EFFECTS OF HUMAN DISTURBANCE ON THE BEHAVIOR AND ENERGETICS OF NONBREEDING SANDERLINGS

by

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(ABSTRACT)

Human disturbance of avifauna and other wildlife is defined as any intentional or unintentional anthropogenic action that elicits a metabolic or behavioral response. I proposed that the energetic response to disturbance should be reflected as increased existence metabolism (EM). If so, then there must be three behavioral responses to increased EM: increased energy intake compensates for increased EM, habituation reduces increased EM, and dispersal avoids increasing EM altogether. I applied this model to captive and free-ranging nonbreeding sanderlings (*Calidris alba*).

I exposed 24 captive sanderlings to a 5-min disturbance event during each of 10 diurnal hours over two 4-d trials. The metabolizable energy of food ingested was determined for each bird daily. Total body electrical conductivity and body mass were measured during trials to account for energy derived from metabolized body tissues. These combined values suggest that EM was elevated by 7% in response to disturbance during 8% of daylight hours. Caged sanderlings responded to disturbance with alert and attempted escape behaviors; *i.e.*, dispersal. Sanderlings spent more time attempting to escape on the first day of each trial and during the first of 10 disturbance events in a day, suggesting some behavioral habituation. There was evidence of compensatory feeding after the trials, but not during them.

Abundance, behavior, and distribution of free-ranging sanderlings were studied at Assateague Island National Seashore, Maryland, during two winters in 1991-93. Increasing pedestrian traffic decreased the probablility of sanderling occurrence on 200-m plots by as much as 45%. Average sanderlings ambulated or flushed when pedestrians and vehicles approached within 20 m and 10 m, respectively, and flushed more frequently in response to pedestrians than vehicles. Mean densities were nearly 60% less on disturbed than undisturbed 200-m plots. Sanderling densities were highest on plots with invertebrate prey and no disturbance, and lowest on those with disturbance and no prey. Apparently, higher food availability can partially compensate for the costs of disturbance.

Disturbed sanderlings spent 177% more time in maintenance behaviors, 151% more time in flight, and 42% less time roosting than undisturbed sanderlings. On average, undisturbed sanderlings expended 6 $kJ \cdot h^{-1}$ whereas disturbed sanderlings expended 9 $kJ \cdot h^{-1}$. More than 90% of the variation in energy expenditure was attributable to time in flight. Although chronic human disturbance can elevate EM in the caged environment, the flush response largely determines the energetic cost of disturbance in free-ranging sanderlings.

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Literature Review

Human disturbance of avifauna and other wildlife may be defined as any intentional or unintentional anthropogenic action that elicits a metabolic or behavioral response. Disturbance generally does not include actions that involve a tactile stimulus, but rather the visual, olfactive, or aural threat of one. For example, an off-road vehicle that destroys a nesting piping plover (*Charadrius melodus*) is not disturbing, it is a direct source of mortality (Melvin *et al.* 1994); however, vehicular noise that causes adjacent brooding adults to leave their nests unattended is a disturbance.

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). Most recently, Knight and Gutzwiller (1995) edited an anthology of writings on researching and managing wildlife-recreationist interactions.

The published record suggests that the effects of human disturbance on wildlife were explicity acknowledged by the research and management communities in the late 1970s. Disturbance of colonial breeders caused by research activities and the subsequent depredation was openly discussed in the ornithological literature by Duffy (1979), MacInnes (1980), and Strang (1980). Human disturbance became a more substantial management issue when a successful legal challenge by the Defenders of Wildlife forced Ruby Lake National Wildlife Refuge to restrict outboard motors and prohibit waterskiing in 1978 because these activities were reducing waterfowl production (Bouffard 1982, Curtin 1993).

However, prior to these developments, I believe that recognition of human disturbance as a topic of study or concern had been impeded somewhat by preconceptions on the part of managers and researchers. This oversight stems, in part, from ecologists historically viewing "man [as] outside nature" (Barrett 1981) and, in part, from wildlife biologists reacting slowly to nongame issues (cf. Peak 1986). Although Sousa (1984) recognized that physical human disturbance can impact faunal communities (*i.e.*, "mobile animals"), recent publications in *stress ecology* have failed to recognize human presence as a source of stress (Barrett and Rosenberg 1981, Rapport *et al.* 1985), probably because developments in this new field have focused at the ecosystem level and, at least initially, on floral systems. Ironically, *stress* has been defined as "a perturbation that is applied to a system by a stressor which is foreign to that system or which may be natural to it but is applied at an excessive level (*e.g.*, phosphorus)" (Barrett 1981), and is disadvantageous to the system (Ivanovici and Wiebe 1981). Certainly this definition includes disturbance induced by human presence or activity as a stressor (cf. Selye 1976).

Among managers, use of wildlife resources has been traditionally viewed as consumptive or nonconsumptive, depending on whether enjoyment of the resource directly resulted in death of an animal (*e.g.*, duck hunting) or not (*e.g.*, birdwatching). Unfortunately, this dichotomy has often been misconstrued to mean those activities that negatively impact wildlife and those that do not. Wilkes (1977) was perhaps the first to explicitly disparage the "myth of the nonconsumptive user", pointing out that this user group tramples and rearranges vegetation patterns, disturbs and displaces wildlife, replaces habitat with the infrastructure required to support recreational uses, and generates refuse. Ultimately, Wilkes argued that there is simply no such thing as a nonconsumptive user. Although Pomerantz *et al.* (1988) suggested that human activities should be viewed in the context of their impacts on wildlife and not on a superficial classification of use, this dichotomy persists in the current literature and, consequently, so does its misuse.

Human disturbance and its effects on avifauna should not be trivialized. In a review of bird species listed as having unstable or declining populations, 6% were directly attributable to human disturbance (Flather and Hoekstra 1989). Furthermore, the potential for conflicting use of time and space by birds and humans is considerable, pervasive, and only likely to increase. In 1991, 76 million Americans ≥ 16 years old recreated with the primary purpose of photographing, observing, or feeding wildlife, activities conventionally viewed as nonconsumptive; 40 million other Americans hunted or fished. These wildlife-oriented activities totaled more than a billion use-days in the U.S. during 1991 (U.S. Fish and Wildlife Service 1992)! In addition to wildlife-oriented activities, many recreational pursuits are outdoors but do not directly depend on wildlife. More than 13 million Americans participated ≥ 10 days during 1992 in each of these outdoor activities: bicycling, swimming in natural waters, motorboating, driving off-road vehicles, camping in developed campgrounds, and day hiking (Flather and Cordell 1995). These activities also would generally be considered nonconsumptive uses of natural resources, but they clearly have the potential to disturb sympatric avifauna.

The effects of disturbance on birds

The single most cited effect of human disturbance on birds is the flush response and its consequences. Flying is energetically costly behavior. Birds in flight consume 9 - 15 times their basal metabolic rate (King 1974). The flush response is mediated by several biological and psychological factors that are often time- and site-specific including:

- Species-specific tolerances. For example, eight waterfowl species varied their responses to different levels of water-based recreational activity on a Welsh lake (Tuite *et al.* 1983), and pink-footed geese (*Anser brachyrhynchus*) responded to helicopters sooner than barnacle geese (*Branta leucopsis*)(Mosbech and Glahder 1991).

- Temporal differences. For example, entire flocks of staging snow geese (*Chen caerulescens*) flushed more readily in response to disturbance during spring than fall (Belanger and Bedard 1989), and bald eagle (*Haliaeetus leucocephalus*) flush distances were partially explained by time of day and year (Fraser *et al.* 1985).

- Predisturbance behavior. For example, bald eagles on the ground almost always flew when approached and generally at much greater distances than eagles in trees (Knight and Knight 1984), and staging black brant (*Branta bernicla*) were more responsive to aircraft overflights when they were resting at high tide (Ward *et al*. 1987).

- Landscape. For example, wintering white-fronted (*Anser albifrons*)(Norris and Wilson 1988) and pink-footed (Madsen 1985*b*) geese congregated in larger flocks and flew shorter distances when disturbed in larger agricultural fields, and flight responses of wintering bald eagles to approaching humans varied in different habitats (Stalmaster and Newman 1978).

- Intraspecific differences. For example, older Canada goose (*Branta canadensis*) broods were more tolerant of repeated disturbance than younger ones (Eberhart *et al*. 1989), but older bald eagles flushed sooner than young eagles in response to an approaching human (Stalmaster and Newman 1978). Similarly, passerines in rural areas flushed sooner in response to an approaching human than their counterparts in suburban areas (Cooke 1980, Kenney and Knight 1992).

This last point may be an important determinant of gregarious species' response to disturbance. The flight response of a goose flock to disturbance may be largely determined by the individual behavior of its most nervous members (Owens 1977, Belanger and Bedard 1989). A larger flock with more sentinels is not only more likely to identify a potential disturbance sooner than a smaller flock, it also is more likely to have members with a wider range of individual tolerances to disturbance.

Birds also must cease whatever other behavior they were engaged in prior to being flushed. For American black duck (*Anas rubripes*) pairs in early spring, this may mean interruption of courtship and/or nesting activity (Stotts and Davis 1960). For nesting hens, this means an unattended nest with increased probability of egg depredation (Choate 1967, Hand 1980), nest abandonment (Balat 1969) and/or interruption of incubation (Bouffard 1983). For molting canvasbacks (*Aythya valisineria*) and redheads (*A. americana*), this means interference with habitat selection and possible use of suboptimal lakes during the flightless period (Bergman 1973). For a migrating bird, this may mean interference with normal flight patterns and increased susceptibility to accidental death (Blokpoel and Hatch 1976), predation, or being shot (Bartelt 1987). For family groups of Canada geese, this may mean disrupted bonding and early brood breakup (Bartelt 1987). For wintering or migrating waterfowl, this may mean cessation of feeding and/or resting activities (Paulus 1984, Korschgen *et al.* 1985, Morton *et al.* 1989*a*, Belanger and Bedard 1990, Laskowski *et al.* 1993).

Although flight in response to acute disturbance is most obvious to human observers, there are costs associated with nonflight responses at chronic levels.

Any behavioral deviation from rest can be energetically expensive. Wintering black ducks, for example, responded to disturbance by spending more time in alert and escape behaviors and less time resting and feeding, even when they failed to flush (Morton *et al.* 1989*a*). An alert black duck, or one that is walking or swimming, consumes 1.8, 1.4, and 1.8 times, respectively, more energy than a bird at rest (Wooley and Owen 1978).

Furthermore, lack of a behavioral response does not mean lack of a metabolic or physiological response. Ball and Amlaner (1980) demonstrated that an alert but caged Herring gull (*Larus argentatus*) showed a consistently increasing heart-rate response to an approaching human. Similarly, MacArthur *et al.* (1982) found that mountain sheep (*Ovis canadensis*) had elevated heart rates when disturbed by aircraft despite showing no evidence of behavioral response. Although there is some question as to the relationship between heart rate and metabolic rate (Wooley and Owen 1977), it is clear that wildlife are responding with a heightened state of vigilance even when there is no apparent behavioral response.

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. 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 addition to factors that mediate an individual's perception of a disturbance event, there are the inherent characteristics of the disturbance itself. These characteristics include the type, duration, magnitude, and frequency of an event. Disturbance types have been categorized in several ways. Belanger and Bedard (1989, 1990) and Morton *et al.* (1989*b*) distinguished natural from human-induced disturbances. Some investigators have separated human disturbances by their actual source (*e.g.*, traffic, pedestrian, aircraft, hunting activity; Fraser *et al.* 1985, Belanger and Bedard 1989) while others have distinguished levels of human activity (Stalmaster and Newman 1978, Anderson and Keith 1980, Watson 1988); this latter classification is more a measure of the *magnitude* of disturbance.

Within this framework, disturbance sources can be further discriminated. For example, Derksen *et al*. (1988, 1989) and Ward *et al*. (1987, 1988) have distinguished fixed-wing from rotary-wing aircraft, and then further quantified noise (*i.e.*, decibels, percent attentuation) as functions of aircraft type, lateral distance, and altitude. Johnson *et al*. (1985) evaluated the effects of three types of auditory stimuli (white noise, pure tone, and distress calls) on starling (*Sturnus vulgaris*) response, and Thompson *et al*. (1968*b*) studied the interaction of lighting and grouping on the responses of starlings to sound. Certainly classification of disturbance can be carried to any resolution depending on the nature of the question posed.

Approaches to studying disturbance

I identified seven approaches in the literature to studying the effects of human disturbance on avifauna and other wildlife:

(1) flush response (flight time, flush distance, flush threshold, flock percentage) can be intentionally or incidentally induced in the field (Owens 1977, Fraser *et al.* 1985, Klein 1993, Ward *et al*. 1994, Kenney and Knight 1992);

(2) behavioral and energetic changes in the field can be measured with time budgets (Morton *et al*. 1989*a*, Belanger and Bedard 1990, Fernandez and

Azkona 1993);

(3) population redistribution or displacement can be demonstrated in the field with observational (Korschgen *et al.* 1985, Keller 1991) or telemetry (Buehler *et al.* 1991, Austin and Humburg 1992) methods;

(4) physiological responses can be assessed with heart-rate telemetry in both field (MacArthur *et al.* 1982) and laboratory (Wooley and Owen 1977, Ball and Amlaner 1980) or with other measures such as blood urea (Fernandez and Azkona 1993);

(5) simulation models (Frederick *et al.* 1987), Habitat Suitability Index models (Chapman and Howard 1984), and statistical models (Montopoli and Anderson 1991) can be used to assess the effects of human disturbance on wildlife populations;

(6) inferences can be drawn from other laboratory and experimental approaches not specifically targeted to examine human disturbance as used in this context, including animal damage control (Thompson *et al.* 1968) or hazing (Boag and Lewin 1980, Craven and Ellis 1982), commercial poultry (Murphy and Duncan 1977, 1978), animal behavior (Bronson 1968, Mueller and Parker 1980), and handling stress (Meier *et al.* 1973); and

(7) inferences can be drawn from studies in which the effects of disturbance induced by research activity are assessed (Duffy 1979, MacInnes 1980, Strang 1980, Gotmark and Ahlund 1984, Erwin 1989, Frederick and Collopy 1989).

