdot h^{-1}$ (Castro 1987) and 20.1 $kJ \cdot l^{-1}$ of oxygen consumed as a conversion factor. BMR multiples for rest, agonism, alert, maintenance, walk, run, and fly behaviors were 1.2, 2.2, 2.2, 2.1, 1.7, 3.5, and 12.5, respectively (King 1974, Albright *et al.* 1983, Buttemer *et al.* 1986). The energetic cost of foraging was the sum of its proportional components: feed (2.2 X BMR), walk (1.7 X BMR), run (3.5 X BMR), and pause (1.7 X BMR). The energetic cost of thermoregulation was the difference between standard metabolic rate (SMR) and BMR. SMR ($kJ \cdot h^{-1}$) was approximated from the following regression equation for ruddy turnstones (*Arenaria interpres*; Kersten and Piersma 1987):

$$SMR = (-0.05 \cdot T_a + 1.708) \cdot 3.6$$

The y-intercept was recalculated such that SMR equalled BMR at the lower critical temperature (assumed to be 22°C). Mean hourly energy expenditure (HEE) was weighted by the sanderling count per plot and expressed as $kJ \cdot h^{-1}$.

SAS 6.04 (SAS Institute 1987) was used for all data analyses. Significance was $P \leq 0.10$ for all statistical inference unless otherwise specified.

RESULTS

NPS data indicate that the mean daily air temperature during the study period was 5.6°C (SE = 0.24, n = 281). Air temperatures during either winter rarely fell below 0°C for extended periods (NPS data; Table 2). A 2-way ANOVA (df = 9,268, P = 0.0001) suggests that mean temperatures did not differ between years (P = 0.139) but did vary among months (P = 0.0001); the year X month interaction also was significant (P = 0.095). Average daily temperatures were similar in November, December, and January during both winters, but were lower in February during 1992 (P = 0.012). The lowest temperatures recorded were -11.7°C on 19 and 20 Jan during the first winter, and -10°C on 2 and 19 Feb during the second winter. Wind speeds were consistently high on AINS. Daily wind speeds averaged 13 $km \cdot h^{-1}$ (SE = 0.35, n = 283) and maximum winds exceeded 36 $km \cdot h^{-1}$ 50% of the time. Winds exceeded 106 $km \cdot h^{-1}$ during the hurricane on 4 Jan 1992.

Plot distribution and beach morphology

A total of 552 plots was sampled during both winters. In 1991-92, 251 plots were sampled from 3 Nov - 3 Apr. In 1992-93, 301 plots were sampled from 7 Oct - 31 Mar. Plots were sampled on 215 d during these two periods, never more than 5 plots per d. Sampling was slightly biased towards weekends; 368 plots (67%) were completed on weekdays and 184 plots (33%) were completed on weekends. Consequently, estimates of disturbance rates for AINS were weighted by 0.7143 for weekdays and 0.2857 for weekends to adjust for this bias in subsequent analyses. The mean observation period was 81.2 min per plot (SE = 9.327, n = 552).

Plots were well distributed spatially and temporally; there was no relationship between time of day (early, mid, late) and location (AN, AS; χ^2 = 0.46, df = 2, P = 0.793). AN (n = 276) and AS (n = 276) were sampled equally. All 552 161-m segments were sampled at least once, and one as many as 10 times, during the study. Mean sampling frequency was 4.6 times per segment (SE = 0.183, n = 120).

Beach profiles of AN and AS were similar in some respects but differed in others (Table 3). The distribution of slope types was similar on both beaches (χ^2 = 0.213, df = 1, P = 0.644). However, mean distance between berm crest and waterline was less on AS than AN (t = 2.31, df = 524, P = 0.021). Plots with undulating surfaces (χ^2 = 55.78, df = 1, P < 0.001) and widths ≤ 100 m (χ^2 = 106.77, df = 1, P < 0.001) occurred more frequently on AS than AN.

Distributions of slope type (χ^2 =34.99, df = 2, P < 0.001) and beach width (χ^2 = 22.20, df = 1, P < 0.001) were dependent on year. During winter 1991-92, beaches tended to be steeper and narrower than in 1992-93. Whereas 44% of plots during the first year had beach widths ≤ 100 m, only 25% of plots were similarly categorized during the second year. Similarly, 8% of plots sampled during the first year were categorized as steep *vs* 2% during the second year. Neither the distribution of beach surfaces (χ^2 = 0.61, df = 1, P = 0.434) nor mean distance between berm crest and waterline (t = -0.24, df = 524, P = 0.808) were affected by year.

Beach slopes were measured with a clinometer during 1992-93. Beaches categorized as gentle had mean slopes of 6.1° (SE = 0.120, n = 263) and ranged from 1 - 10°. Beaches categorized as steep had mean slopes of 11.3° (SE = 0.184, n = 7) and ranged from 11 - 12°. Slopes categorized as edge were too steep to be measured well, but approximated 90°. Edge and steep slopes were pooled in subsequent analyses.

Human activity

Rates of human activity on the AINS beach during winter were generally low. The weighted average of the sum of vehicles, pedestrians, equestrians, and dogs was 0.61 events·h^{-1} (95% CI = 0.54 - 0.69), although rates as high as 41 events·h^{-1} were recorded on one weekend in Oct 1992. Vehicles and pedestrians accounted for most human activities, averaging 0.41·h^{-1} (95% CI = 0.36 - 0.46) and 0.19·h^{-1} (95% CI = 0.15 - 0.22), respectively.

Human activity levels varied spatially over AINS. The occurrence of human activities on a 200-m plot was strongly affected by location (χ^2 = 4.25, df = 1, P = 0.039); 64% of plots on AS *vs* 20% of plots on AN were visited at least once during the observation period (Table 4). Similarly, geometric mean activity rates during the winter were almost 6 times higher on AS than AN (t-test, P = 0.0001; Table 4). A 2-way ANOVA (df = 3, 548, P = 0.0001) suggests that mean rates varied by location, day of week (weekend *vs* weekday), and their interaction (P ≤ 0.002). Human activity averaged 0.20 events·h^{-1} on AN and 1.16 events·h^{-1} on AS (Table 4). Disturbance rates on AN did not differ between weekends and weekdays (P = 0.845), but did so on AS (P = 0.0001). Mean hourly rates on AN were 0.21 events (95% CI = 0.14 - 0.28) on weekdays and 0.19 events (95% CI = 0.09 - 0.29) on weekends. In contrast, mean hourly rates on AS were 1.02 events (95% CI = 0.83 - 1.24) on weekdays and 2.00 events (95% CI = 1.42 - 2.72) on weekends.

Human activity varied temporally over the winter. A 2-way ANOVA (Table 5) suggests that mean activity rates did not differ by year ($P = 0.143$) but differed among months ($P = 0.007$); there also was a year X month interaction ($P = 0.007$). Mean activity rates (excluding Oct) were highest in November ($\bar{x} = 0.94$, 95% CI = 0.70 - 1.22) and lowest in February ($\bar{x} = 0.37$, 95% CI = 0.22 - 0.54), although rates did not differ among January, February, and March ($P \geq 0.185$). The year X month interaction was expected because AINS was closed to public access after 4 Jan during the first winter. Mean activity rates were lower in February than during other months of the first winter ($P \leq 0.002$), but did not differ among months during the second year ($P \geq 0.56$).

Avifauna

A total of 3306 scans was recorded for 552 plots (only 5 scans were recorded for 6 plots because poor lighting restricted visibility). Bird numbers were averaged for each plot ($n = 552$) and weighted by day of week (weekend = 0.2857, weekday = 0.7143). Unless otherwise noted, all density estimates are expressed as number per 200-m plot.

The avian community during winter consisted primarily of sanderlings, dunlins (*Calidris alpina*), black-bellied plovers (*Pluvialis squatarola*), ring-billed gulls (*Larus delawarensis*), herring gulls (*L. argentatus*), and greater black-backed gulls (*L. marinus*). The sanderling was the most abundant wintering shorebird species on the open beach, with a geometric mean density of 1.39 (95% CI = 1.22 - 1.58) and a maximum density of 882. Sanderlings occurred on 57% of plots. Dunlins and black-bellied plovers were much less common, occurring on 5% and 3% of plots, respectively. Densities were low, averaging 0.05 dunlins (95% CI = 0.03 - 0.07) and 0.01 black-bellied plovers (95% CI = 0.01 - 0.02) per plot.

Gulls and terns, which primarily included laughing gulls (*L. atricilla*), Bonaparte's gulls (*L. philadephia*), royal terns (*Sterna maxima*), and caspian terns (*S. caspia*), were generally abundant with a geometric mean density of 0.44 (95% CI = 0.37 - 0.51) and a maximum density of 402. Gulls and terns occurred on 39% of plots. A 2 X 2 contingency analysis suggests that occurrences of sanderlings and *Laridae* on the beach were not independent ($\chi^2 = 14.3$, df = 1, $P < 0.001$). Gulls and terns were absent on 54% of 312 plots on which sanderlings occurred, and were present on 30% of 240 plots on which sanderlings were absent. On plots which sanderlings occurred ($n = 312$), sanderling densities were positively correlated with *Laridae* densities ($r = 0.275$, $P < 0.001$). Observations of other avian species during winter were rare. These other species occurred on 5% of plots and included boat-tailed grackles (*Quiscalus major*), common grackles (*Q. quiscula*), piping plovers (*Charadrius melodus*), semipalmated plovers (*Charadrius semipalmatus*), and American oystercatchers (*Haematopus palliatus*).

Sanderlings were not distributed equitably over AINS. Geometric mean density of sanderlings on AN was nearly twice that of AS ($t = 3.46$, df = 2.75, 275, $P = 0.0006$; Table 4). Sanderlings occurred on 60% of plots on AN, but only on 52% of plots on AS ($\chi^2 = 4.25$, df = 1, $P = 0.039$; Table 15). On plots where sanderlings were present, 69% were characterized as having smooth-surfaced beaches and 66% were wide beaches with dunes absent or > 100 m from the water. These morphological features were characteristic of the beach on AN rather than AS (Table 3).

Use of AINS by sanderlings varied temporally over the winter. A 2-way ANOVA (Table 5) suggests that sanderling abundance did not differ between years ($P = 0.614$) but varied among months ($P = 0.0001$). Mean sanderling density was highest in November, decreased in December, and was least in January - March. The year X month interaction ($P = 0.070$) suggested that variation among months differed between years. Although mean sanderling densities were lower in Nov and Dec 1991 than during the subsequent winter, the population remained at higher mean levels during the latter part (January - March) of the first winter.

A total of 738 flocks was recorded during the two winters. Sanderling flocks averaged 4.05 (95% CI = 3.68 - 4.47) with a mode of 1 and a median of 3. The largest flock observed in flight consisted of ≈ 500 sanderlings, although larger groups of birds were observed roosting on the beach. A 4-way ANCOVA suggests that mean flock size was affected by year, month, and wind speed ($P \leq 0.002$), but not by location or time of day ($P \geq 0.121$). Sanderling flocks, by several measures, were larger during early and late winter than during midwinter, when sanderlings commonly flew as singles and pairs (Table 6). Flock size was negatively correlated with wind speed ($r = -0.22$, $P < 0.001$).

A 2 X 3 contingency analysis weighted by flock size suggests that flight direction was dependent on time of day ($\chi^2 = 377.0$, $P < 0.001$). Most sanderlings flew north in the morning (61%) and at mid day (67%), but flew south (61%) late in the day. A 2 X 2 contingency analysis weighted by flock size also suggests that location influenced flight direction ($\chi^2 = 1110.7$ $P < 0.001$). Whereas 69% of sanderlings observed on AN during the day flew north, 64% of sanderlings observed on AS flew south.