Much of the published literature has focused on documenting that disturbance occurs rather than examining the mechanistic causes of disturbance. Many of these studies pose a problem in that investigators may erroneously conclude that human disturbance *per se* has no effect on the examined parameters (*e.g.*, Watson 1988, Frederick and Collopy 1989), whereas there may be alternative explanations. For example, the "disturbance" source applied in a study may be perceived as a stressor by some individual animals but not by others. Even if the stimulus is appropriately disturbing to a given species, it may not be applied at a level sufficient to elicit an overt behavioral response. An investigator can conclude that a specific type or level of human activity is not disturbing but, by definition, cannot conclude that human disturbance has no effect. Conversely, inverse associations between densities of nest or roost sites and human development may simply demonstrate preferences rather than species tolerance limits.

Studies of disturbance also may be hampered during the design process because of anthropocentric views on what constitutes a "disturbance". For example, Freddy *et al.* (1986) showed that mule deer (*Odocoileus hemionus*) reacted more to humans afoot than on snowmobiles which, at least initially, seems counter-intuitive. Watson (1988) presumed dogs were a source of disturbance to nesting dotterels

(*Charadrius morinellus*), yet dogs are used as attractants in Dutch *endecoy* traps for waterfowl. Aircraft are required to fly above minimum altitudes during fall staging of snow geese in the Arctic National Wildlife Refuge and during breeding of the Hawaiian petrel (*Pterodroma phaeopygia*) in Haleakala National Park, yet staging black brant showed increased response to helicopters with increasing altitude (Ward *et al.* 1988). Distributions of bald eagle perch trees and shoreline development on Chesapeake Bay were negatively correlated (Buehler *et al.* 1991), yet bald eagles perch in large numbers on buildings and telephone poles in Adak, Alaska (pers. obs.). Partly for these reasons, Burger (1995) cautioned that researchers should document when human presence does not cause an effect, as well as when it does.

Proposed Model

I chose to study the effects of human disturbance on sanderlings (*Calidris alba*). As Myers (1989) noted, the sanderlings is the "white rat" of shorebird research in both hemispheres. Many behavioral and ecological aspects of sanderlings have been previously described: nesting (Parmelee 1970), migration (Myers *et al.* 1985, Summers *et al.* 1987), population structure (Myers *et al.* 1986), winter spacing behavior (Myers *et al.* 1980, Myers 1984), energetics (Connors *et al.* 1981, Castro 1987, Castro *et al.* 1992), and feeding (Silliman *et al.* 1976, Myers *et al.* 1980, Maron and Myers 1985). Additionally, sanderlings have been shown to be sensitive to both pedestrian (Burger and Gochfeld 1991) and vehicular traffic (Pfister *et al.* 1992) on the beach.

The breeding range of sanderlings is circumpolar, with a mean latitude of 72°N (Myers 1981). Sanderlings breed from mid-June to mid-Aug, a relatively short 60-d period. Mating is monogamous with occasional double clutching and serial polyandry. Both sexes incubate, but the female leaves shortly after incubation to initiate and care for a second clutch while the male attends the first clutch. In the New World, sanderlings migrating south in the late summer and early autumn tend to use the Atlantic coast.

The nonbreeding season of sanderlings is 10 mos, with the actual winter residence usually 4 - 8 mos 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). Northbound sanderlings from the Pacific tropics tend to use a central flyway and to a lesser extent the Pacific coastline; northbound sanderlings from the Atlantic tropics use the Atlantic coast. Because most sanderlings winter on the Peruvian and Chilean coast, the sanderling metapopulation tends to circumnavigate the New World in a clockwise direction as they complete their annual cycle (Myers *et al.* 1989). Within this larger migration pattern, vehicular traffic on the beach can reduce local sanderling use of staging areas by as much as 50% (Pfister *et al.* 1992).

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). Observations of sanderlings wintering at different latitudes suggest that time spent feeding varies from 36% in Peru to 50% in New Jersey to 85% in Texas (Castro *et al.* 1992). However, at a given beach, the number of people within 100 m of sanderlings consistently explained much of the variation in time spent foraging (Burger and Gochfeld 1991).

A recent summary of the International Shorebird Survey showed that sanderling populations on the East Coast decreased by 80% during 1972 - 1983 (Howe *et al.* 1989). Myers (1989) attributed at least some of this decline to the pervasive use of pesticides in South America and coastal degradation. Human activities that occur on the beaches within the nonbreeding range of sanderlings may constitute a serious form of habitat degradation.

I propose that human disturbance is an additional energetic burden on animals that have evolved, for the most part, in the absence of humans. Consequently, the energetic response to human disturbance should be reflected as increased existence metabolism (*sensu* Kendeigh 1949). I will argue, and hopefully demonstrate, that there are essentially three behavioral responses to increased existence metabolism: (1) compensatory foraging, (2) habituation, and (3) dispersal. Increased energy intake compensates for increased existence metabolism, habituation reduces disturbance-increased existence metabolism, and dispersal avoids increases in existence metabolism altogether. This is most easily tested during the winter months when energy balance may be more critical for nonbreeding sanderling (Maron and Myers 1985).

Existence metabolism

The concept of existence metabolism was originally proposed by Kendeigh (1949), clarified by Kendeigh (1969), and later reinterpreted by Ricklefs (1974:172-175). This model includes three components: existence metabolism, maximum potential metabolism (*i.e.*, available energy), and productive energy (Figure 1). Existence metabolism (EM) is the rate at which energy is used by caged birds maintaining a constant mass (± 1 - 2%) over a period of 3 - 4 days when the birds are not involved in reproduction, molting, migratory unrest, growth, or fat deposition. It includes, by definition, the costs of basal metabolism (BMR), thermoregulation, the heat increment of feeding, and the energy expended in cage locomotor activity (foraging; Kendeigh *et al.* 1977). In effect, it is the minimum amount of energy required for existence in a cage and varies linearly with temperature below the thermoneutral zone (but see Davis 1955, Owen 1970). Wijnandts (1984:39) observed that "EM should theoretically differ from free-living existence only by the cost of locomotion (principally for foraging)".

Maximum potential metabolism was defined by West (1960) as the maximum rate at which energy can be metabolized by a bird. It occurs at the lower limit of temperature tolerance (*i.e.*, the temperature [LD50] at which 50% of newly-caught, locally-acclimatized birds died; Kendeigh *et al.* 1977), but it will be manifested at higher temperatures if the animal is performing excessive exercise (Murton and Westwood 1977; see Kontogiannis 1968). Measurement of maximum potential metabolism caused by cold stress in waterfowl, and perhaps shorebirds, may be difficult; a mallard (*Anas platyrhynchos*) in postabsorptive state was able to maintain body temperature for 1h at -100° C (cited in Prince 1979).

Because of the forementioned problem and difficulties with other assumptions, Ricklefs (1974) used the term *available energy* (AE) as a preferred alternative to maximum potential metabolism. This term includes food availability and "procurement", the latter referring to foraging constraints. Prince (1979) suggested that the highest rate of food consumption by a bird under laboratory conditions may provide an estimate of AE.

Productive energy (PE) is the difference between AE and EM at any given temperature. PE is, in effect, the energy available for reproduction, molt, growth, migratory unrest, and fat deposition. Dunn (1979) pointed out that determination of PE is useful for identifying periods of vunerability to environmental stress during the annual time-energy budget of an avian species. Prince (1979) suggested that most wintering activity in waterfowl falls within EM (rather than PE) but I think this statement overstates the stress that most waterfowl (and shorebirds) experience on their wintering grounds. Since Prince's publication, it has become more apparent that courtship in dabbling ducks occurs throughout the wintering period (*e.g.*, Hepp and Hair 1983), that some waterfowl spend substantial amounts of their time budgets loafing (Paulus 1988), and that some wintering waterfowl reduce food intake and body mass "voluntarily" after midwinter (Hepp 1986, Perry *et al.* 1986).

There is some confusion in the literature about the role of food intake. Whereas Ricklefs (1974) included food intake within the context of AE (as discussed previously), Murton and Westwood (1977:149) suggested that PE is modified by food intake, "since underfed birds will not achieve their maximum potential energy". As I understand the PE concept, and as I plan to use it experimentally, PE cannot include measures of food intake as it is simply the difference between AE and EM.

The concept of EM seems to be appropriate for modelling the energetic costs of responding metabolically or behaviorally to disturbance. Human-induced disturbance is an environmental stressor over and beyond the stressors imposed by a "natural" system. I consider it an additive cost that may or may not be compensated for by additional foraging (i.e., compensatory foraging). And as will be discussed elsewhere, there may be other risks associated with feeding outside the optimum "window".

Assuming that response to human disturbance is additive, then EM should increase. In Figure 1, the the y-intercept increases but the slope remains the same (EM′) in response to disturbance. For every increment that EM′ increases as a result of responding to disturbance, PE should decrease, effectively reducing energy available for fat deposition (primarily) and survival during periods of cold or food stress. This model emphasizes three important points: that disturbance is effectively a component of habitat quality, that human disturbance may be more critical when the difference between EM and AE is minimal (i.e., during periods of cold or heat stress), and that human disturbance may directly affect fitness by reducing PE.

Habituation

Habituation may be defined as the waning of response as a result of repeated or continuous stimulation; "the response decrement is specific to the original stimulus [which] can be reinstated by another, equally strong, stimulus" (Peeke 1984:399), and it "neither results from altered properties of sensory receptors or effectors nor is [it] followed by any kind of reinforcement" (Shalter 1984:351). Davis and File (1984:287-293) summarized the historical development of current theories of habituation, and papers collected in Peeke and Herz (1973a, 1973b) and Peeke and Petrinovich (1984) extensively reviewed research in habituation.

Habituation studies of avian species have been conducted primarily in the context of investigating social releasers (*e.g.*, Tinbergen 1948) or for the purpose of frightening birds away from crops (Krebs 1980) and airports (Larkin 1976). Studies of auditory habituation have included alarm calls (Thompson *et al.* 1968*a*, Shalter 1984), distress calls (Langowski *et al.* 1969, Johnson *et al.* 1985), and territorial songs (Petrinovich and Patterson 1979, Patterson and Petrinovich 1979, Peeke and Petrinovich 1984), whereas studies of visual habituation have been oriented towards predator models (see citations in Shalter 1984). These types of studies generally offer little towards understanding habituation to most human-induced disturbances (*e.g.*, aircraft noise or automobile traffic) in that the stimuli are natural and responses are innately programmed, at least in part. For example, the variance in heart rate of naive mallard ducklings is greater in response to the silhouette of a hawk than to that of a goose (Mueller and Parker 1980). However, it is likely that avian responses to anthropogenic stimuli may be generalized to some degree; many animals react fearfully to novelty and to objects that are approaching them (Bronson 1968).

The response of birds to auditory stimuli is mediated by noise level (dBA), noise type, time of day, and number of birds involved. For example, Ward *et al.* (1988) found that 80% of the variation in flight response of Pacific black brant to aircraft was explained by the noise generated above 65 dBA, despite various combinations of aircraft type, lateral distance, and altitude. However, the type of noise can affect response; starlings (*Sturnus vulgaris*) exhibited high heart rates when subjected to distress calls and intermediate rates when subjected to a human voice or escape call, despite similar sound levels (Thompson *et al.* 1968a). Furthermore, heart rates of starlings were higher during the day than night, and when in a group than when alone, in response to distress calls (Thompson *et al.* 1968b).

As I mentioned previously, studies of visual stimuli have been primarily limited to raptor models. However, in a particularly innovative study, Lazarus (1979) exposed captive red-billed queleas (*Quelea quelea*) to a very brief (80 ms) light to test the early warning response of different size flocks. Additionally, applied studies of poultry have used actual human presence or physical handling to elicit a fear response (Murphy and Duncan 1977, 1978, Barnett and Hemsworth 1989, Hemsworth and Barnett 1989).

Murphy and Duncan (1977, 1978) showed that responses of domestic fowl to humans may be very resistant to modification. Adult hens of two domestic stocks, one docile and one flighty, were generally unaffected by associating human contact with a food reward or with a non-rewarding situation. Chicks of both stocks, raised without human contact for the first six weeks of their lives, showed withdrawal responses when first exposed to humans; however, docile birds habituated (relative to controls) within five days to humans, whereas flighty birds were still showing more withdrawal than their controls after 21 days. These results demonstrate breed-specific (and presumably species-specific) responsiveness to disturbance. They also show that the fear response in both stocks could be modified by rearing without human contact, but that the behavioral modification is in the direction of increasing withdrawal.

One of the difficulties with scoring habituation based on behavioral cues was demonstrated by MacArthur *et al.* (1982) in their study of heart rate-telemetered mountain sheep (*Ovis canadensis*) in Alberta. Sheep had elevated heart rates when disturbed by aircraft despite showing no evidence of behavioral response (*i.e.*, alert to or withdrawing from the disturbance). Mean duration of the heart rate response (in the absence of a behavioral response) was not greater than the mean duration of the behavioral response when it did occur. This is an outstanding example of the dual process of habituation outlined by Groves and Thompson (1970), where the response to a stimulus is the summation of two opposing processes, one which is decremental (habituation) and the other incremental (sensitization; *i.e.*, arousal).

It is critical that experimental stimuli be qualitatively and quantitatively within the range of anthropogenic stimuli experienced by shorebirds. On the other hand, experimental stimuli must be sufficiently generalized such that inferences can be extended to management scenarios. Petrinovich (1973:158-160) discussed this trade-off of structuring experiments in systematic versus representative designs. The former is useful for demonstrating **possibility** whereas the latter investigates **probability**. Petrinovich (1973:160) suggested that in order to understand behavioral habituation it will be necessary to abandon research strategies which give a "spurious air of precision". For example, laboratory researchers may positively correlate fear response with noise level, yet a mouse moving around in the dark can evoke the most persistent orienting response while a jet aircraft taking off may not "ruffle the composure of the most timid rabbits grazing near the runway" (Worden 1973:113). As an alternative, Petrinovich (1973) advocated using a "set of more naturalistic and representative research tools".