Macroinvertebrates

A total of 2759 core samples of benthic macroinvertebrates was collected from the swash zone of 552 plots (only 4 cores were obtained for 1 plot). For analyses, the 5 cores per plot were treated as subsamples and invertebrate numbers in the 5 cores were summed for each plot (n = 552). Unless otherwise noted, all density estimates were expressed as number per 400 cm^2.

The swash-zone macroinvertebrate community during winter consisted of mole crabs (*Emerita talpoida*), amphipods (Order Amphipoda), polychaetes (Class Polychaeta), and coquina clams (*Donax variabilis*). *Emerita* was the most abundant organism, with a geometric mean density of 1.24 per 400 cm^2 (95% CI = 1.02 - 1.49) and a maximum density of 218; it occurred on 40% of plots. Amphipods were abundant also, with a geometric mean density of 1.01 per 400 cm^2 (95% CI = 0.82 - 1.21) and a maximum density of 148; they occurred on 34% of plots. Both polychaetes and *Donax* were much less common, occurring on 11% and 5% of plots, respectively. Densities were low, averaging 0.19 (95% CI = 0.13 - 0.25) polychaetes and 0.07 (95% CI = 0.04 - 0.10) *Donax* per 400 cm^2. However, the importance of polychaetes to foraging sanderlings during winter may be underrepresented by these statistics. Polychaete densities as high as 35 per 400 cm^2 in Jan and 12 per cm^2 in Feb occurred infrequently on plots, a period when prey availability was otherwise low.

Except for *Emerita*, invertebrates were not distributed equitably over AINS. Total invertebrate, amphipod, polychaete, and *Donax* densities were higher on AN than AS (t-test, $P \leq 0.03$, Table 4). Similarly, invertebrate occurrence was associated with location ($\chi^2 = 9.93$, df = 1, $P = 0.002$); whereas invertebrates occurred on 58% of plots on AN, invertebrates were found on only 45% of plots on AS (Table 4).

Separate 2-way ANOVAs (Table 5) suggest that total invertebrates and *Emerita* mean densities were higher during the first winter ($P \leq 0.008$), whereas *Donax* densities were higher during the second year ($P = 0.05$). Total invertebrate, *Emerita*, amphipod, and *Donax* densities varied monthly during the winter ($P < 0.0001$). Mean invertebrate densities were 50.52 (95% CI = 38.69 - 65.88) in October, decreased to 0.20 (95% CI = 0.09 - 0.31) in February, and increased to 1.14 (95% CI = 0.77 - 1.59) in March. *Emerita* population phenology was not identical during both years ($P = 0.0001$). *Emerita* populations in 1991-92 declined precipitously during the third week in December and began increasing during the first week in March; in contrast, populations in 1992-93 declined during the third week in November and showed no evidence of increasing by April.

One-way ANOVAs (df = 3,548) suggest that total invertebrate, amphipod, and polychaete densities within the swash zone were affected by tidal stage ($P \leq 0.001$). Geometric mean

invertebrate density was highest ($\bar{x}$ = 3.78, 95% CI = 2.74 - 5.10) at low tide and least ($\bar{x}$ = 1.43, 95% CI = 0.93 - 2.05) at high tide. Geometric mean densities of both amphipods and polychaetes similarly peaked at low tide, whereas mean *Emerita* and *Donax* densities were not affected by tidal stage ($P \geq 0.54$).

Effect of observer activity on sanderling occurrence

The plot sampling protocol required that 200-m boundaries be established at the start of an observation period. Because sanderlings were sometimes already present on the plot, we were concerned about the effect of observer activity on sanderling activity, particularly if some or all of the sanderlings flushed. To minimize possible observer effects, we chose to wait ≥ 15 min before initiating the first scan regardless of the presence or absence of sanderlings on the plot. Although observers were instructed to minimize their presence, some or all of the sanderlings that were already present flushed from 36 of 141 plots. However, a 2 X 2 contingency analysis suggests that the occurrence of sanderlings on the first scan (*i.e.*, 15 min later) was independent of whether sanderlings that were initially present flushed or not (χ^2 = 1.80, df = 1, P = 0.180).

Although the continued presence of an observer during an observation period may have affected sanderling behavior, there is circumstantial evidence that observer presence did not affect the likelihood of sanderlings occurring on the plot. Occurrences of sanderling on both the first scan (χ^2 = 136.2, df = 1, $P < 0.001$) and on the plot at any time during the observation period (χ^2 = 79.5, df = 1, $P < 0.001$) were dependent on whether sanderlings were initially present on the plot. Sanderlings were subsequently present sometime during the 60 - 80 min observation period on 96.5% of plots that initially had birds present, regardless of whether they were flushed or not. In contrast, sanderlings were only present sometime during the observation period on 54.2% of plots that did not initially have sanderlings present. Because observers continued to be present on plots regardless of the initial presence of sanderlings, these data suggest that the likelihood of sanderlings occurring on a plot varied independently of observer presence.

Intentional disturbance

Of 88 trials, 45 assessed vehicles, 60 were conducted at the water's edge, and 57 were conducted below the berm. Sanderlings eventually flushed in 39, ran around the vehicle or pedestrian in 18, showed only agitation in 4, and did not overtly respond in 27. Mean and median agitation distances were 19.5 m (n = 43, SE = 1.65) and 16.6 m, respectively. Mean and median ambulation distances were 16.6 m (n = 17, SE = 3.74) and 14.5 m, respectively. Mean and median flush distances were 15.1 m (n = 39, SE = 1.58) and 12.9 m, respectively.

T-tests suggest that mean agitation distance did not differ by disturbance type (df = 21, 20, P = 0.331). However, sanderlings generally walked/ran (P = 0.086) or flew (P = 0.015) at greater distances in response to an approaching pedestrian than vehicle. Mean ambulation distances were 21.4 m (n = 11, 5.25) and 8.0 m (n = 6, SE = 1.57), respectively, in response to pedestrians and vehicles. Mean flush distances were 17.8 m (n = 24, SE = 17.83) and 10.8 m (n = 15, SE = 2.88), respectively, in response to pedestrians and vehicles (Figure 4).

Contingency analyses suggest that sanderlings clearly flushed more frequently in response to a pedestrian than vehicle (χ^2 = 4.50, df = 1, P = 0.034), particulary when the disturbance source was approaching at the water's edge (χ^2 = 23.00, df = 1, $P < 0.001$) or below the berm. Of 39 flushes, 61.5% were due to pedestrian approaches, 94.9% were at the water's edge, and 87.2% occurred below the berm. Mean time in flight was at least 12.3 sec (n = 39, SE = 1.71); sanderlings flew out of sight on 7 occasions.

Temporal and spatial relationships among human activity, sanderlings, and invertebrate prey.

Sanderling, human activity, and invertebrate prey densities clearly covary temporally on AINS, probably in response to seasonal changes in ambient air temperature. Weekly averages of sanderlings (n = 26; Figure 5) were positively correlated with invertebrate density (r^s = 0.46, P = 0.018), human activity per hour (r^s = 0.46, P = 0.019), and ambient air temperature (r^s = 0.68, P = 0.0001). Levels of all four variables peaked in October, declined slightly in November and December, were minimal during January and Februrary, and began to increase in late March and early April.

Sanderlings appear to have reduced the impact of conflicting temporal use of AINS by adjusting their spatial distribution. Sanderling densities averaged by 161-m increments (n = 120) continued to be positively correlated with invertebrate density (r^s = 0.36, P = 0.0001; Figure 6) but were now negatively correlated with human activity rate (r^s = -0.16, P = 0.074; Figure 7). Similarly, sanderling occurrence during any of six scans for a given plot (n = 552) was dependent on the occurrence of human activity during any of those scans (χ^2 = 3.15, df = 1, P = 0.076); sanderlings occurred on 58% of undisturbed plots but only 48% of disturbed plots.

Does human activity affect sanderling occurrence?

The likelihood of sanderlings occurring during any one of six scans of a plot was modelled with logistic regression. This analysis must be adjusted by confounding sources of variation; in particular, sanderling populations temporally and positively covary with human use levels, invertebrate populations, and ambient air temperatures (see above). Thirty-four variables were considered in the stepwise model-building procedure (Table 7): human activity (17), invertebrate populations (7), beach morphology (4), time and tide (4), and weather (2). Because some spatial variables were not measured initially, only 3,163 scans of 528 plots were used in the following analyses.

The final logistic regression model selected during the stepwise procedure correctly classified 67% of predicted values for 528 plots (-2 LOG L χ^2 = 3.34, df = 10, P = 0.068; Table 8). The likelihood of sanderlings occurring on a plot was negatively associated ($P \leq 0.07$) with increasing pedestrian traffic within 10 m of the water, total invertebrate density, *Emerita* density, month, wind speed, and undulating beach surfaces. Conversely, sanderling occurrence was positively associated ($P \leq 0.07$) with increasing invertebrate occurrence, ambient temperature, tidal stage and the second winter.

The odds ratio suggests that increasing pedestrian traffic (from 0 to 26) during a scan reduced the likelihood of sanderlings occurring during that scan by as much as 45% (Table 8). Prey availability, season, weather, and beach surface mediated the predicted probability of that occurrence. Surprisingly, increasing prey availability had conflicting effects on sanderling occurrence. Sanderlings were more likely to occur on a plot as invertebrates occurred more frequently (0 - 5) in the five core subsamples. Paradoxically, invertebrate and *Emerita* absolute densities decreased the likelihood of sanderlings occurring on a plot. This anomaly is at least partly explained by the interaction of sanderlings with tide and prey availability. Although mean invertebrate densities in the swash zone were highest at low tide, sanderlings were more likely to occur on the beach as tidal stage increased. Sanderlings at AINS often foraged on the estuarine tidal flats when they were exposed at low tide; as water flooded into the bay, sanderlings moved to the marine beaches where they would mill around in preparation for roosting.

Does human activity affect sanderling density?

Sanderling density was not correlated with different measures of human activity levels (Table 9).

However, sanderling density was positively correlated with invertebrate densities and ambient air temperature, and negatively correlated with wind speed. Consequently, these variables were included in the following analyses.

The effect of the occurrence of human activity on mean sanderling counts per 200 m were assessed with ANCOVA, in which variance was blocked by invertebrate occurrence (0, 1) and adjusted for the effects of Julian date, air temperature, and wind speed as covariates (Table 10). When all plots were included in the model regardless of sanderling occurrence (n = 552), mean sanderling count was 2.4 times higher on plots with no human activity than those with activity (P = 0.029). Sanderling counts averaged 1.52 (95% CI = 1.79 - 1.28) on undisturbed plots and 0.63 (95% CI = 1.39 - 0.47) on disturbed plots. The occurrence of invertebrate prey did not affect mean sanderling densities (Table 10).

However, this same analysis applied only to plots on which sanderlings occurred (n = 312) did not show human activity as a significant effect (Table 10). Mean sanderling counts were 3.72 (95% CI = 3.17 - 4.33) and 3.06 (95% CI = 1.90 - 4.68), respectively, on undisturbed and disturbed plots. However, mean sanderling count was 2.4 times higher on plots with invertebrate prey present than on those with prey absent (P = 0.003).

These two ANCOVAs suggest that sanderlings may have initially selected plots because of the absence of disturbance, but the decision to remain on the plot was dependent on the presence of invertebrate prey. In other words, the absence of invertebrate prey exacerbated the effect of disturbance on sanderling density (Figure 8). Mean sanderling densities were highest on plots with invertebrate prey and no disturbance ($\bar{x}$ = 5.25, 95% CI = 4.22 - 6.50) and lowest on those with disturbance and no invertebrate prey ($\bar{x}$ = 1.79, 95% CI = 0.61 - 3.84).

An unexpected large-scale manipulation occurred during the first year when AINS was closed to public access after 4 Jan due to hurricane-induced wave damage. Although this closure had very little effect on human activity levels on AN, AS became an essentially an undisturbed beach except for NPS employees and the few private landowners that remain within the boundaries of AINS. Consequently, if human activity has the potential to depress sanderling populations over a large area, then sanderling abundance on AS should be higher during the latter part of the first winter, after adjusting for confounding sources of variation.