Compensatory foraging

Shorebird feeding strategies in response to human disturbance have been studied only once previously. Burger and Gochfeld (1991) showed that the number of people within 100 m of wintering sanderlings consistently explained most of the variation in time spent foraging; to compensate, sanderlings apparently fed more at night when pedestrian traffic levels on the beach were lower and birds reacted at shorter distances. Similarly, Barnard and Thompson (1985) presented evidence that plovers can compensate for an energy deficit by increasing diurnal feeding time, feeding at night, or utilizing fat and protein reserves. Robert *et al.* (1989) suggested that some shorebirds wintering in Venezuela may feed at night because of limited feeding space and time induced by tide constraints during the day.

In an unique study, Swennen *et al.* (1989) stressed captive oystercatchers (*Haematopus ostralegus*) by manipulating their tidal regime in an outdoor aviary. Even with foraging time shortened to as little as a third of the normal 5 - 6 hr low tide, the birds were able to maintain their mean consumption (g ash-free dry mass) per tide. These birds achieved increased intake rates by spending proportionally more time foraging during shorter low tides, and by reducing search and handling times. In a similar study under field conditions, Goss-Custard (1981) investigated the ability of redshanks (*Tringa totanus*) to compensate for shortened daylength during the winter (Aug - Mar). Redshanks prefer to feed during the day and daylength varied 10.7-15.2 hr during the study period. Goss-Custard found that redshanks tended to reduce search speed and ingestion rate of small worms, while increasing number of pecks attempted and ingestion rate of large worms in response to reduced daylength.

The possibility of compensatory foraging by waterfowl in response to human disturbance has been suggested by Pedroli (1982), and Tuite *et al*. (1983), and recently modelled by Brackney (1987) and Belanger and Bedard (1990). Using time budget and body composition data from undisturbed flocks (Brackney *et al*. 1987) and reaction times of snow geese to aircraft (Davis and Wisely 1974), Brackney (1987) simulated the interactive effects of compensatory foraging and habituation to aircraft disturbance on daily fat gain in female snow geese staging on the Arctic National Wildlife Refuge. Sensitivity analysis suggested that reduced feeding time and energy intake had greater effects on daily fat gain than increased energy expenditure due to flight; Brackney assumed geese would compensate for disturbance by increasing foraging time at the expense of other behaviors.

Belanger and Bedard (1989, 1990) investigated two responses of staging snow geese to human disturbance in Quebec. In Response A, birds flew away but promptly resumed feeding following a disturbance. In Response B, birds interrupted feeding altogether. Based on diurnal time budget data, a 4% increase in night feeding could theoretically compensate for energy losses caused by additional flight in response A, whereas a 32% increase in night feeding would be required in response B. Variation in observed feeding time during the day was not correlated with disturbance levels.

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.

Optimal foraging theory supposes that animals maximize or minimize some *currency* subject to definable *constraints*; hence, that currency is optimized. In discussions of optimal foraging theory with other students, I find that the concept of *optimality* is frequently misunderstood. Maximization and optimization are often viewed as two different strategies rather than options on a continuum. Stearns and Schmid-Hempel (1987:120) pointed out that *optimal* has one meaning in common usage and quite another in technical usage: in the former, it simply means "the best possible" and in the latter, it "always means the best possible under the given boundary conditions".

Schoener (1971) suggested that animals can approach the problem of acquiring food quickly by being either *energy maximizers* or *time minimizers*. The former maximizes the amount of energy gained in a fixed time and the latter minimizes the time required to gain a fixed ration of energy. Pyke *et al*. (1977) argued that in most situations both currencies are equivalent to rate maximization; they differ from each other only when food comes in lumps (see example in Stephens and Krebs 1986:9). Recently, Masman *et al*. (1988) proposed a third currency, *energy minimization*, based on evidence that kestrels (*Falco tinnunculus*) minimize energy expenditure, rather than foraging time, during winter.

However, I would rarely expect net rate of energy intake by birds to be maximized in a proximate sense for reasons outlined elsewhere in this text; exceptions might be hyperphagia during migrational staging, feeding after prolonged fasting, or feeding by parents of altricial young. In most situations, net rate of energy intake should be submaximal (*i.e.*, optimal) such that an animal can invest both time and energy into other actitivites that maximize its long term fitness. Hainsworth and Wolf (1983) argued that feeding may be regulated proportionally or integrally, with respect to endogenous energy reserves, as a consequence of trade-offs between energy demands and nutrient or predation constraints.

Constraints may be extrinsic or intrinsic (Stephens and Krebs 1986:10). Extrinsic constraints are imposed on an animal by the environment; *e.g.*, tide cycle, ambient temperature, time of day, or wind velocity. Intrinsic constraints are imposed on an animal by its physiology or life history; these can be limitations on species-specific abilities (*e.g.*, maximum flight speed, hearing range) or tolerances within which an animal must live (*e.g.*, nutrient requirements). Conventional foraging models have generally assumed few constraints; much of the recent developmental work in optimal foraging theory has studied the inclusion of additional constraints in models (see Pyke 1984). While it is clearly important to understand how extrinsic factors constrain foraging, it is the intrinsic constraints that shorebirds can relax in order to increase energy intake rate.

Shorebirds (*Charadrii*) use two basic foraging strategies: one group, including sanderlings, most other sandpipers (*Scolopacidae),* and the oystercatcher (*Haematopus* sp.) are predominantly tactile feeders whereas plovers (*Charadriidae*) feed almost exclusively by sight (Pienkowski 1981; but see Paulson 1990). Plovers sometimes vibrate their feet ("foot-trembling") to stimulate prey movement (Pienkowski 1983, Barnard and Thompson 1985). These strategies have coevolved with anatomical structures, mandible length being the most obviously different feature between the two groups (Burton 1974). Search patterns are remarkably different between the two groups; sandpipers *cruise search* and plovers *saltatory search* (O'Brien *et al.* 1990).

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.

Dispersal

Anthropogenic disturbance can affect dispersal and distribution of wildlife. Researchers have generally approached this problem by relating animal distribution to roads (Van der Zande *et al.* 1980, Madsen 1985), to housing development patterns (Vogel 1983, Mann 1985, Buehler *et al.* 1991), and to recreation (Knight and Knight 1984, Korschgen *et al.* 1985). Others (*e.g.*, Stalmaster and Newman 1978, Fraser *et al.* 1985) have made inferences about dispersal from measuring flush response and flush distances. Shorebird studies have been limited; Watson (1988) attempted to relate breeding densities of dotterels to pedestrian traffic, and Bryant (1979) found correlations between densities of shorebirds wintering in Scotland and a disturbance index (based on distance from shore).

Klein (1993) investigated the distribution of foraging waterbirds (Anseriformes, Charadriformes, Ciconiiformes, Gruiformes, Pelecaniformes, Podicipediformes) on the "Ding" Darling National Wildlife Refuge, Florida, in relation to vehicular traffic. In addition to recording waterbird densities within 20 m X 50 m plots, Klein categorized five behavioral responses to experimental exposure to five human disturbance patterns. Shorebirds showed sensitivity at intermediate traffic levels, but shorebird numbers were too low to be included in statistical analyses of the latter experiment. Experimental manipulation of human disturbance, though not unique, is certainly an unusual approach to studying distribution shifts in foraging shorebirds. However, Klein did not consider possible differences in prey availability among strip plots in her experimental design.

Another approach to studying dispersal in response to anthropogenic disturbance is to measure changes in flock size and behavior. For example, Norris and Wilson (1988) correlated increases in maximum sizes of 18 white-fronted goose flocks over two years with lower disturbance levels; this may be partially explained by findings that brant (Owens 1977) and pink-footed geese (Madsen 1985) flushed at greater distances with increasing flock size. Similarly, Barnard (1980) found that house sparrow (*Passer domesticus*) flock means and variances decreased with increasing levels of human activity.

Ironically, results of numerous experimental studies of flocking behavior actually suggest that flock size and human disturbance should be positively correlated. Beveridge and Deage (1986:303) stated that most studies have found that as flock size increases an individual's vigilance decreases and foraging increases). Consequently, flocking by shorebirds may serve as a strategy to share vigilance costs at high disturbance levels; *e.g.*, Lazarus (1979) showed that as group size of red-billed queleas increased, response to a flying goshawk changed from taking wing to flight intention movements to orienting behaviors, despite increasing probabilities of detecting the predator. Alternatively, flocking may serve as a foraging strategy to compensate for increased disturbance costs; *e.g.*, Ekman and Hake (1988) recently demonstrated that green finches (*Caruelis chloris*) foraging in groups reduced food intake variablity by taking advantage of cues from flock mates, thereby minimizing starvation risks.

Theoretical predictions and empirical observations of flocking may not match because increased rates of "looking up" may not imply enhanced vigilance for predators (*i.e.*, human disturbance). Rather, as Beveridge and Deag (1986) pointed out, increased rates of "looking up" may be associated with attention to flock companions, either to observe feeding success or to observe possible competitors. The flock vigilance hypothesis ignores interspecific and intraspecific aggression within the flock. For example, Burger *et al.* (1979) documented that aggression generally increased as migrating shorebirds densities increased (although there were exceptions). Also, there is controversy over the role of mixed-species flocking; Barnard and Thompson (1985) argued that mixed-species foraging flocks take flight earlier than single-species flocks because of enhanced vigilance, whereas Stinson (1988) argued that interspecific feeding interference causes some species to abandon feeding sites more readily.

The central questions to my dissertation are the following:

Does human disturbance increase the existence metabolism of sanderlings?

Can sanderlings compensate for increased existence metabolism or disturbed foraging activity by relaxing foraging constraints?

Can sanderlings habituate to disturbance stimuli?

How does human disturbance disperse wintering sanderling populations?

The first question must be answered with captive sanderlings. The second two questions can be partly answered with both captive and free-ranging sanderlings. The last question must be addressed with free-ranging sanderlings.

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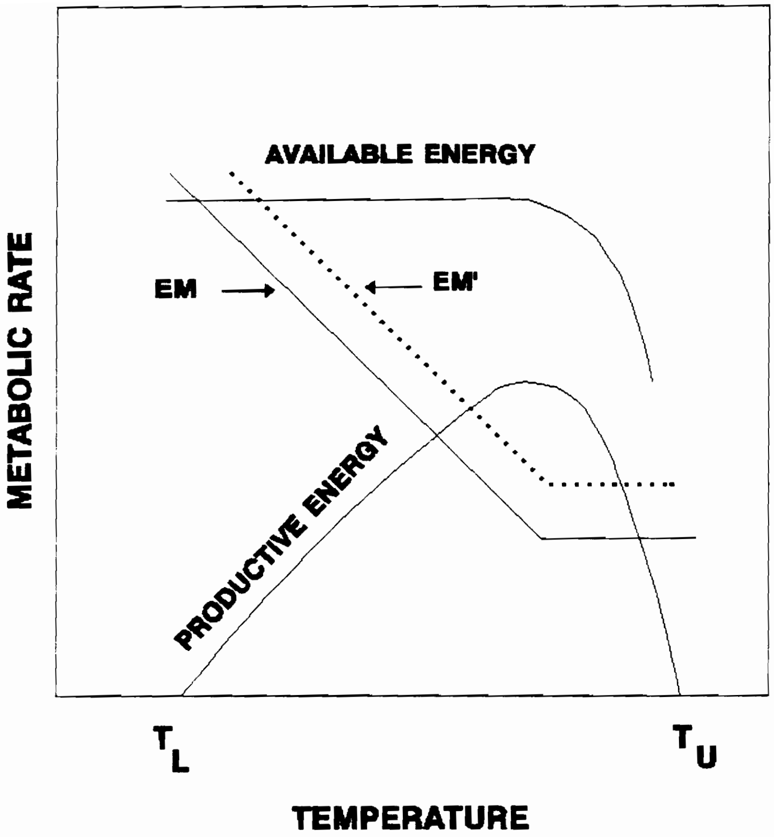

Adapted from Ricklefs (1974).

Figure 1. Hypothetical effect of anthropogenic disturbance on existence metabolism (EM).

CHAPTER 2

Effects of Low Level Human Disturbance on Nonbreeding Dunlin and Sanderling Energy Metabolism

Introduction

Human disturbance has been increasingly recognized as an environmental threat to wild avifauna, including raptors (Knight and Skagen 1986), waterfowl (Morton *et al.* 1989, Dahlgren and Korschgen 1992), seabirds (Manuwal 1978, Anderson and Keith 1980), waterbirds (Kaiser and Fritzell 1984, Bratton 1990, Klein 1993), shorebirds (Yalden and Yalden 1989, Burger and Gochfield 1991, Pfister *et al.* 1992), and other groups (Wunz 1971, Cooke 1980). The effects of research activity on avian subjects also has been openly discussed within the scientific community (Duffy 1979, MacInnes 1980, Strang 1980).

The single most cited response to disturbance is flight and its consequences. Flying is an energetically costly behavior; estimates range from 9 to 15 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.

Despite the potential impacts that human disturbance may have on birds, the phenomenon of disturbance has not been modelled or generalized to any degree. Because disturbance is a recently recognized problem, studies have tended to anecdotally document that it occurs or, at best, have quantified the effects (not the causes) of disturbance. The fact that bird-human interactions are clearly multivariate in complexity does not make even conceptual modelling a simple task: there are species-specific tolerances that may vary behaviorally, temporally, spatially, with individual experience, and/or with type, frequency, duration, and magnitude of the disturbance stimulus itself.

Anderson (1988) proposed that human disturbance and its impacts on wildlife are analagous to the dose-response relationship in toxicology. As with toxicants, there is a range of doses (*i.e.*, disturbances levels) over which there is a graded response and a minimum effective dose; *i.e.*, a threshold which must be reached before an animal responds. This is similar to the dual-disturbance threshold model that McGarigal *et al*. (1991) proposed for explaining bald eagle (*Haliaeetus leucocephalus*) flush response. These are functional approaches to studying the symptoms of disturbance and have important management applications, but contribute little to understanding the ecological tradeoffs a bird makes when it choses to overtly respond (*e.g.*, flush).