We tested this hypothesis with a 3-way ANCOVA model in which the effects of year, beach location (AN vs AS), and season (early *vs* late) on mean sanderling density was assessed, after correcting for varying invertebrate density and air temperature (Table 11). The location X year X season interaction term was significant (P = 0.029). Mean sanderling densities declined from early to late season on AN during the first winter, and on both AN and AS during the second winter ($P \leq 0.001$); however, mean density did not differ between early and late season on AS during the first winter (P = 0.927). During the first year, mean sanderling counts on AS were 1.01 per 200 m (95% CI = 0.44 - 1.79) during the early season and 0.97 per 200 m (95% CI = 0.56 - 1.49) during the late season. During the second year, mean sanderling densities on AS were 2.97 per 200 m (95% CI = 1.89 - 4.44) during the early season and 0.33 per 200 m (95% CI = 0.05 - 0.68) during the late season; this suggests a 9-fold decrease in sanderling use of AS during the day because AINS remained open for public access.

Does human activity affect time and energy expenditures?

On average (n = 312), sanderlings spent 50% of their time foraging, 26% of their time resting, and 15% of their time in non-foraging locomotion (Table 12). When sanderlings foraged, 65% of their time was spent actively searching or pausing; only 35% of their foraging time was spent probing, gleaning, or pecking. Including search time during foraging bouts, sanderlings spent a total of 45% of their diurnal hours flying, running, or walking. This time budget results in a mean energy expenditure of 8.75 $kJ \cdot h^{-1}$ (n = 312, SE = 0.91) or 210 $kJ \cdot d^{-1}$.

Several expressions of human disturbance were associated with sanderling behavior (Table 13). In general, increasing levels of human activity were positively correlated with increasing time spent in flight and maintenance behaviors, and negatively correlated with time spent roosting and ambulating. Ambulation was curtailed, whether it occurred during foraging or at other times, suggesting that sanderlings were forced to fly around disturbance sources rather than walk or run. Total vehicles, parked vehicles, and moving vehicles were positively correlated with time spent vigilant.

MANOVA suggests that sanderling behaviors differed on disturbed and undisturbed plots (Table 14). On average, disturbed sanderlings spent 177% more time in maintenance behaviors (P = 0.0001) and 151% more time in flight (P = 0.0002), and 42% less time resting (P = 0.036) than undisturbed sanderlings. Sanderlings were frequently observed stretching wings and legs as pedestrians or vehicles approached, and preening after the disturbance source passed.

Mean foraging time did not differ between disturbed and undisturbed sanderlings (P = 0.541), suggesting that disturbance did not reduce total time allocated to foraging. However, disturbance may have reduced foraging efficiency; a separate MANOVA of the three foraging subcategories (df = 3,308, P = 0.001) suggests that disturbed sanderlings paused more (P = 0.002) and moved less (P = 0.020) while foraging than undisturbed sanderlings. This would be a reasonable outcome if behaviors scored as *pause* included more subtle forms of vigilance.

A 2-way ANOVA with interaction was initially used to assess the influence of disturbance and invertebrate occurrences on mean hourly energy expenditure (HEE). Invertebrate occurrence was included in the model because their densities were so highly correlated with time spent foraging and resting (Table 13). Although the full model was significant (df = 3,308, P = 0.0001), neither the main effects nor interaction term were significant ($P \geq 0.280$). A re-analysis without the interaction term suggests that mean HEE was higher on plots where human activity occurred (P = 0.056) and higher where invertebrate prey occurred (P = 0.0001). Arithmetic means of HEE for sanderlings on undisturbed and disturbed plots were 6.3 $kJ \cdot h^{-1}$ and 9.6 $kJ \cdot h^{-1}$, respectively (Table 15).

Monthly means of HEE suggested a distinct bimodal distribution of energy expenditure over the winter season (Figure 9). The first pulse of HEE was likely due to migration-induced hyperphagia by transient sanderlings; the second pulse was likely due to fattening by winter-resident sanderlings. These premises were partially supported by the fact that the variation in proportion of time spent foraging coincided well with varying HEE (Figure 9). In addition, mean HEE for sanderlings on disturbed plots coincided with HEE averaged for all plots after November, suggesting that disturbance rates were not high enough to significantly affect the mean HEE of sanderlings that wintered on AINS. However, it is apparent that mean HEE in October was substantially elevated because of high disturbance levels (Figure 9).

Energy expenditure differed for sanderlings that used different areas of AINS during the nonbreeding season. Mean HEE was 9.0 $kJ \cdot h^{-1}$ for sanderlings on AS and 6.0 $kJ \cdot h^{-1}$ for sanderlings on AN. Higher energy expenditures on AS were presumably due to more time spent foraging and flying, and less time spent resting and ambulating (Table 16). On average, sanderlings spent 38% more time foraging (Table 16) on AS, an area which averaged 42% fewer invertebrates than AN (Table 4). Paradoxically, foraging time and invertebrate abundance were positively correlated for those plots on which sanderlings occurred (Table 13). This suggests that sanderlings were not increasing their foraging time on AS due to fewer invertebrates; rather, sanderlings were extending their feeding time <u>despite</u> lower prey abundance, implying that they were compensating for higher energy costs.

Most of the variation in HEE was clearly attributable to time spent in flight. Stepwise multiple regression modeling suggested that HEE increased with increasing invertebrate abundance, foraging time, flying time, and the number of parked vehicles, but decreased with increasing air temperatures (R^2 = 0.932, df = 5,306, P = 0.0001). Partial correlations suggest that time spent

in flight and air temperature accounted for 92% and 37%, respectively, of the variation in HEE; the number of parked vehicles only explained an additional 1% of the variation.

DISCUSSION

Because tradeoffs between foraging or dispersing are intrinsically linked to food quality and availability (Madsen 1985*c*, Sincock *et al.* 1966), it is easy to understand why some researchers argue that human disturbance effectively lowers habitat quality, carrying capacity, or functional availability of habitats (Williams and Forbes 1980, Korschgen *et al.* 1985, Morton *et al.* 1989*b*, Belanger and Bedard 1989, Ebbinge 1991). Habitat Suitability Index models (U.S. Fish and Wildlife Service) that incorporate disturbance as a parameter are based on this premise. Several studies do, in fact, show that chronic levels of disturbance may ultimately affect habitat selection (Williams and Forbes 1980, Tuite *et al.* 1983, Madsen 1985*b*) and spatial distribution (Norris and Wilson 1988, Keller 1991) of waterfowl. There is also a landscape component to human disturbance that is likely to be missed in most studies. Sincock *et al.* (1966) recognized that waterfowl tolerance of disturbance is likely relative to the level of disturbance on adjoining areas; they argued that waterfowl response to hunting and boating activity in Back Bay, Virginia, was dependent on the level of similar activities immediately south in Currituck Sound, North Carolina.

In many respects, the concept of compensatory foraging touches on issues central to theories about allocation of time and energy resources by birds (cf. Paladino 1989). That a free-ranging bird can alter its time budget to accomodate increased foraging draws attention to the plasticity of loafing time (see Herbers 1981, Krebs and Harvey 1986, and Skutch 1989) and the importance of maintenance behaviors (since they remain fairly constant despite adjustments in other parts of the time budget). That a free-ranging bird can voluntarily increase rate of food intake (although I suspect at the expense of increased predation risk or reduced foraging efficiency) seems to imply that food may not proximately limit avian populations (but see Lack 1954 and Newton 1980).

King and Murphy (1985) argued that the evidence actually suggests that food is a plausible limiting factor in the absence of other constraints, but not necessarily as a *proximate* regulator. In much the same way that "the ghost of competition past" is now recognized as contributing to avian community structure, so must nutritional stress in the past be acknowledged as structuring foraging strategies. King and Murphy (1985) suggested that there is little empirical evidence of nutritional stress in contemporary wild populations because birds have developed compensatory mechanisms for buffering against periods of nutritional stress (also see Herbers 1981). These adaptations take the form of nutrient reserves and reallocation of nutrient expenditures; the extent of the buffer depends not only on the difference between nutrient supply and demand, but also on metabolic and behavioral plasticity (see Dugan *et al.* 1981, Davidson 1981).

Although King and Murphy (1985) did not mention compensatory foraging, certainly alternative foraging strategies could be considered plastic behavior. It is not surprising that there are alternative strategies for acquiring food (within a species); rather, it is unexpected that birds do not choose the strategy that maximizes net gain. As I indicated previously, birds can clearly forage faster and longer than normal when stressed. One explanation for this observation is that birds operate within an *optimal working capacity*, proximately limited by physiological constraints (cf. Drent and Daan 1980). Interpreted loosely, this concept suggests that there is some maximum substainable metabolic expenditure that individuals may exceed for short periods, but only at the risk of reduced condition (i.e., fitness) due to physiological and muscular fatigue. Alternatively, Mrosovsky and Powley (1977) presented persuasive evidence that many terrestrial vertebrates operate within set points for whole body and/or lipid masses.

It was apparent from the outset of this study that the potential for conflicting use of AINS by human recreationists and sanderlings was high. Peak monthly sanderling counts by AINS personnel were, in fact, positively correlated ($r_s = 0.334$, $P = 0.008$, $n = 62$) with estimates of human visitation during 1988 - 1992. These similar temporal patterns confound analyses because of their seasonal overlap. Pfister *et al.* (1992), for example, had to account for variation in census data due to migration phenology before they were able to demonstrate the negative effect of vehicular traffic on shorebird abundance. Other variables such as food availability and weather also may mask the effects of disturbance. Sincock *et al.* (1966) recognized that waterfowl will tolerate more human disturbance on their wintering grounds where food quantity or quality is high. Schueck and Marzluff (1995) recently showed that weather explained more variation in raptor abundance than did disturbance due to military activity at a study site in Idaho.

To a certain extent, we had expected analytical difficulties because of the multivariate nature of the problem. Underwood (1989) discussed concerns (that are relevant to this study) with the assessment of stress in nonexperimental studies; *i.e.*, nonreplicated comparisons of perturbed and unperturbed populations, and correlations and spatial comparisons. Most of his criticisms stem from failure to adequately account for spatial and temporal variation. However, multiple replication (of AN and AS) on a large scale was not feasible. To minimize these concerns, we measured food availability *in situ* and used an approach where plots were randomly allocated within beach location (AS, AN) and time of day strata; the latter also balanced tide considerations. Depending on the analysis, we adjusted *posthoc* for variation due to weather (temperature, wind speed), prey availability, seasonality (Julian date), and spatial characteristics. Where appropriate, ANCOVA was the preferred technique, either blocking with a binomial variable or adjusting with a covariate. We also reduced data by summing or averaging counts over spatial and temporal increments (*i.e.*, cumulative counts) and then applying correlation or contingency analyses.

Some human activities on the beach at AINS were clearly disturbing to migrating and wintering sanderlings. Of the human activities that were assessed in this study, pedestrians within 10 m of the swash zone was the most disturbing to sanderlings. Increasing levels of pedestrian traffic decreased the likelihood of sanderling occurrence on 200-m plots by as much as 45% (Table 8). Our data suggest that the average threshold of response to pedestrians may be 20 m for wintering sanderlings. Sanderlings generally showed agitation and began to ambulate and/or flush when pedestrians approached within 20 m; in contrast, sanderlings responded to vehicles at only half that distance (Figure 4). Similarly, 20-m stretches of beach with an average of ≤ 2 persons were tolerable to foraging sanderlings in Florida (Burger and Gochfeld 1991). The effect of pedestrian traffic on sanderlings was aggravated because of the duration of the stimulus: pedestrians at 4.8 kph remain within a 20-m radius for 30 sec whereas ORVs at 16 kph remain within a 10-m radius for only 1 sec. Pfister *et al.* (1992) also considered pedestrians to be more disturbing to sanderlings than vehicular traffic.