Perhaps anthropogenic disturbance should be viewed more simply as an additional stressor of natural systems. Stress has been defined as a "perturbation that is applied to a system by a stressor that is foreign to that system or which may be natural to it but is applied at an excessive level" (Barrett 1981), and is disadvantageous to the system (Ivanovici and Wiebe 1981). Certainly this definition includes human presence or activity as a stressor (*sensu* Selye 1976) of avian systems. Although it could be argued that most avian species have evolved with *Homo sapiens in abstentia* or, until relatively recently, at low densities (and is therefore foreign), it is unnecessary to do so. It should be apparent that human presence and activity have exceeded tolerable levels for avian populations in many urban and special public use areas (*e.g.*, National Parks).

In this context of human disturbance as a stressor, I hypothesized that the metabolic response to it will be to increase maintenance costs (Chapter 1). Birds have three possible behavioral responses to increased maintenance costs: increased energy intake, habituation, and/or dispersal. Increased energy intake compensates for increased costs, habituation effectively reduces disturbance-induced costs, and dispersal avoids disturbance altogether. Failure to respond adequately with one or more of these three strategies may ultimately result in reduced body mass and, presumably, reduced fitness of individuals.

I chose to test this idea with the productive energy model proposed by Kendeigh (1949), clarified by Kendeigh (1969), and reinterpreted by Ricklefs (1974:172-175). This model includes three components: existence metabolism (EM), available energy, and productive energy (Figure 1). EM is the rate at which energy is used by caged birds maintaining body mass (± 2%) over a period of 3 - 4 d when the birds are not involved in reproduction, molting, migratory unrest, growth, or fat deposition. Available energy is the maximum rate at which energy can be metabolized by a bird (West 1960); it generally occurs at the lower limit of temperature tolerance, but it will be manifested at higher temperatures if the animal is performing excessive exercise (Kontogiannis 1968). Productive energy is the difference between available energy and EM at any given temperature. Productive energy represents the energy available for reproduction, molt, growth, migratory unrest, and fat deposition and, as such, is a measure of potential fitness.

Increased maintenance costs associated with metabolic and behavioral responses to disturbance should be manifested as increased EM; the resulting elevated value is defined as EM′. For every increment that EM′ increases, productive energy should decrease (Figure 1); therefore, this model could theoretically show the cost of disturbance to potential fitness. Dunn (1979) pointed out that determination of productive energy is useful for identifying periods of vulnerability to environmental stress during the annual time-energy budget of an avian species.

I applied this model to nonbreeding dunlins (*Calidris alpinus*) and sanderlings (*Calidris alba*). Both species are common wintering shorebirds on the mid-Atlantic coast, the former on estuarine tidal flats and the latter on marine beaches. Human disturbance on beaches, in particular, has been implicated as a factor contributing to reduced sanderling abundance (Pfister *et al.* 1992) and diurnal foraging time (Burger and Gochfeld 1991). In this chapter, I report the results of two experiments that were conducted, the first with dunlins in a pilot study and the second with sanderlings, to test the hypothesis that EM differed between disturbed and undisturbed treatments.

Experiment 1: Dunlin energy metabolism

Methods

Dunlins (*Calidris alpinus*) were mistnetted at Chincoteague National Wildlife Refuge, Virginia, during Oct - Nov 1990. Birds were aged by plumage (Prater *et al.* 1977:100), identified with aluminum leg bands, and transported to the vivarium at Virginia Polytechnic Institute and State University. Initial capture weights were measured with a spring scale to the nearest 0.5 g; subsequent weights were measured with an electronic balance to the nearest 0.1 g.

Dunlins were maintained in quarantine and relative isolation at 20° C on a 10L:14D photoperiod (0730 - 1730). Maximum and minimum room temperatures were recorded daily. During the acclimation period, 2 - 4 birds were kept in 61 X 61 X 41 cm stainless steel rabbit cages. Grated cage floors were covered with Shepherd™ cageboard. Separate bathing and drinking water (the latter with dissolved Nekton K™ vitamin supplement) were provided daily. Crushed oyster shells and 2mm granulated salmon grower (Biosponge™) were provided *ad libitum*.

This feed is 45% protein, 16% fat, and 3% crude fiber. Nekton MSA™ amino acid and calcium supplement was supplied with the salmon grower.

Because only one room was available for trials, dunlins received undisturbed (control) and disturbed treatments sequentially with two replications; *i.e.*, 1C-1D-2C-2D. The first trial (1C) was initiated on 20 Feb and the last trial (2D) was completed on 26 Mar. Trials were conducted over 4 d, with 4-d intervals between trials. Nine adult and 9 immature dunlins were randomly assigned by age to 6 cages 3 weeks before trials (each cage contained 3 birds of the same age). Initial and final body masses were recorded at 0900 on the day before a trial was initiated and on the day a trial was completed, respectively. The mean of initial and final body mass for sanderlings in each cage was raised to the 0.704 power to derive metabolic body mass ($BM^{.704}$; (Kersten and Piersma 1987). Body mass changes during trials were tested for significance with paired t-tests.

In disturbed trials, dunlins were exposed to a 5-min disturbance event (on the hour ± 10 min) during each of 10 diurnal h for 4 d. During each event, I walked back and forth in front of the cages while human voices were broadcast from a tape player at approximately 70 dBA (measured at 1.5 m from cage doors with a Realistic™ sound level meter). Both disturbed and undisturbed subjects were exposed daily to 15 min of human activity at 0900 while water and feed were replaced.

Drinking water and weighed amounts of salmon grower were provided *ad libitum* during the experimental period. Plexiglas was used in place of cageboard during trials; the plexiglas was replaced daily so that excrement and spilled feed could be removed and sorted. Bath water was removed during trials because feed and fecal matter were inseparable when partially dissolved in it. However, bath water was provided daily during intervals between trials. Wet feed intake$\cdot$cage$^{-1}\cdot$day^{-1} was determined for trials and intervals between trials.

Two 10-g grab samples of salmon grower were taken daily during trials and freeze-dried for 24 h to obtain dry weights; these values were later used to correct wet weights of daily food provided (by day) for varying moisture content. Food remaining and feces were dried for 24 h and weighed to the nearest 0.01 g. Four samples each of food and feces were combusted in a Parr™ adiabatic bomb calorimeter to obtain mean energy content; these values were applied to dry food mass ingested and dry fecal mass egested to derive apparent metabolized energy (ME). ME was divided by BM$^{.704}$ in the subsequent analysis to standardize values for varying body mass among sanderlings.

Because all four trials were conducted sequentially in a single room, I considered each trial a single sample, with two repetitions per treatment and six cages per repetition. I applied this nested analysis of variance (ANOVA; df = 13, 10) to assess the effect of treatment on ME, dry feed ingested, and dry feces egested, after dividing these values by metabolic body mass. The treatment effect (df = 1) was tested with the mean square for repetitions nested within treatment (df = 2); the repetition within treatment effect was tested with the mean square for cage nested within repetition (df = 10). Paired-*t* tests were used to assess the change in body mass for dunlin by cage ($n = 6$) within trials. Significance for all statistical inference was $P \leq 0.10$.

Results

Most dunlins appeared to acclimate to captivity well. Mean body mass of 22 dunlins recorded between capture date and 19 Feb (12 - 16 weeks), the beginning of experimental trials, was at least as high as body mass at capture. Capture weights of adult and immature dunlins averaged 54.9 g (SE = 1.6, $n = 10$) and 52.4 g (SE = 2.9, $n = 12$), respectively. On 19 Feb, mean weights of adults and immatures were 56.9 g (SE = 1.5, $n = 10$) and 51.3 g (SE = 0.9, $n = 12$), respectively. Dunlins were able to metabolize 69.8% of the dry salmon grower, which contained 22.3 $\text{kJ}\cdot\text{g}^{-1}$ of energy (Table 1).

ME was higher for undisturbed than disturbed dunlins ($P = 0.086$; Table 2). On average, three dunlins metabolized 31.1 $\text{kJ}\cdot(\text{BM}^{.704})^{-1}$ (SE = 0.8, $n = 12$) in an undisturbed caged environment and 28.6 $\text{kJ}\cdot(\text{BM}^{.704})^{-1}$ (SE = 0.8, $n = 12$) in a disturbed caged environment over a 4-d period. These values represented 1118 kJ•4d^{-1} in the former and 1020 kJ•4d^{-1} in the latter (Table 3). Neither dry feces egested ($P = 0.318$) nor dry feed ingested ($P = 0.152$) differed between treatments (Tables 2, 3).

Differences in ME between treatments did not manifest themselves clearly in body mass changes during the experimental period. Paired *t*-tests of body mass change by cage suggested that the average group of three sanderlings ($n = 6$) gained 1.95 g (SE = 0.69, $P = 0.036$) during trial 1C but lost 3.92 g (SE = 0.75, $P = 0.003$), 4.68 g (SE = 1.05, $P = 0.001$), and 2.5 g (SE = 0.92, $P = 0.042$) during trials 2C, 1D, and 2D, respectively. Dunlins regained body mass during the 4-d intervals between trials, but not enough to fully compensate for the loss during trials (Figure 2). Mean body mass ($n = 18$) declined from 54.1 g (SE = 1.16) to 53.3 g (SE = 0.95) by 31 Mar, 4 d after the last trial.

There was no evidence that dunlins altered their feeding times during disturbance trials. Wet feed intake•cage^{-1}•day^{-1} of 4 nonexperimental dunlins (2 birds•cage^{-1}) was determined between 0900 - 1700 and between 1700 - 0900 during the second disturbance trial (2D) and subsequent post-trial 4-d interval. While disturbed, the mean proportion of wet feed•cage^{-1} ingested between 0900-1700 was 0.215 (SE = 0.300, $n = 4$) and 0.284 (SE = 0.032, $n = 4$). During the post-trial interval, this proportion remained relatively constant at 0.191 (SE = 0.0350, $n = 4$) and 0.264 (SE = 0.242, $n = 4$) for the same cages. However, mean wet feed intake•day^{-1} (n = 8) increased by 24% and 30% during the 4-d intervals after control and disturbance treatments, respectively. Regardless of whether dunlins were disturbed or not, ≥ 70% of feed intake apparently occurred between 1700 and 0900 the next day.

Ambient room temperatures during the experimental period varied from 18 - 25° C. Averages of maximum and minimum daily temperatures (n = 4) were 20.4° C (SE = 0.43), 20.4° C (SE = 0.52), 19.1° C (SE = 0.13), and 22.9° C (SE = 0.32) during trials 1C, 1D, 2C, and 2D, respectively.

Discussion

Without accounting for varying body mass, results of this pilot study suggest the opposite of what was expected. In response to a low level of disturbance that spanned 50 min•d^{-1} or 8.3% of daylight hours, energy metabolized by disturbed dunlins averaged 98.2 kJ•cage^{-1}•4d^{-1} lower than by undisturbed dunlins; *i.e.*, 8.8% lower. EM estimates for disturbed and undisturbed dunlins were 85.0 kJ•d^{-1} and 93.2 kJ•d^{-1}.

Undisturbed dunlins gained 0.6 g during the first repetition and lost 1.3 g during the second repetition (Table 3). In contrast, disturbed dunlins lost 1.6 g and 0.8 g during the first and second repetitions, respectively. Variations in body mass and food intake were poorly associated, presumably because each bird (*n* = 18) was weighed pre- and post-trial whereas food intake was measured daily for each cage (*n* = 6). The tendency to lose body mass during three of four trials and then regain most of that loss during the 4-d intervals between trials, regardless of treatment (Figure 1), suggest that the experimental protocol itself was stressful. Both lack of bathing water and accumulation of fecal matter on dunlins' feet may physically distress the birds.

However, mean body mass of four nonexperimental dunlins that were held in the same room as the 18 experimental dunlins, but not at the expense of bathing water or cageboard, declined similarly over the experimental period (Figure 3); simple linear regression suggests that the slopes were -0.288 (SE = 0.138) for the former and -0.284 (SE = 0.095) for the latter. Additionally, mean body mass had been declining since 31 Dec, 7 weeks prior to the start of the first trial. This phenomenon could have been caused by a nutritional deficiency, muscle atrophy, or an endogenously-regulated rhythm (see Pienkowski *et al.* 1984:45 and Appendix 1).

I suggest that the accelerated weight loss during disturbed trials was due to the treatment itself. Proximate analysis of 83 sanderlings suggested that a 1-g weight difference consisted of 22.7% lipids, 29% dry lean mass, and 48.3% water, which approximates 14.5 kJ (Castro *et al.* 1989). If body mass changes shown here are assumed to be similar (Table 1), then undisturbed and disturbed dunlins metabolized 94.4 $kJ \cdot d^{-1}$ and 89.4 $kJ \cdot d^{-1}$, respectively, from feed and body reserves combined. These similar data suggest that total metabolized energy may not vary in response to the energetic costs of disturbance in a caged environment. Rather, birds may reduce body mass and, effectively, EM so as to balance the additional energetic costs of disturbance. In this case, average dunlins cumulatively lost 2.4 g in two disturbed trials as opposed to 0.7 g during two undisturbed trials, despite similar estimates of total metabolized energy.

I had initially considered using a more quantifiable and repeatable machine-generated stimuli than the one chosen for this exploratory study. However, the question of ecological relevance eventually outweighed statistical concerns. The combination of human presence coupled with human voices is a disturbance that wintering sandpipers are constantly challenged with along shorelines. The relatively low level was selected because higher levels would have elicited a flush response and, consequently, physical duress and negative conditioning when dunlins encountered the cage walls or ceiling. The hourly exposure was selected because there is evidence that birds respond differently to environmental stress at different times of the day (Fraser *et al.* 1985, Meier *et al.* 1973).

Generally, dunlins responded to the disturbance used in this study with alert behavior (standing, necks outstretched), alarm calls, and agitation (preening, walking back and forth). I observed flush behavior rarely during these trials. In the middle of the day, there was a tendency to respond less actively; paradoxically, some birds occasionally fed while others remained resting on one leg with head tucked.

Inherent weaknesses in the experimental design and protocol confounded the difficulty of measuring small changes in energy expenditure by captive animals. Further attempts to measure the energetic cost of disturbance must incorporate a statistical design and/or sampling methodology to better account for varying body mass and composition, a shortened experimental period or change in experimental protocol to reduce stress, and estimation of fecal energy egested from all experimental subjects (rather than an average) so as to account for individual variation. In the following experiment with sanderlings, all parameters are measured on individual birds (rather than three), each bird is exposed to only two trials (rather than four), the interval between trials was increased from 4 d to 10 d, plexiglas was replaced by linoleum flooring, metabolized lipid mass during trials were estimated from measurements of total body electrical conductivity, and the experimental design was changed from a nested ANOVA to a 2-way factorial design with metabolic body mass as a covariate (ANCOVA).