We did not attempt to categorize pedestrian traffic by group size or activity type. Groups of people are both ephemeral and amorphous, and it is often difficult to determine exactly what they are doing, particularly while scanning the activities of sanderlings. In one recent survey of AINS, however, 76% of respondents were in groups of 3 - 10 persons and only 4.1% were singles or pairs (Wright and Van Horne 1991). These data are one reason that we believe that the presence or absence of human activity on 200-m study plots generally explained variation in sanderling abundance and occurrence better than actual counts of pedestrians. It is not the number of people *per se*, but their distribution in time and space on the beach, that determines their impact. Incidental observations of sanderling-human interactions suggest that a single, cohesive group of 10 persons walking through the swash zone, for example, was much less disturbing to sanderlings than 10 individuals passing through the same stretch of beach over 30 min. Similarly, 10 persons above the berm, regardless of their grouping, were much less disturbing than 10 persons below the berm.

Although sanderlings avoided pedestrians, ORVs traveling just above the swash zone or below the berm continued to be problematic. In several intentional disturbance trials, sanderlings ran around the approaching vehicle at the last instant simply to avoid being run over. Mortality due to vehicular traffic has been documented for piping plovers (*Charadrius melodus*), another shorebird species that frequently uses the high-energy beach (Melvin *et al.* 1994). Parked ORVs also posed a problem because human activity (*e.g.*, fishing, sunbathing, picnicking) was usually associated with them. Sanderlings clearly responded to increasing numbers of both parked and moving vehicles that were on the same 200-m stretch of beach; ORVs were positively correlated with vigilance, flight, and maintenance behaviors, and negatively correlated with walking, running, and roosting. Pfister *et al.* (1992) similarly found that sanderling abundance showed a monotonic decline (up to 50%) in response to increasing levels of vehicular disturbance.

Because sanderlings occurred less frequently where pedestrians were present, mean densities were nearly 60% less on disturbed than undisturbed plots. Sanderling abundance at a staging area in Massachusetts was similarly reduced by 50% at higher levels of vehicular disturbance (Pfister *et al.* 1992). At AINS, however, this outcome was mediated by the occurrence of invertebrate prey within the swash zone. Mean sanderling density on plots with prey but no human activity was 3 times higher than on plots with human activity but no prey (Figure 8). Sincock *et al.* (1965) similarly argued that wintering waterfowl are more tolerant of disturbance in areas of high food quality or quantity (or at least higher than adjoining areas).

Higher prey availability not only compensates for increased energy expenditure due to disturbance, it may also compensate for the apparent reduction in foraging efficiency due to disturbance. Most human activities reduced active search time (*i.e.*, walking, running) during foraging in order to increase time spent pausing or feeding, or both (Tables 13, 14). Behavior scored as **pause** probably included more subtle forms of vigilance. Behavior scored as **feed** probably included more subtle forms of agitation; we frequently observed caged sanderlings peck at the cage floor when they were exposed to disturbing stimuli (Morton 1996).

Migrating and wintering sanderlings that used the high-energy beach at AINS spent 50% of their time foraging and 26% of their time roosting (Table 12). Mean energy expenditure, estimated from diurnal time budgets, was 210 $kJ \cdot d^{-1}$ or 4 times BMR. Castro *et al.* (1992) reported that nonbreeding sanderlings in New Jersey, 200 km to the north of AINS, spent 50% of their time foraging but almost 40% of their time roosting; daily energy expenditure (DEE), estimated from double-labeled water, was 200 kJ (SE = 12.8) or 4.2 times BMR. These corroborative estimates of DEE for sanderlings at similar latitudes alleviate some concerns about the reliability of using time budgets to estimate DEE (*e.g.*, Weathers *et al.* 1984).

Sanderlings wintering at AINS were clearly existing at or near their maximum sustainable metabolic rate. Undisturbed sanderlings at AINS expended 151 $kJ \cdot d^{-1}$ or 2.9 times BMR; in contrast, disturbed sanderlings expended 231 $kJ \cdot d^{-1}$ (Table 15) or 4.4 times BMR. Estimates of DEE by nonbreeding sanderlings at other latitudes ranged from 100 kJ in Panama to 135 kJ in Texas or 2.1 - 2.8 times BMR (Castro *et al.* 1992). DEE estimates for shorebirds in general range from 2.9 - 3.1 times BMR (Kersten and Piersma 1987). The high energetic cost of wintering at AINS is to be expected, as 38° N latitude is approaching the northern-most point of their nonbreeding range (see Root 1988 for additional discussion). Nonetheless, it is apparent that human disturbance has elevated the energetic cost of wintering at AINS.

We had originally proposed that human disturbance would affect sanderlings by increasing existence metabolism (EM) and that logical responses would be to increase energy intake, habituate, and/or disperse (Morton 1996). Balance trials with captive sanderlings suggest that EM does, in fact, increase in response to low-level chronic disturbance, albeit slightly (Morton 1996). The existence metabolism of undisturbed sanderlings was 95 $kJ \cdot d^{-1}$; in contrast, disturbed sanderlings expended 102 $kJ \cdot d^{-1}$. Almost 50% of behaviors observed during disturbances were scored as escape, suggesting that increased EM was largely due to the

costs of additional locomotion within the caged environment.

However, it is apparent that most of the variation in DEE is attributable to activities outside of a caged environment. Whereas mean energy expenditure for caged sanderlings increased only 7% in response to chronic disturbance, mean energy expenditure for free-ranging sanderlings was 53% higher when disturbed. Castro *et al.* (1992) showed that minimum air temperature and carcass mass explained 70% of the variation in DEE (estimated from double-labeled water). We found, however, that although *in situ* air temperature was important, the proportion of time spent in flight explained 92% of the variation in HEE (estimated from time budgets). Similarly, Bryant and Tatner (1991) positively correlated intraspecific variation in DEE of several avian species with time spent flying. This is not surprising given that theoretical estimates of the energetic cost of avian flight are extremely high, ranging from 5 - 43 times BMR (King 1974).

Time in flight ultimately determines the energetic cost of disturbance. Mean time in flight in response to intentional disturbance was at least 12.3 sec (n = 39, SE = 1.71); this datum coincides with the observation by Burger and Gochfeld (1991) that sanderlings may flush as many as 5 times in one minute in response to repeated disturbance. On average, then, sanderlings expend 93.5 J each time they flushed, which represents an additional 1% of undisturbed HEE. It is apparent that sanderlings using AINS may have a difficult time compensating for increases in flight time and HEE that would occur at human disturbance rates as high as $41 \cdot h^{-1}$.

Time spent flying varied widely despite the fact that sanderlings both avoided the most disturbing of human activity, *i.e.*, pedestrians, and were generally reluctant to flush in response to vehicles. Less than 39% of flushes during intentional disturbance trials were due to vehicles and, except in one case, all occurred because the vehicle was traveling at the water's edge; *i.e.*, the sanderlings were in danger of being trampled. Klein (1993) similarly reported that only 50% of egrets and herons flushed in response to intentional human disturbance. Yet, it is clear that time in flight was varying in response to human disturbance. Not only were most measures of disturbance positively correlated with time in flight (Table 13), but disturbed sanderlings averaged 152% more time in flight than undisturbed sanderlings (Table 14).

In addition to avoiding some human activities altogether, sanderlings appear to have further compensated for relatively high disturbance rates at AINS by using AN and AS differently. Human activities were prohibited or restricted on AN, effectively creating a 5.9-km *refugium* from human disturbances that occurred elsewhere on AINS. Disturbance levels averaged 6 times lower on AN than AS, with an even greater disparity on weekends. Concomitantly, invertebrate abundance was 1.7 times higher on AN as AS. This undisturbed environment with high food availability consequently supported a sanderling population on AN that averaged nearly twice that of AS (Table 4). At least during diurnal hours, sanderlings on AN rested more and fed less, expending 50% less energy than those on AS (Table 16).

There is some evidence that sanderlings may have redistributed themselves at night to accommodate higher levels of disturbance on AN during the day. Sanderlings occurred on 9.3% more sample stations on AS during nocturnal surveys than during diurnal surveys earlier that same day (Morton 1996). Most sanderlings were observed flying north in the morning and at mid-day, presumably to roost on the undisturbed beach at AN. Conversely, most sanderlings flew south late in the day, presumably to redistribute themselves over AINS in preparation for late afternoon and nocturnal feeding bouts.

An unintentional large-scale manipulation occurred when the NPS closed AINS to public access during the latter part of the first winter because of beach damage by hurricane-induced waves. Sanderling densities on AS were maintained at similar levels throughout the first winter. In contrast, the mean sanderling density on AS was 9 times lower during the latter part of the second winter, even after adjusting for varying ambient temperatures and invertebrate densities. Human disturbance rates showed an inverse pattern in response to the park closure,

suggesting that disturbance was at least partly responsible for this large-scale disparity in sanderling distribution over AINS during the two winters. This redistribution of winter-resident sanderlings and their selective use of AINS resulted in an average energy expenditure that would not be significantly different had sanderlings existed in an undisturbed environment (Figure 9). However, it is clear that transient sanderlings that migrate through AINS during the autumn either were unable to or lacked the site-specific familiarity to compensate for the higher disturbance levels at that time of year. Mean HEE during Oct was nearly 40% higher for all sanderlings than for undisturbed sanderlings only. Sanderlings that stage at AINS in autumn may have difficulty reaching an optimal nutritional status for migration because of elevated energy expenditure.

Management recommendations

Disturbance by human recreationists on the beaches at AINS are clearly impacting nonbreeding sanderling populations. Although sanderlings have compensated for the effects of disturbance by redistributing themselves and their behavior to less disturbed areas of AINS, wintering sanderling abundance is depressed, wintering sanderlings are at or approaching their maximum sustainable metabolic rate, and staging sanderlings in autumn may have difficulty reaching an optimal nutritional status for migration because of elevated energy expenditure.

Perhaps the most important message to managers of public lands is that human disturbance is not simply an inconvenience to their wildlife resources but, as in this case, a significant negative impact on their life history. Wilkes (1977) was perhaps the first in the literature to criticize the distinction that managers make between consumptive and nonconsumptive users, arguing that this dichotomy has allowed certain activities to flourish on public lands when, in fact, they have been extremely detrimental to wildlife and other living resources. Additionally, the demand on natural resources by this user group is expected to increase; "nonconsumptive" recreational participants in the U.S. are projected to increase nearly 150% over the next 50 years (Flather and Cordell 1995).

On the other hand, many researchers have been careless in their use of disturbance as a term. Human activity is not intrinsically synonymous with disturbance. Some published researchers have concluded that disturbance has no impact on populations; that is literally impossible. Disturbance is just that: Disturbing! An activity may be deemed to have no impact and therefore is not a disturbance. Such an inference needs to be further constrained. A human activity may not be disturbing to some animals during certain periods in their life history, but may be to other conspecific or interspecific individuals at the same or different times. Burger (1995) recognized the importance of this concept when she recommended that researchers document when human presence does not cause an effect as well as when it does.

Assateague Island National Seashore was established in 1965 (PL 89-195) for the general purposes of public outdoor recreation, including conservation of natural features contributing to public enjoyment. However, subsequent amendments (PL 94-578) in 1976 required consideration of "measures for the full protection and management of the natural resources and natural ecosystems of the seashore". The NPS clearly has a legal mandate to consider the impacts of human disturbance on sanderlings and other living resources on AINS. Recommendations for managing the effects of human disturbance at AINS are the following [also see Morton (1995) and Burger (1995)]:

(1) Levels and types of human activities need to be monitored as part of the routine biological surveys conducted by NPS personnel. Specific recommendations for modifying the existing biweekly beach survey are discussed in Chapter 3. The vehicle counters that the NPS maintains on roads also are an important tool for indexing disturbance trends. Pfister *et al.* (1992), for example, acknowledged that although the most serious disturbance was probably caused by pedestrians and unleashed dogs, the vehicle count provided an

index of disturbance that was easiest to obtain.