Experiment 2: Sanderling energy metabolism

Methods

Twenty-four sanderlings were mistnetted at Chincoteague National Wildlife Refuge, Virginia, during 9 - 20 Jan 1993. Birds were aged by plumage (Prater *et al.* 1977:80), identified with aluminum leg bands, and weighed with an Avinet™ 100-g spring scale to the nearest 0.5 g. Lengths of both flattened wings were measured with a ruler to the nearest 1 mm, and lengths of culmen and both tarsi were measured with calipers to the nearest 0.1 mm (Prater *et al.* 1977:24). An electronic balance (± 0.01 g) was used to obtain all subsequent weights. Mean lengths of wing and tarsus were used in subsequent analyses.

Total body electrical conductivity (TOBEC) was measured within 2 h after capture with an EM-SCAN SA-1 Small Animal Body Composition Analyzer™ (Walsberg 1988, Castro *et al.* 1990). Each sanderling was held immobile by a nylon stocking, attached to the shuttle with a rubber band, placed on its dorsum with spine straight, aligned along the long axis of the chamber, and centered in the middle of the measurement chamber. An index of lean body mass (I_{LM}) was calculated as

$$I_{LM} = (S - E)/R;$$

where S = average of four chamber measurements with sample, E = average of four empty chamber measurements, and R = average of two calibration measurements. Sanderlings were held captive outdoors in a 2 X 0.5 X 0.75 m cage until transport to the vivarium at Virginia Polytechnic Institute and State University (VPISU) on 22 Jan 1993. Whole body mass and TOBEC were measured again immediately before (21 Jan), and one week after, transport (1 Feb).

Sanderlings were randomly assigned within age class to two identical rooms in the VPISU vivarium (10 mature and 2 immature birds/room). Birds were maintained individually in 61 X 61 X 41 cm stainless steel rabbit cages (6 cages/rack) at 20°C (± 2°) on a 10L:14D photoperiod (0730 - 1730). During the 3-week acclimation period, sanderlings were provided with Zeigler™ salmon starter No. 3 (50.0% protein, 15.4% fat, 1% fiber, 10.8% ash, 10% moisture), oyster shell fragments, drinking water, and bathing water *ad libitum*.

Two trials were conducted over 4 d each, with a 10-d interval between trials. In each trial, 12 sanderlings within one room were exposed to a 5-min disturbance event on the hour (± 10 min) during each of 10 diurnal hours. Each event consisted of a radio played at approx. 70 dBA (measured 1.5 m from cage doors with a Realistic™ sound level meter), while I walked back and forth 1.5 m in front of the cages. Concurrently, 12 sanderlings in the other room were undisturbed; *i.e.*, they were used as a control. Both treatment groups were exposed to a brief morning visit (≈ 20 min) during which time food, water, and cage linings were changed. To eliminate a possible room effect, I applied the same disturbance to the other room during Trial 2 (*i.e.*, switchback); rooms contained the same sanderlings during both trials. Trial 1 was initiated on 12 Feb and Trial 2 was completed on 2 Mar. Body mass and TOBEC were measured at 0900 on the day before trials were initiated and on the day trials were completed.

Salmon starter and drinking water were provided *ad libitum* during trials. Linoleum was used as the cage floor during trials and replaced daily so that excrement and spilled feed could be removed, sorted, and weighed. Bath water was removed during trials because feed and fecal matter were inseparable when partially dissolved in it; however, bath water was provided daily during the 10-d interval between trials.

Two 10-g grab samples of salmon starter were taken daily and freeze-dried for ≥ 12 h to obtain dry weights; mean values ($n = 2$) were used to correct weights of wet feed provided daily for varying moisture content. These 10-g samples of feed were then pooled by trial, ground with pestle and mortar, and freeze-dried again for ≥ 12 h. Three 1-g grab samples of dried feed per trial ($n = 6$) were subsequently pelleted and combusted in an adiabatic bomb calorimeter to obtain caloric content.

Egested fecal matter and uningested feed for each bird$\cdot$d^{-1} were freeze dried for ≥ 12 h and weighed to the nearest 0.01 g. Dried fecal matter was pooled for each bird by treatment, ground with pestle and mortar, and freeze-dried again for ≥ 12 h. A single 1-g grab sample of the pooled feces for each bird X treatment combination (*n* = 48) was subsequently pelleted and combusted in an adiabatic bomb calorimeter to obtain caloric content. Duplicate 1-g samples of dried fecal matter from 5 birds also were combusted to assess the relative error in the bombing process. Energy content of dried ingested and egested masses was subsequently expressed in joules (1 j = 4.184 cal). Apparent metabolized energy (ME) was the difference in energy content between ingested and egested dry masses.

Behaviors of disturbed sanderlings were scored during both trials. After the first minute of each 5-min disturbance event, I systematically recorded a single behavior (focal point sampling; Altmann 1977) of a different sanderling on alternate passes as I walked back and forth; 12 observations were recorded per disturbance event or 10$\cdot$bird$^{-1}\cdot$d^{-1}. I reversed the observation sequence of birds at the initiation of each hourly disturbance event so as to minimize a possible time effect. Behavioral categories included fly, run, walk, hop (1-legged), alert, and maintenance (drink, preen, wing stretch). The proportion of time spent in different behaviors (*i.e.*, time budgets) was calculated by both bird and hour. Time budgets were converted to energy budgets by weighting each behavioral category by an appropriate multiple of basal metabolic rate (BMR). BMR was estimated for each sanderling using an oxygen consumption value of 1.98 $ml \cdot g^{-1} \cdot h^{-1}$ with a conversion factor of 20.1 kJ per liter of oxygen consumed (Castro 1987); body mass was the average of weights taken at trial initiation and completion. BMR multiples for fly, alert, maintenance, hop, walk, and run behaviors were 12.5, 2.2, 2.1, 3.5, 1.7, and 3.5, respectively (King 1974, Wooley and Owen 1978).

After whole body mass and TOBEC were measured at the completion of Trial 2, birds were euthanized immediately by thoracic compression, double-bagged in plastic, and frozen. Partially-thawed carcasses were plucked, ingesta removed, sexed by gonadal examination, and weighed to obtain plucked wet carcass mass. Carcasses were sectioned, partially frozen, and freeze-dried for ≥ 48 h to obtain dry carcass mass. Carcasses were then homogenized in a Waring blender and freeze-dried again for 12 h to remove absorbed water. Lipids in one 6 - 15 g sample from each carcass homogenate were extracted for 12 h using ethyl ether in a Soxhlet apparatus after oven-drying samples at 55°C for 12 h. Water mass was the difference between plucked wet carcass and dry carcass masses. Nonlipid dry mass (*hereafter* lean mass) was the difference between dry carcass and lipid masses. Lean, water, and lipid masses sum to plucked wet carcass mass.

A calibration equation for estimating lipid mass in live sanderlings was developed by regressing lipid mass on body mass, I_{LM}, sex, age, and body size (see Morton *et al.* 1991) using PROC GLM (SAS Institute 1986). The variance-covariance matrix scores from the first Principal Component axis of the log-transformed morphometric variables (PROC PRINCOMP, SAS Institute 1986) were used as a measure of body size. This technique reduces several morphometrics, in this case culmen, wing, and tarsus lengths, to a single variable that expresses body size (Pimental 1979). The final model was chosen by sequentially eliminating nonsignificant variables from the full model.

The final regression model was used to estimate total lipids in each sanderling at initiation and completion of both trials. Metabolized lipid mass was the difference between lipid estimates within trial for each sanderling. I used a value of 39.3 $kJ \cdot g^{-1}$ lipid (Kersten and Piersma 1987) to adjust ME for lipids metabolized during trials; *i.e.*, EM_{ADJ} was the energy derived from exogenous (ME) and endogenous (metabolized lipids) sources. The effects of trial, treatment, and initial metabolic body mass ($BM^{.704}$; Kersten and Piersma 1987) on dry matter intake, dry feces egested, ME, body mass change, and EM_{ADJ} were analyzed in separate 2-way ANCOVAs (df = 4,43; PROC GLM; SAS Institute 1986). Significance for all statistical inference was $P \leq 0.05$.

Results

This sample of sanderlings included 16 mature females, 4 mature males, 3 immature females, and 1 immature male. Although sanderling distribution was stratified by age *apriori*, birds were not sexed until trials were completed. I was unable to statistically adjust for sex because all 5 males were assigned, by chance, to the same room. However, a 2-way ANCOVA (df = 4,19) suggests that mean body mass at time of capture differed between sexes ($P = 0.030$) but did not vary by age ($P = 0.885$), body size ($P = 0.359$), or the sex X age interaction ($P = 0.369$). Mean body masses of male and female sanderlings at capture were 48.3 g (SE = 1.06, $n = 5$) and 56.8 g (SE = 1.31, $n = 19$), respectively. Consequently, the use of body mass as a covariate in analyses of treatment and trial effects on energy balance presumably removes much of the variance associated with sex.

Sanderlings appeared to acclimate to captivity well. Mean body weights ($n = 24$) did not change during captivity ($r = 0.441$, $P = 0.381$, n = 6) and were never less than that recorded at time of capture (Figure 4). However, mean I_{LM} values decreased after sanderlings were transferred to the VPISU vivarium (Figure 4; $r = -0.995$, $P = 0.0001$, n = 6), suggesting that dry lean mass and/or water mass decreased with capture time.

Five duplicate samples of combusted fecal matter suggest that the relative error in the bombing process was minimal. Duplicates differed by an average of 110 joules (SE = 30.2, *n* = 5), which represents a deviation of only 0.8% from the first sample. Consequently, duplicate estimates were averaged and mean values for these five samples were used in subsequent analyses.

Body composition and TOBEC

This sample (*n* = 25) included an additional sanderling (mature female) that had died shortly after capture and had been kept frozen until processing. Whole body mass averaged 56.3 g (SE = 1.84) and ranged from 45.8 - 93.1 g. TOBEC averaged 59.0 I_{LM} units (SE = 1.24) and ranged from 47.4 - 67.9 units. Lipid mass averaged 12.7 g (SE = 1.54) and ranged from 3.6 - 45.4 g. Lean mass averaged 11.3 g (SE = 0.18) and ranged from 9.4 - 12.6 g. Water mass averaged 27.2 g (SE = 0.40) and ranged from 23.4 - 31.5 g.

TOBEC was positively correlated with body mass (r = 0.607, P = 0.0013), body size (r = 0.470, P = 0.0178), NLDM (r = 0.846, P = 0.0001), and water mass (r = 0.828, P = 0.0001). The standardized partial coefficients of the regression of TOBEC on lipid, lean, and water masses (P = 0.0001, df = 3,21) were 0.135, 0.482, and 0.363, respectively. These data suggest that the relationship between TOBEC and body composition was most explained by varying lean and water masses. However, variation in body composition was primarily lipid mass; the standardized partial coefficients of the regression of body mass on lipid, lean, and water masses ($P = 0.0001$, df = 3,21) were 0.846, 0.081, and 0.275, respectively.

Variation in lipid mass was best explained ($R^2 = 0.948$, $F = 202.1$, $P = 0.0001$, df = 2,22) by the following regression model (Eq. 1):

$$\text{Lipid mass} = -17.361742 + 0.948339\ (\text{BM}) - 0.395496\ (\text{TOBEC})$$

Squared partial correlation coefficients for body mass (BM) and TOBEC were 0.940 ($P = 0.0001$) and 0.551 ($P = 0.0001$), respectively.

Initial and final values of body mass and TOBEC were used to estimate changes in lipid mass during trials from the regression model developed above (Eq. 1). Mean body and lipid mass losses in both trials ($n = 48$) were 4.39 g (SE = 0.411) and 3.27 g (SE = 0.358), respectively. The energy content of estimated lipid mass loss was summed with ME to obtain estimates of EM_{ADJ}.

Metabolic response to disturbance

Dry salmon grower contained 22.65 kJ•g^{-1} (SE = 0.03, *n* = 6), 69.5% of which was metabolizable by sanderlings (Table 1). Dry fecal matter excreted by sanderlings contained 14.11 kJ•g^{-1} (SE = 0.092, *n* = 24). Preliminary two-way ANCOVAs suggested that dry matter intake, fecal mass egested, ME, and body mass lost were unaffected by treatment ($P \geq 0.305$) or BM$^{.704}$ ($P \geq 0.136$)(Table 4). Dry matter intake, dry fecal mass, and ME were higher in Trial 1 than Trial 2 ($P \leq 0.055$), whereas mean body mass loss was higher in Trial 2 than Trial 1 ($P = 0.003$).

Dry matter intake, dry fecal mass, and ME were affected by the treatment X trial interaction ($P \leq 0.020$)(Table 4), suggesting a room effect. Despite identical dimensions and the same cooling system, room temperatures varied slightly. The room in which Trials 1D (18.5°) and 2C (18.5°) were conducted had lower mean temperatures than the room in which Trials 1C (21.6°) and 2D (21.0°) occurred (Table 5). Although sanderlings were maintained within the thermoneutral zone, data from captive dunlins suggest that even small changes in ambient temperatures can affect feed intake (Appendix 1). This additional variation can be accounted for by summing ME with energy derived from metabolized lipid mass; *i.e.*, EM$_{ADJ}$.

EM$_{ADJ}$ was higher for disturbed than undisturbed sanderlings. The least square means (which correct for varying BM$^{.704}$) of EM$_{ADJ}$ for undisturbed and disturbed sanderlings were 379.84 kJ•4 d^{-1} (SE = 8.91, n = 24) and 406.91 kJ•4 d^{-1} (SE = 8.91, n = 24), respectively. Two-way ANCOVAs suggest that EM_{ADJ} was affected by treatment (P = 0.037) and $BM^{.704}$ (P = 0.001), but was unaffected by trials (P = 0.149) and the treatment X trial interaction (P = 0.077)(Table 4). Estimates of both ME and EM_{ADJ} increased linearly and positively with the body mass of sanderlings at the end of the trial. The Pearson correlation coefficient between ME and final body mass was 0.424 (P = 0.003) and between EM_{ADJ} and final body mass was 0.530 (P= 0.0001).