(2) ORV traffic should remain above the berm and vehicles should be parked ≥ 30 m (100 ft) from the swash zone regardless of where the berm is. This single restriction would mitigate much of the impact of vehicular traffic on sanderlings. Although a minimum distance from the water's edge could be specified for travel (*e.g.*, 30 m), the water's edge varies widely with wave action; consequently, both compliance and enforcement are difficult.

(3) At the very least, maintain existing public use restrictions on AN. In this regard, NPS management goals should be developed with a regional perspective. As long as the Chincoteague National Wildlife Refuge continues to provide disturbance-free beaches to the south of AINS, NPS need not restrict AN any further than it already is. On the other hand, the NPS needs to be prepared to implement more restrictive policies on AINS should management policies on CNWR change.

(4) Public education may be the single most effective means for reducing human disturbance, particularly by pedestrians. The publics that use AINS, particularly for recreational activities during the winter months, can be sensitized to their effects on sanderlings and other wildlife that share the open beach. People can be taught to walk around sanderling flocks (particularly those that are roosting), restrain their dogs, and observe wildlife from a distance. Klein (1993) found that people who spoke with roving staff (as opposed to auditorium-held seminars) at Ding Darling National Wildlife Refuge were less likely to disturb wildlife than other recreational users. She specifically recommended that educators emphasize the effects of disturbance, particularly the visitor's potential role in reducing wildlife access to foraging habitat, in an effort to help them associate their actions with national conservation issues.

(5) Enforce the existing regulation that requires dogs to be leashed. Although data collected here were inadequate to assess the impacts of dogs, leashed or otherwise, it is apparent that most dogs enjoy chasing shorebirds.

(6) Continue to rebuild the artificial dune system on AS. The existing artificial primary dune system is intended to minimize beach erosion and protect the existing infrastructure (*i.e.*, camping areas, parking lots, roads, buildings). However, this system of a sand wall, snow fence (to trap blowing sand), and specific access points also serves to visually screen and contain the high levels of human activity that occur on the bayside of the dune. This recommendation is specific to areas of the dune system adjacent to buildings, camping areas, and parking lots; it should not be construed as an endorsement of dune creation elsewhere on AINS.

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Table 1. Public participation in selected recreational activities on the Maryland portion of AINS during 1985-86[a].

Activity	Secondary (%)	Primary (%)	$\bar{x}$ hrs spent in primary activity
Backpack	1.2	0.8	4.6
Camp	2.3	4.5	5.5
Primitive camp	1.3	22.2	71.7
Swim	47.2	35.9	16.7
Wildlife photography	48.2	7.1	5.3
Nature study	10.7	2.2	14.5
Photography	27.6	0.5	9.7
Day hike	9.8	0.7	20.0
Walk	64.2	3.4	10.9
Jog	8.3	0.4	2.3
Off-road vehicle	5.8	1.3	4.3
Saltwater angle	11.9	5.8	13.5
Picnic	37.2	0.5	1.9
Sightsee	54.8	6.4	8.4

[a]*n* = 5,993 respondents; from Wright and Van Horne (1991).

Table 2. Mean minimum and maximum air temperatures (°C) and total precipitation (cm) during the study period on AINS[a].

	1991-92			1992-93		
Month	Minimum	Maximum	Precip	Minimum	Maximum	Precip
Oct[b]	-	-	-	8.2 (0.77)	17.6 (0.63)	7.8
Nov	6.0 (1.95)[c]	14.4 (1.68)	0.7	6.6 (0.89)	13.4 (0.76)	13.9
Dec	2.3 (0.97)	9.9 (0.77)	10.7	2.7 (0.67)	8.5 (0.54)	10.0
Jan	0.2 (0.97)	7.5 (0.68)	5.3	2.2 (0.59)	8.0 (0.48)	10.0
Feb	1.2 (0.65)	8.1 (0.66)	13.4	-1.5 (0.74)	5.4 (0.80)	5.9
Mar	2.7 (0.69)	9.8 (0.70)	11.1	2.0 (0.65)	7.9 (0.65)	16.3

[a]Based on NPS data (Furbish 1992, unpubl. data).

[b]Data not available for Oct 1991.

[c]Standard error of mean in parenthesis.

Table 3. Beach morphology on north (AN) and south (AS) portions of the AINS study area.

Characteristic	AN	AS
SLOPE		
Gentle (≤ 10°)	231 (87.2)	238 (88.5)
Steep (> 10°)	34 (12.8)	31 (11.5)
SURFACE		
Smooth	207 (78.4)	124 (47.0)
Undulate	57 (21.6)	140 (53.0)
DUNE-WATER DISTANCE		
≤100 m	33 (12.4)	146 (54.7)
>100 m or dune absent	233 (87.6)	121 (45.3)
BERM-WATER DISTANCE		
$\bar{x}$ (SE)	17.5 (0.78)	15.3 (0.53)
n	261	265

[a]Slope, surface, and dune-water distance are expressed as frequency of occurrence; number in parenthesis is percentage of plots that occur within type. Berm-water distance expressed as mean and standard error.

Table 4. Geometric mean density[a], 95% confidence interval, and relative frequency of occurrence (%) of avian taxa, macroinvertebrate taxa, and human activities on 552 plots randomly distributed on AN and AS.

	AN (n = 276)			AS (n = 276)		
	$\bar{x}$	95% CI	%	$\bar{x}$	95% CI	%
Shorebirds	1.87	1.54 - 2.24	61.2	1.06	0.88 - 1.26	53.3
Sanderling	1.86	1.53 - 2.22	60.1	1.00	0.83 - 1.19	52.2
Dunlin	0.05	0.02 - 0.07	5.1	0.06	0.03 - 0.10	5.4
Black-bellied plover	0.01	0.00 - 0.02	2.2	0.02	0.01 - 0.03	2.9
Laridae	0.40	0.30 - 0.50	37.7	0.47	0.38 - 0.58	40.2
Total invertebrates	3.13	2.43 - 3.96	58.3	1.83	1.39 - 2.36	44.9
Emerita talpoida	1.35	1.03 - 1.71	44.9	1.14	0.85 - 1.48	35.5
≤10 mm	1.03	0.77 - 1.33	35.9	0.95	0.71 - 1.23	33.0
>10 - ≤20 mm	0.30	0.22 - 0.39	22.8	0.31	0.19 - 0.43	15.9
>20mm	0.15	0.09 - 0.20	13.0	0.12	0.07 - 0.17	9.1
Donax variabilis	0.14	0.08 - 0.21	9.8	0.00	0.00 - 0.01	0.4
Amphipoda	1.40	1.06 - 1.79	39.9	0.68	0.49 - 0.69	29.0
Polychaeta	0.35	0.23 - 0.48	18.5	0.05	0.01 - 0.09	4.3
Total human activities	0.20	0.16 - 0.25	20.3	1.16	1.02 - 1.32	64.1
Pedestrian	0.05	0.03 - 0.07	5.8	0.34	0.27 - 0.42	23.9
Vehicle	0.15	0.11 - 0.18	15.9	0.74	0.65 - 0.84	55.1
Dog	0		0	0.05	0.03 - 0.07	8.0
Aircraft	0.08	0.06 - 0.10	12.3	0.03	0.01 - 0.04	4.4

[a]Geometric mean and confidence interval derived from log-tranformed data and expressed as invertebrates per 400 cm^2 (depth = 4 cm), and human activities and birds per 200-m plot; activities and birds were weighted by day of week (weekend = 0.2857, weekday = 0.7143).

Table 5. Mean squares from 2-way ANOVA models of the effects of year and month on human activity rate (per min), sanderling abundance (per 200 m), and invertebrate prey densities (per 400 cm^2).

					Mean Square[a]			
Source	df	Human[b] activity	Sanderling	Invertebrate	*Emerita*	*Donax*	Amphipod	Polycheate
MONTH[c]	4	1.54**	25.87***	103.92***	52.06***	0.25***	54.23***	0.25
YEAR	1	0.92	0.28	6.61**	41.66***	0.12*	1.73	0.22
MONTH x YEAR	5	1.54**	2.40	2.95**	8.18***	0.09*	0.89	0.32
ERROR	499	0.43	1.10	0.91	0.42	0.03	0.76	0.27

[a] * $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$; F statistic.

[b]Human activity = pedestrians + vehicles + dogs.

[c]Oct data deleted because collected during only one year, and Mar and Apr data pooled because of small sample sizes; consequently, MONTH includes Nov, Dec, Jan, Feb, and Mar.

Table 6. Statistical characteristics of 738 sanderling flocks observed in flight during winters 1991-92 and 1992-93.

Month	*n*	$\bar{x}^a$	95% CI	Maximum	Median	Mode
Oct-Nov	84	13.3	10.0 - 17.6	500	12	7
Dec	138	3.9	3.2 - 4.8	150	3	1
Jan	256	2.4	2.1 - 2.7	300	2	1
Feb	108	2.5	2.0 - 3.0	50	2	1
Mar-Apr	152	7.7	6.0 - 9.9	500	6	1

[a]Geometric mean and confidence interval derived from log-transformed data.

Table 7. Untransformed variables used in statistical analyses.

Variable	Type[a]	Units	Range
Disturbance[b]			
pedestrians ≤ 10m	C	$\Sigma \cdot 200\ m^{-1}$	0 - 26
pedestrians > 10m	C	$\Sigma \cdot 200\ m^{-1}$	0 - 12
all pedestrians	C	$\Sigma \cdot 200\ m^{-1}$	0 - 26
parked vehicles	C	$\Sigma \cdot 200\ m^{-1}$	0 - 11
moving vehicles	C	$\Sigma \cdot 200\ m^{-1}$	0 - 3
all vehicles	C	$\Sigma \cdot 200\ m^{-1}$	0 - 11
all disturbances[c]	C	$\Sigma \cdot 200\ m^{-1}$	0 - 32
pedestrian rate	C	$\Sigma \cdot min^{-1} \cdot 200\ m^{-1}$	0 - 23.9
vehicle rate	C	$\Sigma \cdot min^{-1} \cdot 200\ m^{-1}$	0 - 21.1
disturbance[c] rate	C	$\Sigma \cdot min^{-1} \cdot 200\ m^{-1}$	0 - 28.4
Biological[d]			
sanderlings (per scan)	C	$\underline{\Sigma} \cdot 200\ m^{-1}$	0 - 882
sanderlings	C	$\bar{x} \cdot 200\ m^{-1}$	0 - 602.5
Laridae (per scan)	C	$\underline{\Sigma} \cdot 200\ m^{-1}$	0 - 402
Laridae	C	$\bar{x} \cdot 200\ m^{-1}$	0 - 282.7
Emerita	C	$\Sigma \cdot (400\ cm^2)^{-1}$	0 - 218
Donax	C	$\Sigma \cdot (400\ cm^2)^{-1}$	0 - 52
amphipod	C	$\Sigma \cdot (400\ cm^2)^{-1}$	0 - 148
polychaete	C	$\Sigma \cdot (400\ cm^2)^{-1}$	0 - 66
invertebrates	C	$\Sigma \cdot (400\ cm^2)^{-1}$	0 - 323
Spatial			
berm-water distance	C	m	0 - 60
dune-water distance	O	m	≤ 100, > 100
beach surface	N	-	smooth, undulate
beach slope	O	deg	≤ 10, > 10
Temporal[e]			
year	N	-	1, 2
month	N	-	Oct - Mar/Apr (1 - 6)
time	O	-	early, mid, late
time after sunrise	C	min	-13 - 713
tide	O	-	low, flood/ebb, high
time from high tide	C	min	0 - 381
Weather			
temperature	C	°C	-9.5 - 26.0
wind speed	C	$km \cdot h^{-1}$	0 - 71

[a]C = continuous, O = ordinal, N = nominal.