Behavioral response to disturbance

A total of 960 observations were equally distributed over 24 sanderlings, 10 h, and 4 d. Time budgets were estimated by averaging the proportion of time spent in each behavior using individual sanderlings as the sample unit (n = 24; Table 6). Mean proportion of time that sanderlings spent in alert, escape (hop, walk, run and fly summed), and maintenance behaviors were 0.525 (SE = 0.052), 0.463 (SE = 0.054), and 0.012 (SE = 0.004), respectively. When sanderlings attempted to escape in this caged environment (n = 444), 9.7% hopped, 64.0% walked, 17.8% ran, and 8.5% flew.

MANOVAs (Wilks' λ) suggest that alert and escape behaviors varied among days, hour, and individual sanderlings ($P \leq 0.002$), but not by the day X hour interaction

(*P* = 0.086). Sanderlings tended to spend proportionately more time in escape behaviors ($P \leq 0.065$) and less time being alert ($P \leq 0.088$) on the first days of 4-d trials. Sanderlings spent proportionately more time in escape behaviors and less time in alert during the first disturbance of every day (0730) than during subsequent disturbances ($P \leq 0.007$; Figure 5). Variation among individual sanderlings was much greater than that attributable to day or time, accounting for ≥ 79% of the model sums of squares for either behavior. Some sanderlings spent as much as 95% of their time alert, whereas others spent as much as 100% of their time in escape behaviors (Table 6). Of 24 sanderlings, two spent 32 - 35% of their time attempting to fly whereas 16 never flushed. Mean energy spent by sanderlings during 200 min of disturbances over 4 d, based on behavioral responses, was 20.0 kJ (SE = 1.46, n = 24).

Discussion

Existence metabolism is the rate at which energy is used by caged birds maintaining a constant mass (± 1 - 2%) over a period of 3 - 4 d. In this study, sanderlings lost an average of 7.3% (SE = 0.7, n = 48) of their initial body mass during experimental trials. Clearly, I was not measuring existence metabolism as defined. Hinsely (1992) solved this problem by discarding data from birds whose body mass changed ± 2.5% during trials. Castro *et al.* (1988), on the other hand, adjusted estimates of EM by approximations of the energy content of observed mass changes. I chose this latter approach because a previous metabolism study of captive dunlins suggested that mass change may be a short-term, and perhaps a long-term, response to the increased energy costs of disturbance (*sensu* Moreno 1989, Cooch *et al.* 1991).

I used TOBEC methodology to estimate changes in body mass that were attributable to metabolized lipids. By summing ME and energy derived from metabolized lipids, I estimated the total energy metabolized by sanderlings existing under disturbed (EM_{ADJ}') and undisturbed conditions (EM_{ADJ}). This procedure assumes that lipids can be estimated well in live sanderlings, and that the difference between lipid and body mass loss is water (not lean mass). In support of the first assumption, the regression model developed from TOBEC and body mass as independent variables explained 95% of variation in ether-extracted lipid mass. In support of the second assumption, standardized partial coefficients from the regression of body mass on lean, water, and lipid masses suggest that only 7% of varying body mass (within the range experienced in these trials) may be attributable to lean mass. Additionally, only 1.12 g (SE = 0.16, *n* = 48) of body mass loss was, on average, unattributable to metabolized lipid mass in individual sanderlings; *i.e.*, lean mass changes were negligible even if they occurred.

Least squares estimates of EM_{ADJ} for undisturbed and disturbed sanderlings at 20°C were 95.0 $kJ \cdot d^{-1}$ and 101.7 $kJ \cdot d^{-1}$, respectively. Similarly, EM estimates for nonbreeding sanderlings fed *Tenebrio* larvae and *Limulus* eggs at 25°C were 82.7 $kJ \cdot d^{-1}$ and 116 $kJ \cdot d^{-1}$, respectively (Castro *et al.* 1989). Although I did not record behavior during undisturbed trials, it is apparent that sanderlings had negative reactions to disturbance. Almost 99% of behaviors observed during disturbances were scored as alert or escape, and sanderlings were never observed feeding during these intervals. Of 24 sanderlings, 8 attempted to flush at least once during disturbance trials. The energetic cost of responding behaviorally to disturbance ($n = 24$) was positively associated with metabolized lipids ($r = 0.480$, $P = 0.018$), negatively associated with ME ($r = -0.392$, $P = 0.058$), and not associated with EM_{ADJ} ($r = 0.195$, $P = 0.360$). At least in a caged environment, sanderlings balanced the additional energetic demands of disturbance by increasing endogenously-derived energy and decreasing exogenously-derived energy, suggesting both behavioral and metabolic dimensions.

By constraining birds in a caged environment, the time and energy costs of having remained in the presence of repeated disturbance can be estimated. A 5-min disturbance during each of 10 diurnal hours apparently increased EM_{ADJ} by 6.7 kJ (7%) during that 24-h period, suggesting that productive energy decreased by that same increment. Sanderlings in this study showed evidence of habituation as the day progressed (Figure 5), despite high variability in behavioral response among individuals. There was no evidence of compensatory feeding during trials, despite having feed available *ad libitum*; however, increased body mass during the 10-d interval between trials suggests compensatory intake after the stressor was removed (Figure 4). Habituation and any compensatory feeding that may have occurred were apparently inadequate, resulting in body mass loss during trials.

Reducing fat mass and food intake, although easy to dismiss in laboratory conditions as "stress-related", is a viable strategy for decreasing energy expenditure. Body mass of sanderlings at the end of trials explained 28% of the variation in EM_{ADJ}. Rogers and Smith (1993) argued that individual birds are sensitive to, and can control, both predation and starvation risks by varying body fat. More fat presumably conveys both a survival advantage during periods of prolonged stress and a competitive advantage during conspecific interactions, but also results in longer foraging times, increased predation risks, and higher daily energy expenditures to maintain it. Individual birds must balance these tradeoffs.

Under persistent suboptimal conditions, an animal may eventually acclimatize at a lower steady state of productivity (Yousef 1988). Castro *et al.* (1992) showed that lean, dry carcass mass explained 14% of the variation in the daily energy expenditure of free-ranging sanderlings. Based on mean oxygen consumption of 1.98 $ml \cdot g^{-1} \cdot h^{-1}$ for nonbreeding sanderlings at 25°C and a conversion factor of 20.1 $kJ \cdot l^{-1}$ O_2 (Castro 1987), a 1-g loss of body mass represents a 0.9552 $kJ \cdot d^{-1}$ reduction in BMR. As anthropogenic disturbance becomes more pervasive in the natural system, this is one possible outcome. Cooch *et al.* (1991) have similarly suggested that long-term declines in body size and mass of lesser snow geese (*Anser caerulescens caerulescens*) may be responses to environmental degradation.

Shorebirds appear to respond to stressors in the wild as these sanderlings did in a caged environment. Burger and Gochfeld (1993) showed that diurnal foraging time (and presumably intake) of wintering sanderlings decreased in response to human presence within 100 m. Dugan *et al.* (1981) provided evidence that body fat in nonbreeding shorebirds is, in fact, stored for situations such as this, where energy demands exceed intake for relatively short periods.

Wintering sanderlings in the wild still have opportunities to choose relatively undisturbed habitat. Among free-ranging populations, at least some sanderlings likely disperse in order to avoid disturbance and maintain body fitness. Pfister *et al.* (1992), for example, used census data to show that human disturbance may be displacing individuals of at least some shorebird species (including sanderlings) at a staging area in coastal Massachusetts. Similarly, Bryant (1979) found correlations between densities of shorebirds wintering in Scotland and a disturbance index (based on distance from shore).

Although dispersal is an immediate solution to avoiding the short-term costs of disturbance, it must be balanced by the risks and costs of dispersing. Locomotion behaviors, particularly flight, are energetically expensive. Bryant and Tatner (1991) positively correlated intraspecific variation in daily energy expenditure with time flying in several avian species. For average sanderlings, flight expends 0.42 $kJ \cdot min^{-1}$ (based on an energy coefficient of 12.5 X BMR, where BMR = 48.13 $kJ \cdot d^{-1}$; Castro 1987) but, as shown in this study, the costs of remaining in the proximity of even low levels of disturbance can be high. Sincock *et al.* (1966) implicitly recognized this tradeoff when they suggested that tolerance of disturbance by waterfowl (and presumably other birds) is relative to the level of disturbance and food availability on adjoining areas. As ambient disturbance levels increase in the future, however, sanderlings and other avifauna may be unable to avoid it completely. This study suggests that sanderlings may compensate for disturbance by reducing costs associated with foraging and maintaining body mass. Reduced fitness may be the outcome.

Results of this study are certainly not definitive. Questions remain concerning the possible effect of additional stress induced by the experimental protocol, whether EM′ increases linearly over all temperatures, and the appropriateness of artificial stimuli. However, Kendeigh's model is useful for understanding the cost of stressors such as anthropogenic disturbance: it allows measurement of the hidden metabolic cost of disturbance (EM′), directly associates that cost with potential loss of fitness (*i.e.*, productive energy), and is suggestive of the energetic tradeoffs that birds must consider in order to cope with that potential loss of fitness.

Ironically, Hinsely (1992) disparaged the use of metabolic measurements that required integration over relatively long periods, such as EM trials, because "they include all energy expenditures due to stress-related activity and alertness". Although her criticism may be appropriate for studies that are designed to measure metabolism in a relatively stress-free environment, this description explains exactly why EM trials are appropriate for measuring stress; *i.e.*, they provide an integrated end-point. Yousef (1988) lamented the fact that after almost 8 decades of stress research, there is not a single universally acceptable index of stress. Reiterating Moberg (1985), Yousef recommended that "scientists should de-emphasize the traditional approach of measuring discrete physiological responses to stress, *e.g.*, heart rate or the plasma concentration of adrenal corticoids, and instead examine the effects stress has on reproduction, immunity and metabolism, which would serve as indicators of well-being". Productive energy has this attribute.

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Table 1. Dry matter and energy content of BioSponge™ and Ziegler™ 2-mm salmon chow[a] fed, respectively, to 18 dunlins and 24 sanderlings during 4-d trials.

	Dunlin			Sanderling		
	n	$\bar{x}$	SE	*n*	$\bar{x}$	SE
Dry matter (%)	30	97.3	0.1	16	95.3	0.1
Metabolizable dry matter (%)	24	53.5	0.3	24	51.0	1.8
Metabolizable energy (%)[b]	24	69.8	0.2	24	69.5	1.1
Gross energy ($kJ \cdot g^{-1}$)	4	22.3	0.6	6	22.7	0.0
Metabolizable energy ($kJ \cdot g^{-1}$)[b]	24	15.5	0.0	24	15.7	0.3

[a] BioSponge™ salmon grower contains 45% protein, 16% fat, and 3% fiber; Ziegler™ No. 3 salmon starter contains 50% protein, 15.4% fat, 1% fiber, and 10.8% ash.

[b] Based on mean fecal energy of 14.46 $kJ \cdot g^{-1}$ (SE = 0.16, *n* = 4) and 14.11 $kJ \cdot g^{-1}$ (SE = 0.09, *n* = 24) for dunlin and sanderling, respectively.

Table 2. Mean squares from nested ANOVA models of dry feed ingested[a] (g), dry feces egested[a] (g), and metabolized energy[a] (kJ) by 18 dunlins in 6 cages (3 per cage) during 4-d trials.

		Mean Square[b]		
Source	df	Dry feed ingested	Dry feces egested	Metabolized energy
TREATMENT	1	0.1176	0.0101	38.166*
REP(TREATMENT)	2	0.0230	0.0110	3.771
CAGE(TREATMENT)	10	0.0534**	0.0133**	12.780**
ERROR	10	0.0067	0.0020	1.429

[a] All values divided by metabolic body mass (see text).

[b] * $P \leq 0.10$, ** $P \leq 0.01$; F statistic.

Table 3. Mean[a] metabolic responses of 18 captive dunlins in 6 cages (3 per cage) exposed to undisturbed and disturbed[b] treatments during four 4-d trials.

	UNDISTURBED		DISTURBED	
TRIAL	1C	2C	1D	2D
Dry feed ingested (g)	70.9 (2.61)	72.3 (3.71)	64.6 (3.75)	67.6 (2.46)
Dry feces egested (g)	32.0 (1.19)	33.8 (1.91)	30.3 (1.99)	32.2 (1.34)
Gross energy intake[c] (kJ)	1579.0 (59.99)	1609.4 (82.47)	1437.5 (83.52)	1505.5 (54.73)
Fecal energy[d] (kJ)	463.2 (16.94)	488.6 (27.65)	437.8 (28.73)	465.0 (19.37)
Metabolized energy (kJ)	1115.7 (41.42)	1120.8 (55.45)	999.7 (55.5)	1040.5 (36.32)
Initial body mass (g)	162.3 (4.82)	162.8 (4.51)	164.1 (4.04)	160.1 (3.98)
Final body mass (g)	164.2 (4.57)	158.9 (4.83)	159.4 (4.45)	157.6 (4.06)

[a] Number in parenthesis is standard error of mean of 6 cages of 3 dunlins each.

[b] Disturbance stimuli repeated 5 $\text{min} \cdot \text{h}^{-1}$ for 10 diurnal hours during two 4-d trials.

[c] Based on $4.184\ \text{J} \cdot \text{cal}^{-1} \cdot 5320.5\ \text{cal} \cdot \text{g}^{-1}$ dry mass ($SE = 14.2$, $n = 4$).

[d] Based on $4.184\ \text{J} \cdot \text{cal}^{-1} \cdot 3457.0\ \text{cal} \cdot \text{g}^{-1}$ dry mass ($SE = 39.2$, $n = 4$).

Table 4. Mean squares from 2-way ANCOVA models of dry feed ingested (g), dry feces egested (g), metabolized energy (kJ), and adjusted metabolized energy[a] (kJ) by 24 sanderlings during 4-d trials.

		Mean Square[b]			
Source	df	Dry feed ingested	Dry feces egested	Metabolized energy	EM_{ADJ}
TREATMENT	1	0.21	0.01	116.92	8774.18*
TRIAL	1	180.66*	28.92	49174.45*	4103.41
TREATMENT X TRIAL	1	200.06*	43.09*	51969.52**	6240.62
METABOLIC BODY MASS	1	5.96	1.66	1427.51	23039.90**
ERROR	43	31.35	7.44	7720.21	139906.62

[a] EM_{ADJ} = ME + energy content of estimated metabolized lipids (see text for details).

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

Table 5. Mean metabolic responses[a] of 24 captive sanderlings exposed to undisturbed and disturbed[b] treatments during two 4-d trials.

	UNDISTURBED		DISTURBED	
TRIAL	1C	2C	1D	2D
Dry feed ingested (g)	16.1 (1.13)	16.8 (1.84)	20.7 (1.48)	12.4 (1.84)
Dry feces egested (g)	7.5 (0.55)	8.1 (0.93)	9.5 (0.75)	5.9 (0.84)
Gross energy intake (kJ)	365.7 (25.61)	381.1 (41.77)	469.9 (33.6)	281.4 (41.62)
Fecal energy (kJ)	106.8 (8.61)	113.1 (13.73)	136.0 (11.36)	83.1 (11.78)
Metabolized energy (kJ)	258.9 (17.79)	268.1 (28.27)	333.9 (22.56)	198.2 (30.02)
EM (kJ)	347.3 (8.84)	414.6 (17.54)	409.8 (11.48)	401.8 (16.64)
EM_{ADJ} (kJ)[c]	358.4 (12.99)	401.3 (13.16)	409.4 (12.59)	404.5 (12.62)
Initial body mass (g)	56.9 (1.17)	64.6 (3.34)	60.5 (1.62)	59.5 (1.58)
ΔBody mass (g)	-3.6 (0.42)	-4.5 (0.79)	-2.6 (0.52)	-6.9 (0.96)
ΔTOBEC (I_{LM})[d]	-2.9 (0.85)	-0.2 (1.06)	-0.2 (1.11)	-3.3 (0.89)
ΔLipid mass (g)[e]	-2.2 (0.54)	-3.7 (0.59)	-1.9 (0.43)	-5.2 (0.88)
Room temperature (°C)	21.6 (0.13)	18.5 (0.20)	18.5 (0.20)	21.0 (0.20)

[a] SE in parenthesis; $n = 12$ for all variables except temperature ($n = 4$).

[b] Disturbance stimuli repeated 5 $\mathrm{min \cdot h^{-1}}$ for 10 diurnal hours during two 4-d trials.

[c] EM_{ADJ} = ME + energy content of metabolized lipids, using 39.3 $\mathrm{kJ \cdot g^{-1}}$ lipid as a conversion factor.

[d] TOBEC = total body electrical conductivity (measured with EM-SCAN SA-1 Small Animal Body Composition Analyzer™).

[e] Estimated by the following regression equation: lipid mass = -17.362 + 0.948 (BM) - 0.395 (TOBEC).

Table 6. Energetic (kJ) and behavioral responses (%) of 24 captive sanderlings to human disturbance repeated 5 min•h^{-1} for 10 diurnal hours over 4 d.

RESPONSE[a]	$\bar{x}$	SE	Minimum	Maximum	CV
Alert	52.5	5.24	0.0	95.0	48.87
Hop	4.5	2.22	0.0	50.0	240.76
Walk	29.6	3.69	0.0	70.0	61.07
Run	8.2	3.24	0.0	60.0	192.66
Fly	4.0	1.93	0.0	35.0	239.17
Maintenance[b]	1.3	0.37	0.0	5.0	144.46
Energy[c]	20.0	1.46	13.7	43.8	35.86

[a] Behavioral responses of each sanderling based on 40 observations.

[b] Maintenance behaviors include drink, preen, wing stretch.

[c] Energy = Σ (behavioral proportion•BMR coefficient•BMR) where BMR coefficients for alert, hop, walk, run, fly, and maintenance behaviors are 2.2, 3.5, 1.7, 3.5, 12.5, and 2.1, respectively. BMR = 1.98 ml•g^{-1}•h^{-1} with a conversion factor of 20.1 kJ per liter of oxygen consumed and g = body mass of each sanderling averaged between trial initiation and completion.

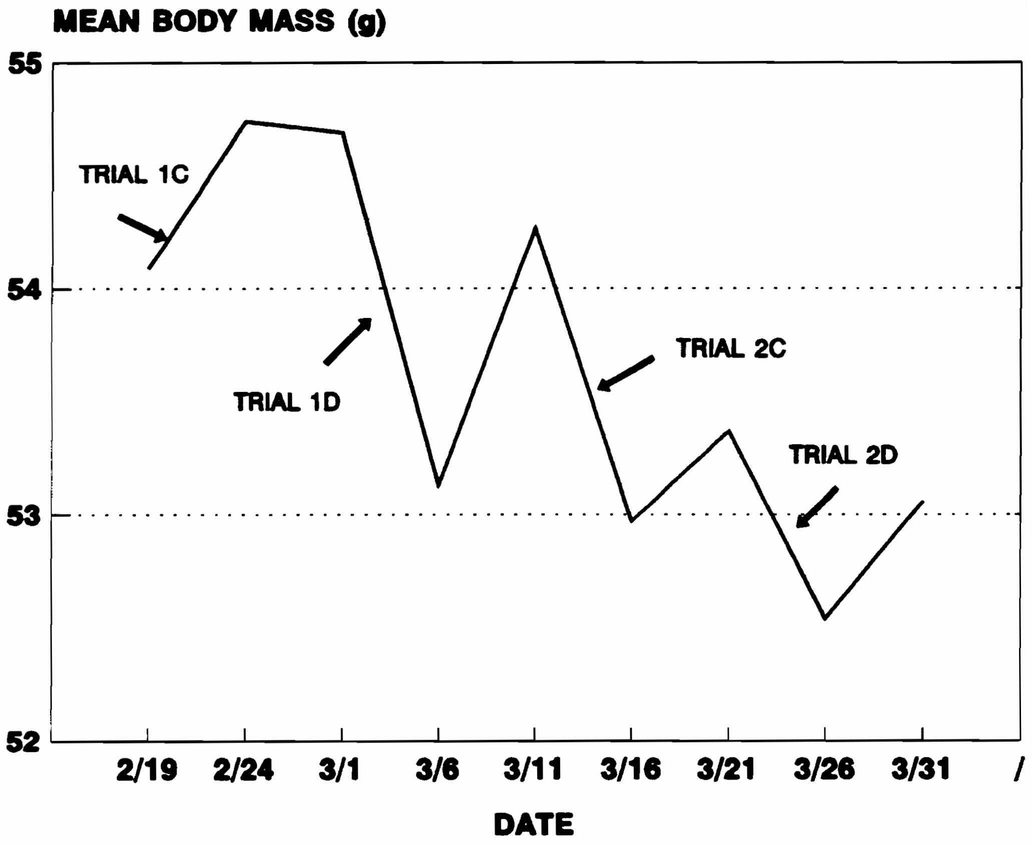


Figure 2. Mean body mass of 18 captive dunlins during the experimental period.

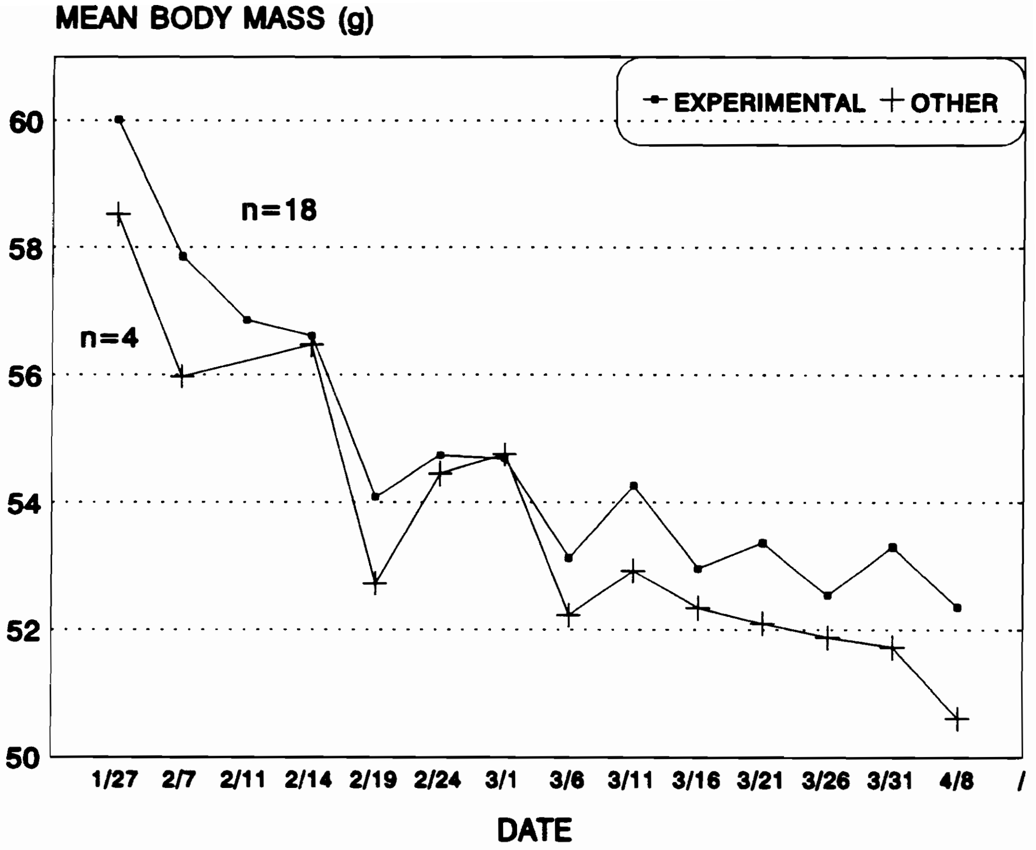
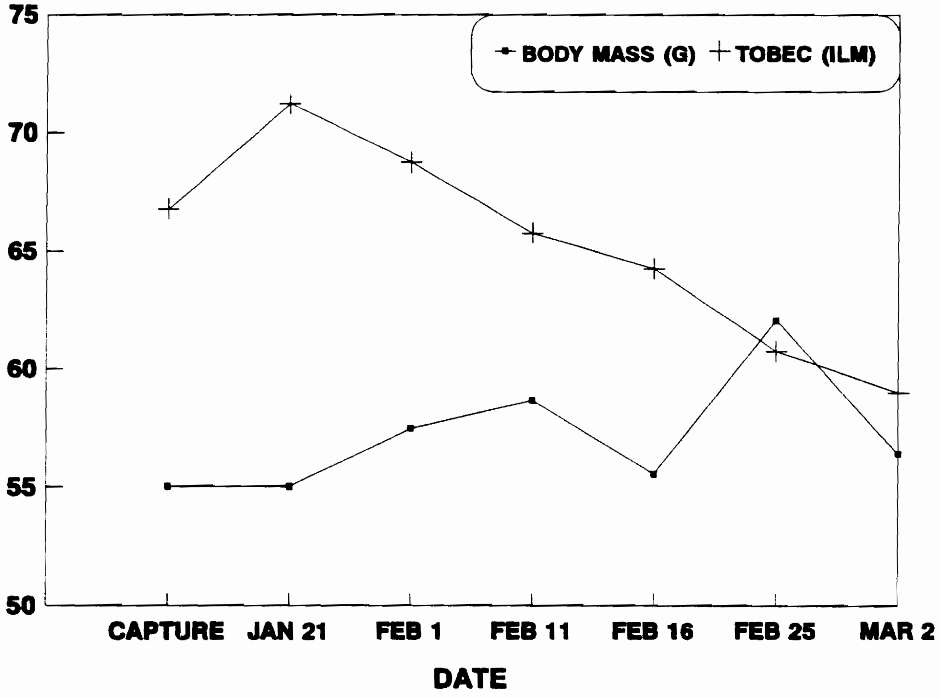


Figure 3. Mean body mass of 22 captive dunlins after assignments to experimental cages.



Capture dates = 9 - 20 Jan 1993.
Trials 1 and 2 initiated 12 and 26 Feb, respectively; body mass and TOBEC measured on 11 and 25 Feb.

Figure 4. Changes in mean body mass and total body electrical conductivity (TOBEC) of 24 captive sanderlings.

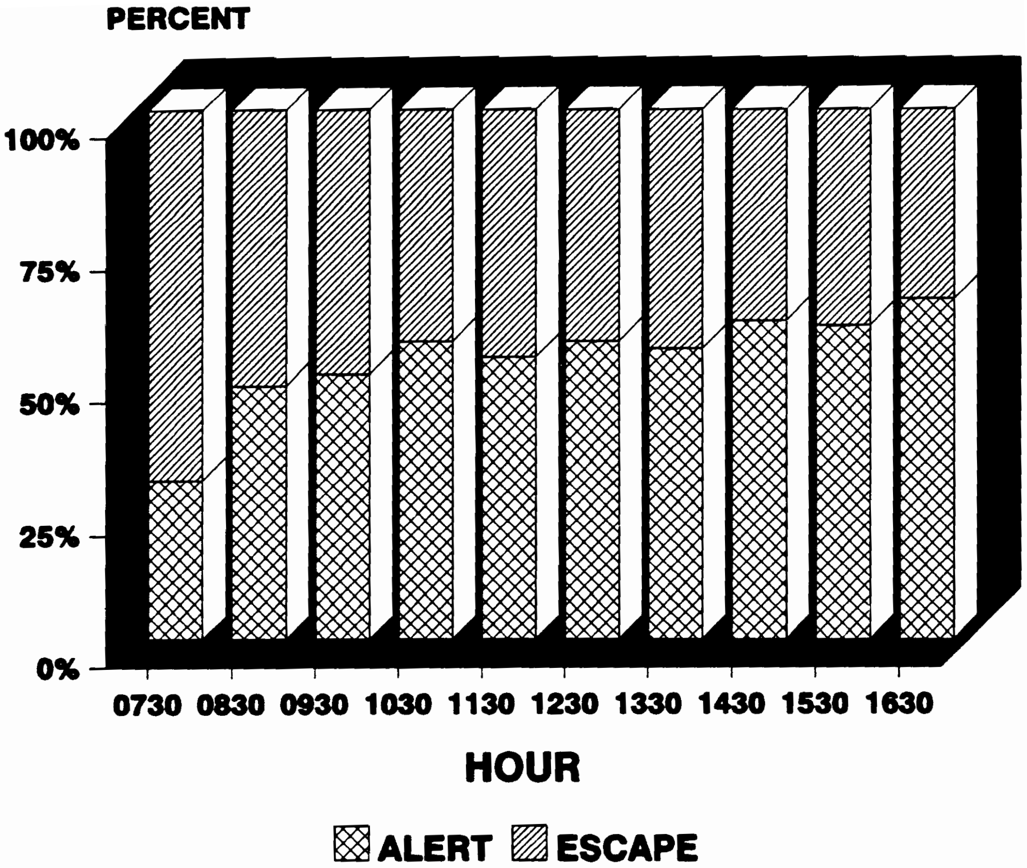


Figure 5. Behavioral responses of 24 captive sanderlings to hourly disturbance.