[b]Occurrence of sanderlings, *Laridae*, vehicles, pedestrians, and disturbances on plot also expressed as binomial (0, 1) or ordinal variable (0 - 6 scans); see text for details.

[c]Disturbances = pedestrians (including anglers, swimmers) + equestrians + vehicles + dogs.

[d]Occurrence of *Emerita*, *Donax*, polychaetes, amphipods, and total invertebrates on plot also expressed as binomial (0, 1) or ordinal variable (0 - 5 core samples); see text for details.

[e]Times corrected for Sandy Hook, NJ (NOAA 1991, 1992, 1993). Time pre- and post-high tide was absolute value.

Table 8. Selected[a] logistic regression model[b]: effects of human activity, prey availability, weather, and temporal and spatial characteristics on the occurrence of sanderlings on 528 200-m beach plots at AINS.

Variable[c]	Parameter ^	SE	Wald χ^2	*P*	Odds Ratio
Intercept	2.03	0.76	7.1	0.01	
Pedestrians ≤ 10m	-0.60	0.29	4.4	0.04	0.55
Total invertebrate	-0.51	0.28	3.4	0.07	0.60
Invertebrate occurrence (0 - 5)	0.52	0.18	8.0	0.01	1.68
Emerita	-0.77	0.18	17.7	0.00	0.46
Year	0.53	0.21	6.2	0.01	1.70
Month	-0.39	0.09	18.5	0.00	0.68
Tide	0.26	0.14	3.3	0.07	1.30
Temperature	0.06	0.02	6.1	0.01	1.06
Wind speed	-0.05	0.02	8.0	0.01	0.96
Beach surface	-0.84	0.21	16.0	0.00	0.43

[a]Stepwise regression; *P* for entry = 0.30, *P* for stay = 0.05.

[b]Somners' D = 0.484, -2 LOG L χ^2 = 3.34 (df = 10, *P* = 0.068); correctly classified 67% of predicted values.

[c]All variables expressed as defined in Table 12.

Table 9. Human activity, invertebrate density, *Laridae* density, air temperature, and wind speed correlated (Pearson's) with sanderling density on 200-m plots.

Variable[a]	All plots $n = 552$	Sanderlings present $n = 312$
Σ disturbances	0.004 (.92)	0.074 (.19)
disturbance rate	0.007 (.87)	0.060 (.29)
pedestrian	0.011 (.80)	0.080 (.16)
pedestrian ≤ 10m	-0.031 (.47)	0.052 (.36)
pedestrian > 10m	0.045 (.29)	0.068 (.23)
pedestrian rate	0.064 (.13)	0.117 (.04)
vehicle	-0.016 (.71)	0.033 (.56)
moving vehicles	-0.024 (.57)	0.038 (.50)
parked vehicles	0.009 (.84)	0.032 (.57)
vehicle rate	-0.031 (.47)	0.003 (.96)
Σ invertebrates	0.304 (.00)[b]	0.485 (.00)
Emerita	0.201 (.00)	0.448 (.00)
Donax	0.127 (.00)	0.201 (.00)
amphipod	0.292 (.00)	0.371 (.00)
polychaete	0.105 (.01)	0.118 (.04)
$\bar{x}$ *Laridae*	0.207 (.00)	0.275 (.00)
temperature (°C)	0.271 (.00)	0.341 (.00)
wind speed ($k \cdot h^{-1}$)	-0.141 (.00)	-0.165 (.00)
time from high tide	-0.061 (.15)	-0.038 (.51)

[a]All biological variables (*i.e.*, temperature and wind speed excluded) are log-tranformed; see Table 2 for additional details.

[b]*P* value in parenthesis for H_o: $r = 0$.

Table 10. Mean squares from 2-way ANCOVA models of the effects of human disturbance and prey occurrences on mean sanderling abundance, after adjusting for season and weather.

Source	df	Mean Square[a]	
		All plots	Plots with sanderlings
DISTURBANCE	1	5.76*	0.71
PREY	1	3.15	9.56**
DISTURBANCE X PREY	1	0.51	0.26
JULIAN DATE	1	24.15**	22.94**
TEMPERATURE	1	5.83*	1.21
WIND SPEED	1	3.80	4.89*
ERROR	[b]	1.20	1.04

[a] *$P \leq 0.05$, **$P \leq 0.01$; F statistic.

[b] df = 545, 305, respectively.

Table 11. Mean squares from 3-way ANCOVA model of sanderling abundance on 508[a] 200-m plots.

Source	df	Mean square[b]
YEAR	1	0.27
LOCATION	1	15.51**
YEAR X LOCATION	1	0.01
SEASON[c]	1	92.22**
YEAR X SEASON	1	14.02**
LOCATION X SEASON	1	1.58
YEAR X LOCATION X SEASON	1	4.49*
PREY	1	5.75*
ERROR	499	537.38

[a]Oct data deleted because only collected during one year.

[b] $*P \leq 0.05$, $**P \leq 0.01$; F statistic.

[c]Early season includes Oct and Nov data; late season includes Jan - Apr data.

Table 12. Diurnal time budget of sanderlings using AINS during Oct - Apr.

BEHAVIOR	$\bar{x}$ % (SE)[a]
Forage	49.9 (7.31)
Feed	34.8 (3.18)
Search	60.1 (3.17)
Pause	4.7 (1.08)
Rest	26.2 (6.88)
Alert	4.1 (1.30)
Maintenance	3.4 (0.89)
Ambulate	5.2 (2.44)
Fly	9.5 (3.69)
Agonism	0.4 (0.26)
Other	1.3 (0.95)

[a]Arithmetic means (n = 312 plots) weighted by sanderling count per plot.

Table 13. Pearson correlation coefficients (weighted by sanderling count) between sanderling behavioral proportions and densities[a] of human activity and invertebrate prey, time, and weather.

	Forage									
	Forage	FEED	MOVE	PAUSE	Agonism	Alert	Fly	Groom	Ambulate	Rest
Disturbance	.037	.123[2]	-.136[2]	.131[2]	.059	.057	.194[3]	.276[3]	-.091	-.123[2]
Pedestrian	.039	.115[2]	-.121[2]	.081	.092[1]	.015	.161[3]	.160[3]	-.106[1]	-.108[1]
Pedestrian ≤ 10m	.054	.068	-.079	.062	-.006	-.027	.034	.104[1]	-.080	-.053
Pedestrian > 10m	.018	.103[1]	-.109[1]	.079	.140[3]	.058	.163[3]	.168[3]	-.083	-.102[1]
Vehicle	-.019	.108[1]	-.132[2]	.170[3]	.018	.144[3]	.216[3]	.376[3]	-.026	-.101[1]
Moving vehicle	.001	.090	-.117[2]	.189[3]	.004	.136[2]	.185[3]	.376[3]	-.016	-.095[1]
Parked vehicle	-.047	.117[2]	-.134[2]	.106[1]	.063	.127[2]	.203[3]	.281[3]	-.042	-.081
Invertebrate	.436[3]	.345[3]	-.361[3]	.163[3]	.213[3]	.016	.240[3]	.241[3]	-.197[3]	-.504[3]
Emerita	.264[3]	.254[3]	-.260[3]	.132[2]	.194[3]	.177[3]	.249[3]	.333[3]	-.084	-.402[3]
Donax	.173[3]	.087	-.105[1]	.153[3]	.043	-.001	.043	.107[1]	-.063	-.149[3]
Polychaete	.254[3]	.209[3]	-.237[3]	.089	.049	-.108[1]	-.035	.108[1]	-.125[2]	-.193[3]
Amphipod	.381[3]	.265[3]	-.255[3]	.019	.104[1]	-.186[3]	.234[3]	.010	-.251[3]	.392[3]
Time	.294[3]	.070	-.016	.013	.097[1]	-.109[1]	-.033	.036	-.446[3]	-.136[2]
Tide	.456[3]	.264[3]	-.262[3]	-.053	-.038	-.056	.307[3]	-.010	-.283[3]	-.536[3]
Temperature	-.095[1]	.081	-.015	.002	.006	-.093[1]	.062	.043[3]	-.191[3]	.123[2]
Wind speed	.544[3]	.185[3]	-.255[3]	.290[3]	.150[3]	.063	.252[3]	.114[2]	-.089	-.600[3]

[a]Proportions were angular transformed; counts were natural-log transformed.

[1] = $P \leq 0.10$, [2] = $P \leq 0.05$, [3] = $P \leq 0.01$ ($n = 312$).

Table 14. Arithmetic means and standard errors (weighted by count) of percent time spent in different behaviors by disturbed and undisturbed sanderlings at AINS.

BEHAVIOR[a]	UNDISTURBED n = 273	DISTURBED[b] n = 39	P[c]
Forage	49.6 (8.07)	52.5 (15.22)	0.541
Rest	28.1 (7.72)	11.7 (6.57)	0.036
Alert	4.0 (1.40)	4.6 (3.50)	0.227
Maintenance	2.8 (0.81)	7.7 (3.44)	0.000
Ambulate	5.8 (2.77)	1.2 (1.16)	0.185
Fly	8.1 (3.32)	20.4 (17.28)	0.000
Agonism	0.4 (0.28)	0.4 (0.74)	0.844

[a]All proportions were angular transformed for analysis.

[b]Anthropogenic disturbance includes vehicles, pedestrians, equestrians, swimmers ≤ 10 m of the beach, and dogs.

[c]Probability that F > F (ANOVA) based on least square means and standard errors. MANOVA test for no DISTURBANCE effect on overall time budget: Wilks' λ = 0.818, df = 7,304, F = 9.61, P = 0.0001.

Table 15. Arithmetic means and standard errors (weighted by count) of energy expended ($kJ \cdot h^{-1}$) in different behaviors by disturbed and undisturbed sanderlings at AINS.

BEHAVIOR	BMR MULTIPLE[a]	UNDISTURBED	DISTURBED[b]
		n = 273	*n* = 39
Forage	[c]	2.77 (0.45)	3.09 (0.85)
Rest	1.2	0.74 (0.20)	0.31 (0.17)
Alert	2.2	0.19 (0.07)	0.22 (0.17)
Maintenance	2.1	0.13 (0.10)	0.36 (0.16)
Ambulate	[d]	0.24 (0.12)	0.06 (0.05)
Fly	12.5	2.22 (0.91)	5.59 (4.73)
Agonism	1.1	0.02 (0.01)	0.02 (0.04)
HEE[e]		6.31 (0.84)	9.64 (3.88)

[a]Basal metabolic rate (BMR) = 2.189 $kJ \cdot h^{-1}$ for 55-g sanderling; see text for details. BMR multiples derived from coefficients found in King (1974), Albright *et al.* (1983), and Buttemer *et al.* (1986).

[b]Anthropogenic disturbance includes vehicles, pedestrians, swimmers $\leq$ 10 m of the beach, and dogs.

[c]Forage = Σ energy expended in feed (2.2 X BMR), search walk (1.7 X BMR), search run (3.5 X BMR), and search pause (1.7 X BMR).

[d]Ambulate = Σ energy expended in walk (1.7 X BMR) and run (3.5 X BMR).

[e]Hourly energy expenditure (HEE) = Σ energy expended in all behaviors + thermoregulation.

Table 16. Arithmetic means and standard errors (weighted by count) of percent time spent in different behaviors and energy expenditure ($kJ \cdot h^{-1}$) by sanderlings using AN and AS.

BEHAVIOR[a]	AN n = 168	AS n = 144	P^b
Forage	45.8 (12.3)	63.3 (5.94)	.000
Rest	32.1 (12.0)	1.2 (2.41)	.000
Alert	3.8 (2.04)	5.0 (1.50)	.086
Maintenance	3.1 (1.31)	4.3 (1.14)	.096
Ambulate	6.6 (4.43)	0.9 (0.56)	.001
Fly	7.2 (4.75)	17.2 (5.47)	.000
Agonism	0.4 (0.34)	0.4 (0.41)	.105
HEE[c]	6.0 (1.21)	9.0 (1.22)	.000

[a]All proportions were angular transformed for analysis.

[b]Probability that $F > F$ (ANOVA) based on least square means and standard errors. MANOVA test for no LOCATION effect on overall time budget: Wilks' λ = 0.800, df = 7,304, F = 10.87, P = 0.0001.

[c]Hourly energy expenditure (HEE) = $\sum$ energy expended in all behaviors + thermoregulation.

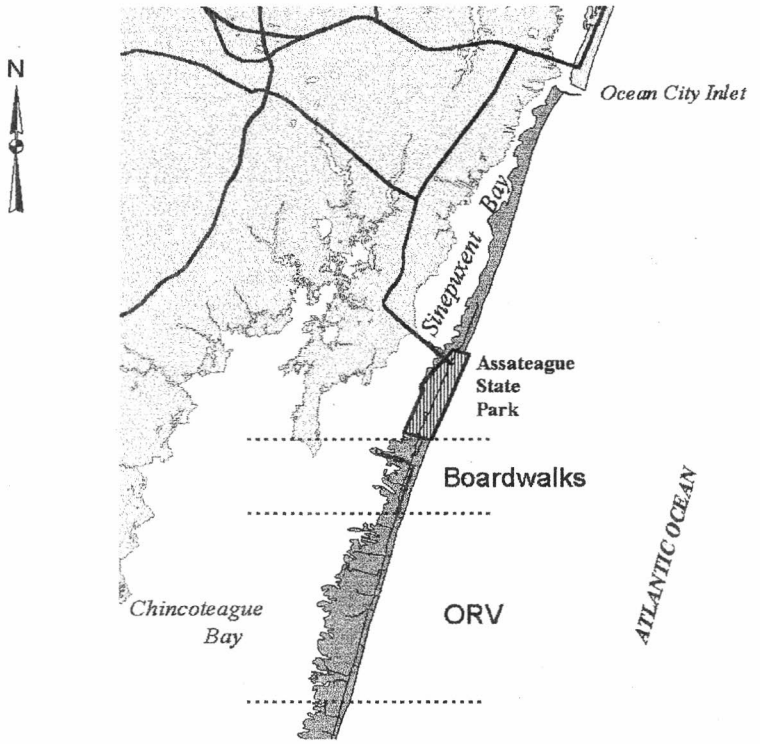


Figure 1. Study area on Assateague Island National Seashore in Maryland.

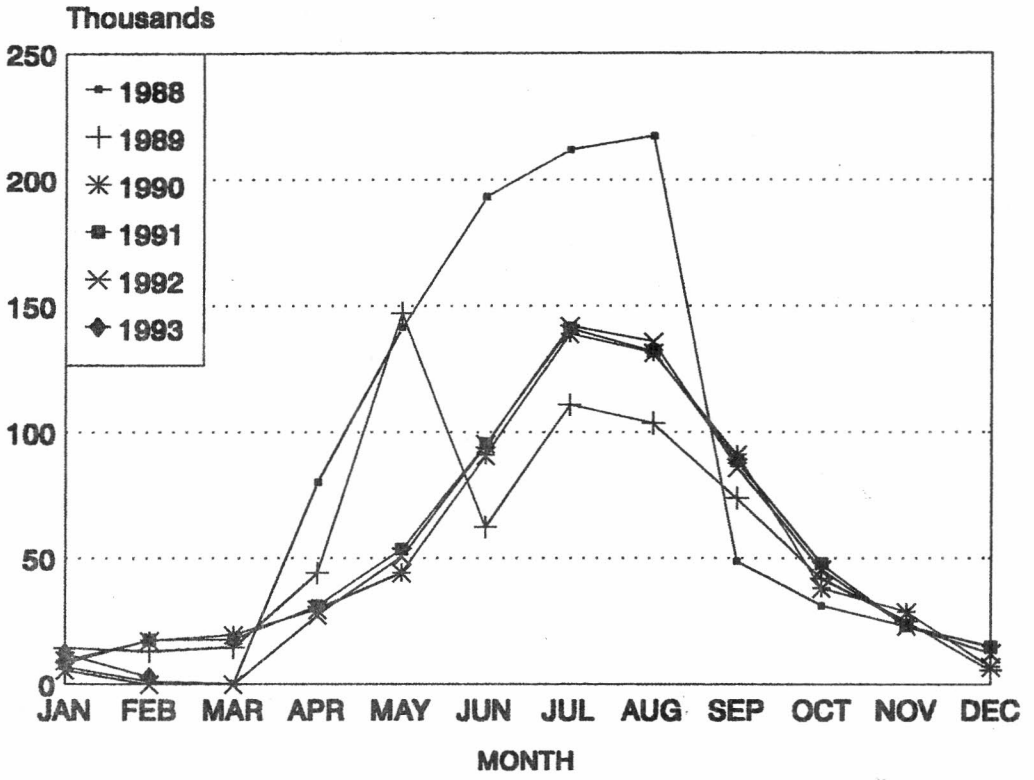


Figure 2. Number of visitors to the Maryland portion of Assateague Island National Seashore (1988-93).

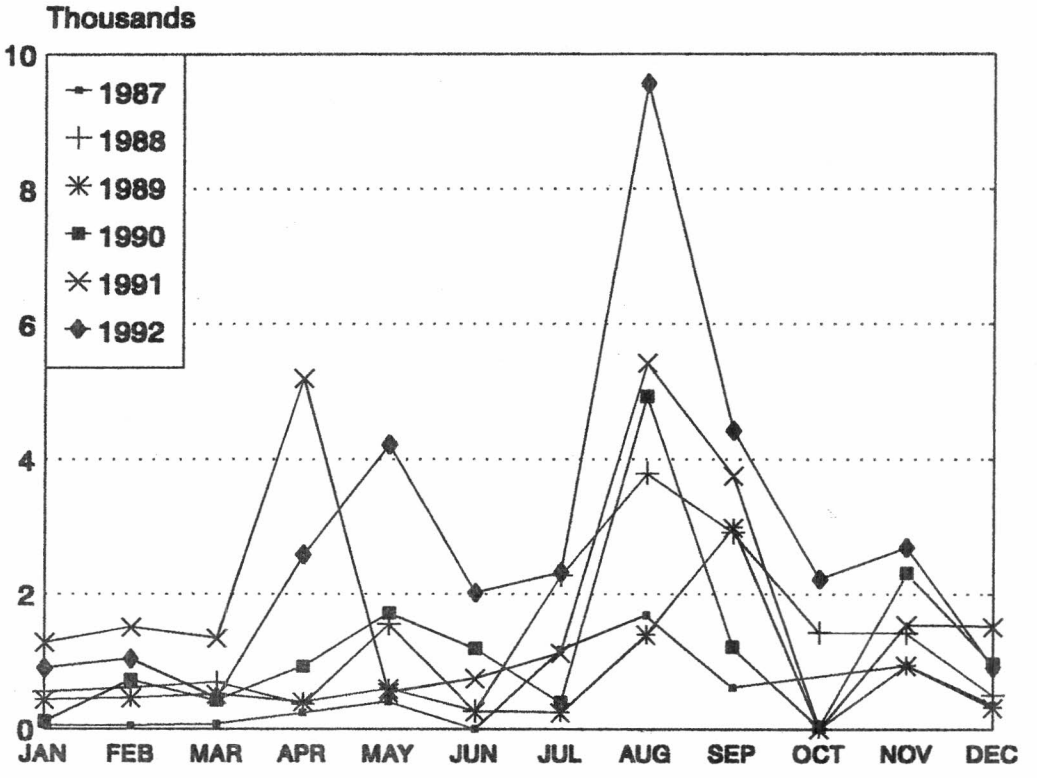


Figure 3. Seasonal trends in sanderling populations on Assateague Island National Seashore (1987-92).

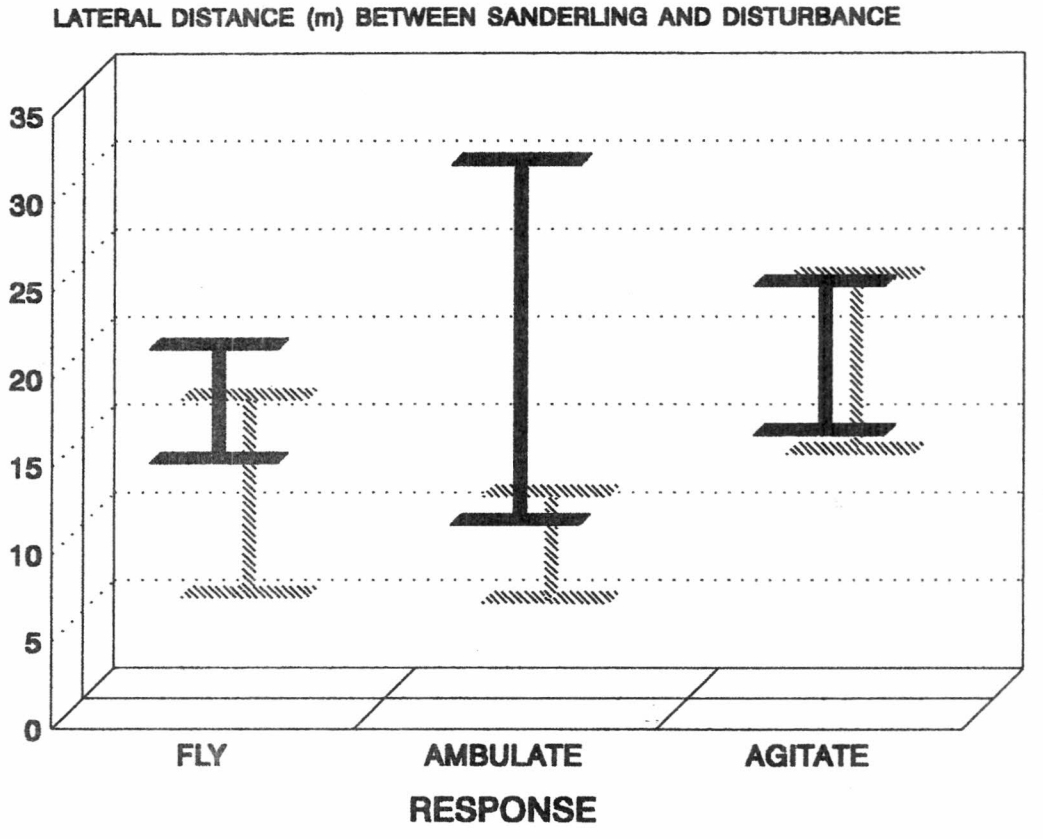
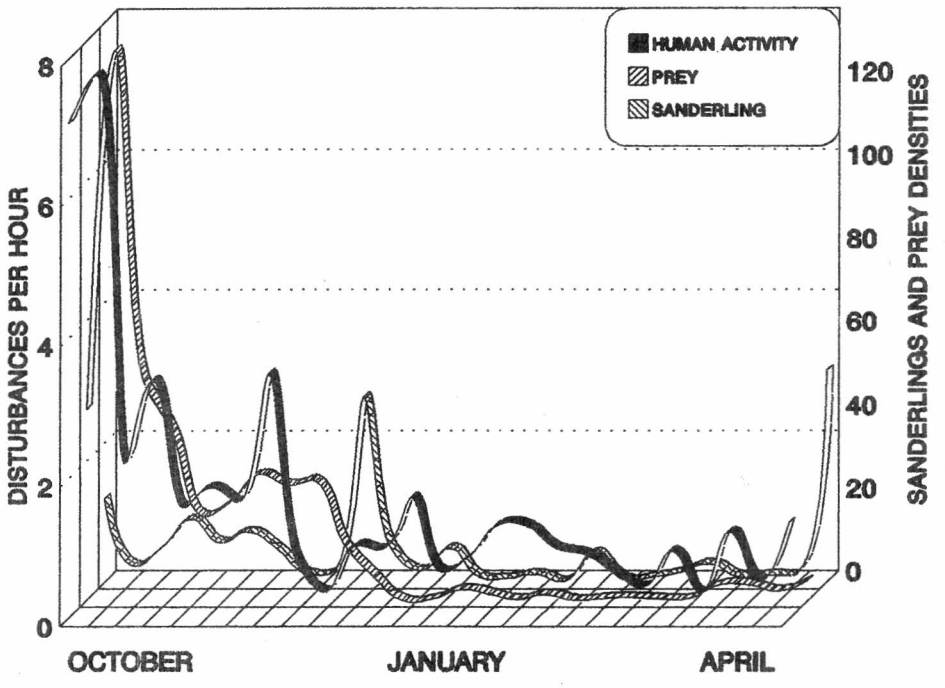


Figure 4. Mean distances (95% CI) at which sanderlings respond to an approaching vehicle (striped) or pedestrian (solid).



Sanderling count = mean of 6 scans per plot.
Prey estimate = *Donax* + *Emerita* + polychaete + amphipod.
Human activity = pedestrians + equestrians + vehicles + dogs.

Figure 5. Sanderling, invertebrate prey and human disturbance on 200-m beach plots averaged by week.

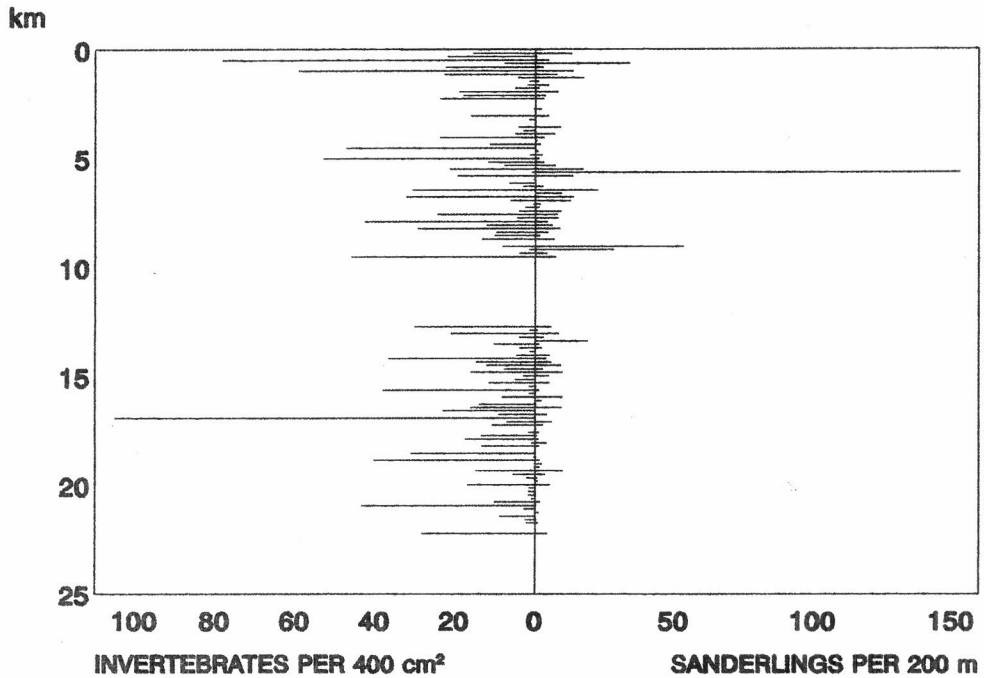
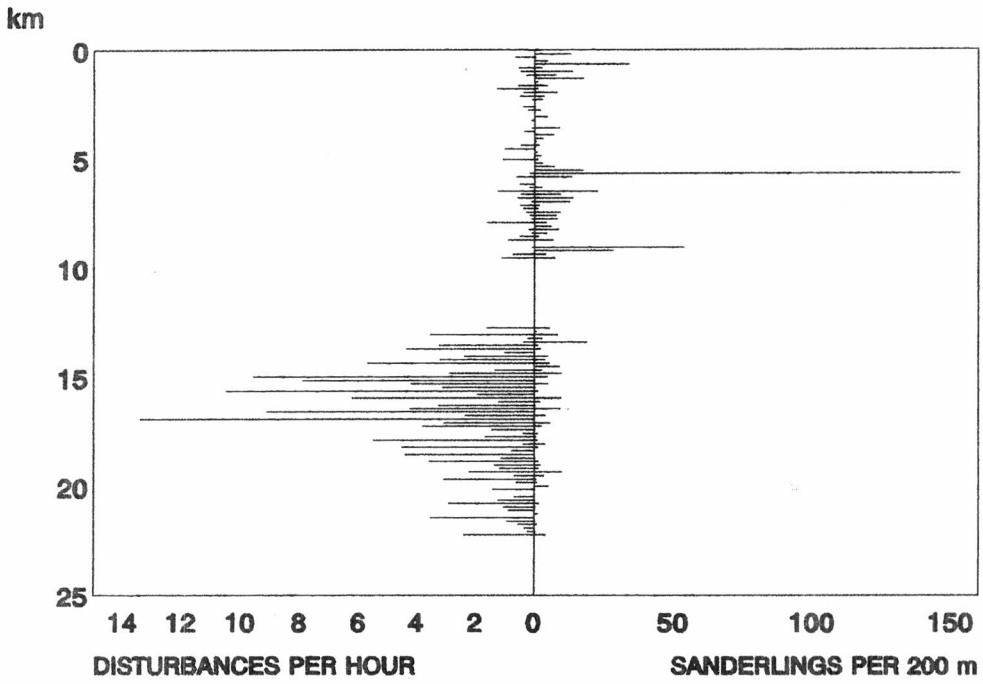


Figure 6. Mean sanderling and invertebrate prey densities at 161-m increments from the north end of Assateague Island National Seashore.



n = 552 plots averaged over 120 increments.
Sanderling count = mean of 6 scans per plot.
Disturbance = pedestrians + equestrians + vehicles + dogs.

Figure 7. Mean sanderling density and disturbance rate at 161-m increments from the north end of Assateague Island National Seashore.

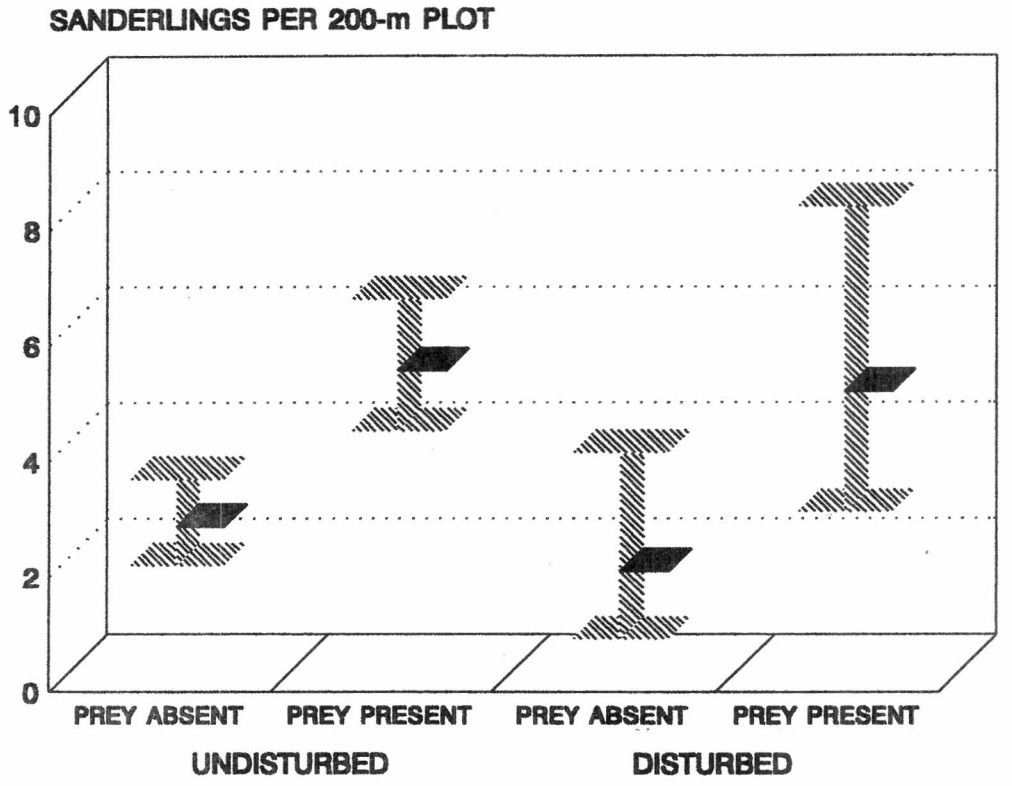


Figure 8. Least square means (± 1 SE) of sanderling abundance within 312 200-m plots on which human activity and invertebrate prey are present or absent.

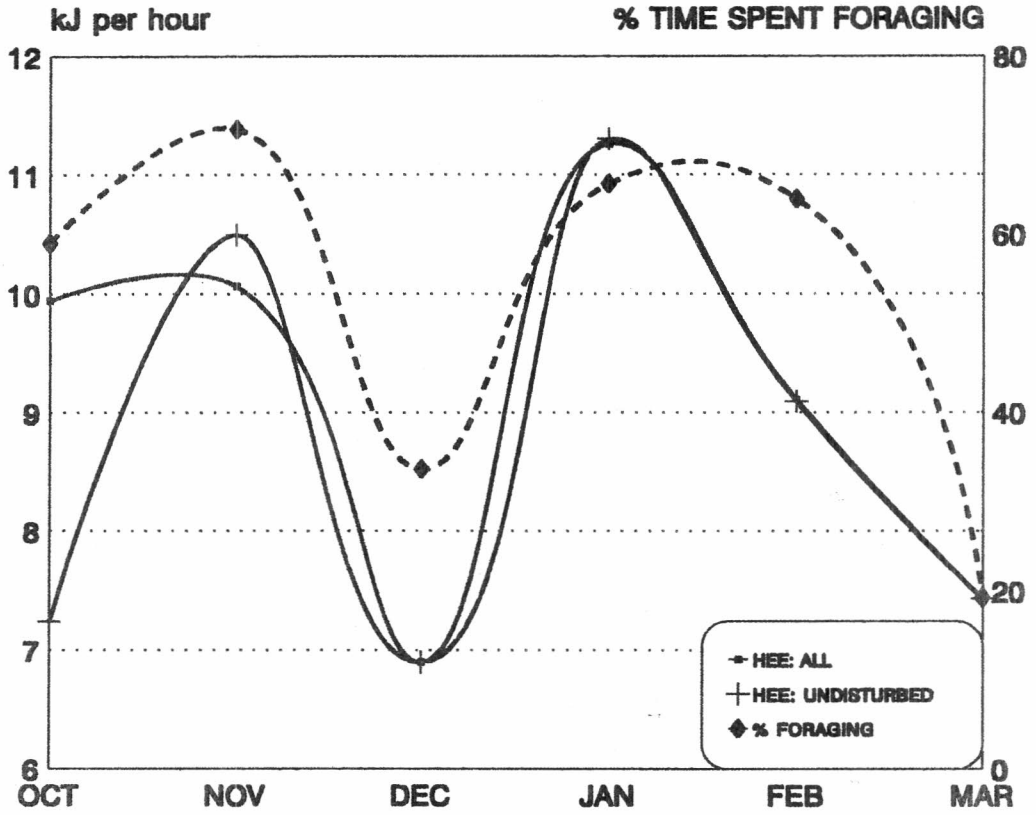


Figure 9. Monthly averages of percent time spent foraging and hourly energy expenditure by sanderlings on all plots (n = 312) and undisturbed plots only (n = 273).