CHAPTER 3

Weekly Surveys of Beach Use at Assateague Island National Seashore

Introduction

A recent summary of the International Shorebird Survey showed that sanderling (*Calidris alba*) populations on the East Coast decreased 80% from 1972 to 1983 (Howe *et al.* 1989). Although reasons for this decline are not known (Myers 1989), studies by Burger and Gochfeld (1991) and Pfister *et al.* (1992) suggest that human disturbance may be displacing sanderlings on their wintering and staging areas.

I examined the possible effects of human activities on sanderlings at Assateague Island National Seashore (AINS). AINS is an important stopover for migrating sanderlings and is located on the northern extreme of their nonbreeding range. As part of the ongoing biological monitoring program at AINS, National Park Service (NPS) personnel count bird populations by species during biweekly surveys of the open beach. NPS data from 1987 - 1993 show that temporal use of AINS by sanderlings has a bimodal distribution, with a vernal migration pulse in Apr - May and a larger autumnal pulse in Jul - Aug (Figure 6). Sanderling counts during the nonbreeding season (Nov - Mar) range from 30 - 2700. Minimum counts during Jan, usually the month when sanderling populations are lowest, averaged 397 (SE = 128.8, n = 7). 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.

AINS also is one of the most highly visited public areas by recreationists in North America. Data from vehicle counters suggest that public use of the Maryland portion of AINS averaged 714,800 visitors annually from 1988 to 1992 (Figure 6). Visitation tends to peak in Jul or Aug, with numbers exceeding 100,000 during either month. Even in Jan, which is usually the month of least visitation, visitors averaged 9,563 (SE = 1,341.8) from 1988 to 1993.

It is apparent that the potential for human activities to affect sanderling populations at AINS is great. However, those effects are difficult to distinguish because seasonal use of AINS by sanderlings and humans tends to covary. Peak monthly sanderling counts were positively correlated (r_s = 0.334, P = 0.008, n = 62) with estimates of human use during 1988 - 1992. Despite this relationship, sanderlings may, in fact, be avoiding or minimizing encounters with human activities by subtle adjustments in their spatial and temporal use of AINS. To assess possible changes in spatial use, I modified the NPS survey methodology to include simultaneous counts of sanderlings and human activities within relatively short segments of beach. To assess possible changes in temporal use, I conducted these surveys during both night and day, and on weekends and weekdays. In this paper, I report the results of these modifications to the NPS survey methodology.

Study area

Assateague Island is a 60-km long barrier island off the Atlantic coast of Maryland and Virginia (38° 15′ N). The island was designated as part of the International Shorebird Reserve in 1990. The Maryland portion of Assateague Island consists of two public lands and a few scattered private inholdings (Figure 7). The NPS administers the 3,200-ha AINS and the Maryland Department of Natural Resources administers the 275-ha Assateague State Park. 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).

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 that extends north of Assateague State Park, and land access is restricted to entry from the south. Consequently, the frequency of disturbance diminishes rapidly the further one goes north. The south end 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, equestrians, dogs, and off-road vehicles 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. The north and south parts of AINS are separated by 3.2 km of beach that is part of Assateague State Park.

Methods

Shorebirds, other avifauna, and humans on the AINS beach were counted during weekly surveys conducted between 1000 - 1400 h. Additional surveys were conducted on weekends whenever possible to assess the response of sanderling populations to increased disturbance on weekends. Paired surveys were generally conducted on Friday and Saturday or, infrequently, on Sunday and Monday.

Birds and human activities were counted from a vehicle for 19 km, from the north end (AN) of Assateague Island to 9.5 km south (AS) of Assateague State Park. The 3.2-km beach administered by the Maryland Department of Natural Resources was excluded in this survey; consequently, AN and AS were each 9.5 km in length. Only birds actually on the beach (between dune crest and waterline) were counted; birds flying by or loafing offshore were not included. Only human activities that occurred between the dune crest and ≤ 10 m offshore were counted. Birds and human activities were counted in 483-m segments (0.3 mile) during 1991-92 using the vehicle odometer. Because preliminary analyses suggested that human activities may have a narrower zone of influence on sanderlings, counts were delimited in 161-m segments (0.1 mile) during 1992-93. Data from winter 1992-93 were subsequently summed by 483-m segments for comparison with the previous winter.

In addition to diurnal counts of sanderlings during 1992-93, the presence or absence of sanderlings was recorded at every 161-m segment during both day and night. Behaviors were categorized as foraging, flushed, or other. A Star-Tron™ night-vision scope was used to observe sanderlings on most nights. Nocturnal surveys were conducted between 2200 h and 0200 h, approximately 12 h after diurnal surveys were completed. During some nocturnal surveys, a 750,000-candlepower spotlight was used to detect sanderlings because of poor lighting conditions due to a new moon or inclement weather.

Spearman correlation analysis was used to measure the association between cumulative numbers (*i.e.*, summed over surveys) of human activities and sanderlings within 161-m and 483-m segments. Two-way analysis of covariance (ANCOVA) was used to assess the effects of day of week and location on levels of human activity, after adjusting for wind speed and ambient temperature. Paired t-tests were used to test differences between the number of sanderlings that occurred on AS during weekend vs weekday surveys, and on AS during diurnal vs nocturnal surveys for a given date. The Cochran-Mantel-Haenszel χ^2 statistic (CMH) was used in multi-way contingency analyses to assess the association between occurrences of human activity and sanderlings; the Mantel-Haenszel estimator (CH) of the odds ratio was used to assess the likelihood of sanderlings occurring in the presence of human activity. SAS 6.04 (SAS Institute Inc. 1987) was used for all statistical analyses; $P \leq 0.05$ was used for all statistical inference.

Results

Diurnal surveys

In 1991-92, 24 beach surveys were completed during 19 weeks from 22 Nov to 3 Apr. Paired surveys were conducted until 4 Jan, when public facilities at AINS were damaged by hurricane-induced waves; only single surveys were conducted thereafter because public access was prohibited. In 1992-93, 40 beach surveys were completed during 21 weeks between 9 Oct and 20 Mar. Paired surveys were completed on all weekends except for two in March when spring tides precluded beach access. A total of 24 paired surveys over 40 weeks was completed during both winters. Seasonal variation in counts was estimated from surveys conducted only on weekdays (*n* = 19 in 1991-92, *n* = 21 in 1992-93).

Mean counts of sanderlings, dunlins, and black-bellied plovers on the study area were 597.9 (SE = 128.4), 50.9 (SE = 30.1), and 1.8 (SE = 1.3), respectively, in 1991-92 (*n* = 19)(Table 7). Mean counts of sanderling, dunlin, and black-bellied plover were 608.5 (SE = 126.3), 9.9 (SE = 4.4), and 3.0 (SE = 1.5), respectively, in 1992-93 (*n* = 21). Mean gull and tern counts (*Laridae*) were 386.3 (SE = 74.6) in the first winter and 321.0 (SE = 78.9) in the second winter. Herring (*Larus argentatus*), greater black-backed (*L. marinus)*, and ring-billed (*L. delawarensis*) gulls were common throughout both winters, occurring on ≥ 95% of surveys. Other *Laridae* species infrequently observed included laughing gull (*L. atricilla*), black-headed gull (*L. ridibundus*), Bonaparte's gull (*L. philadelphia*), royal tern (*Sterna maxima*), caspian tern (*S. caspia*), and Forster's tern (*S. forsteri*). Other shorebird species infrequently observed in late fall or early spring included American oystercatcher (*Haematopus palliatus*), ruddy turnstone (*Arenaria interpres*), piping plover (*Charadrius melodus*), and semipalmated plover (*C. semipalmatus*).

Sanderling counts showed dissimilar seasonal patterns during the two years (Figure 8). In 1991-92, counts showed a bimodal distribution with an autumn peak of 2,364 on 14 Dec and a vernal peak of 1,166 on 8 Mar. In 1992-93, counts showed an autumn peak of 2,137 on 16 Oct but failed to show any migrational pulses as late as 20 Mar. During both years, sanderling populations on the study area typically ranged from 50 - 500 during Jan - Mar. Mean proportions of total sanderlings that occurred on AS were 0.38 (SE = 0.08, n = 19) in 1991-92 and 0.29 (SE = 0.06, n = 21) in 1992-93; a t-test applied to the transformed data (angular; Sokal and Rohlf 1981:427) suggested that these means did not differ (t = 1.08, df = 38, P = 0.285).

Human activity levels were lower on AS during winter 1991-92 than was typical. Public access to Assateague Island was either restricted or partially restricted during two periods because of damage by hurricane-induced waves. The over-sand route was closed to ORVs from the start of the study through 27 Nov. Both AINS and Assateague State Park were closed to the general public from 4 Jan - 31 Mar. Disturbance on AS was created by pedestrians until 4 Jan, by ORVs during 28 Nov - 3 Jan, and by AINS personnel during the entire winter. Disturbance on AN was minimal during the entire winter, although aircraft overflights were relatively frequent due to the proximity of the Ocean City airport on the eastern shore of Sinapuxent Bay.

Several types of potential human disturbances occurred on the study area during weekly surveys (Table 8). Pedestrians represented 76.2% of total activities. Of pedestrian activities, 67.4% were classified as beachcombing or walking and 22.0% as fishing. Vehicles represented 18.7% of total activities. All but one vehicle recorded on AN were owned or contracted by AINS, or were used by authorized researchers. On AS, 78.3% of recorded vehicles in 1991-92 were operated by NPS staff or researchers; this datum reflects closure of AINS to public access after 4 Jan 1992. In contrast, only 7.8% of recorded vehicles in 1992-93, respectively, were operated by NPS staff or researchers. Helicopters and fixed-wing aircraft $\leq$ 150 m above ground level (AGL) were infrequently observed during weekly surveys, representing $< 1\%$ of total disturbances.

Human activity levels on AN were low relative to those on AS (Figure 9). During 1991-92 ($n = 24$), total numbers of vehicles, pedestrians, equestrians, and dogs averaged 0.4 (SE = 0.2) per survey on AN compared to 12.0 (SE = 3.7) per survey on AS. During 1992-93 ($n = 40$), total disturbances averaged 1.4 (SE = 0.3) per survey on AN and 34.5 (SE = 8.9) per survey on AS. Mean activity levels were about 3 times lower during the first winter due to closure of AINS after 4 Jan 1992. Activity levels also were about 3 times higher on weekends than weekdays when AINS was open to public access. Total numbers of vehicles, pedestrians, equestrians, and dogs averaged 15.7 (SE = 3.0, $n = 27$) on weekday surveys and 51.3 (SE = 14.3, $n = 24$) on weekend surveys. The highest human-use weekend occurred on 10 Oct 1992 when 220 pedestrians, 6 dogs, and 39 vehicles were recorded on the study area during a single survey.

Two-way ANCOVAs suggest that human activity levels observed during midday surveys of AINS were strongly affected by day of the week (weekday, weekend), location (AN, AS), and ambient temperature (Table 9). Day of the week (P = 0.012), location ($P < 0.001$), their interaction (P = 0.019), and temperature ($P < 0.001$), but not wind speed (P = 0.901), affected total numbers of vehicles, pedestrians, and dogs in 1992-93. In contrast, day of the week (P = 0.012), location ($P < 0.001$), and their interaction (P = 0.011), but not wind speed or temperature ($P > 0.400$), affected disturbance levels in 1991-92. Ambient temperature likely did not affect disturbance during the first winter because surveys were initiated later in the fall and public access was prohibited after midwinter. Declining disturbance levels on AINS during the winter can probably be attributed to declining seasonal temperatures.

A simple 2 X 2 contingency analysis suggests that the occurrence of sanderlings at 483-m segments (n = 2560) was not associated with the presence or absence of human activity (χ^2 = 0.19, df = 1, P = 0.666). However, after controlling for temporal variation due to year and month, sanderling occurrence within 483-m sections of beach was found to be associated with human activity (CMH = 6.52, df = 1, P = 0.011). The odds ratio suggests that beaches with no human activity were 14% more likely (CH = 1.14, 95% CI = 1.03 - 1.26) to have sanderlings occur there. Conversely, the presence of any human activity decreased the likelihood of sanderling occurrence by 14% (CH = 0.86, 95% CI = 0.76 - 0.97).

Increased human activity levels also were associated with decreased sanderling abundance. For comparison between winters, total disturbances and sanderlings were summed over all surveys for each 483-m segment (*i.e.*, cumulative) along the beach (Figures 10, 11). Spearman correlation analysis ($n = 40$) suggest that cumulative sanderling and disturbance counts before the 4 Jan storm in 1991-92 were negatively associated ($r_s = -0.333$, $P = 0.036$); with inclusion of data from the relatively undisturbed surveys after 4 Jan, this association breaks down ($r_s = -0.160$, $P = 0.324$). Similar analysis of 1992-93 data using 483-m segments suggest that cumulative sanderling and disturbance counts tend to be negatively associated ($r_s = -0.259$, $P = 0.107$). An analysis of 1992-93 data using 161-m segments ($n = 118$) suggest that the negative association between cumulative sanderling and disturbance counts is more certain ($r_s = -0.197$, $P = 0.033$) at higher resolution.

Paired t-tests ($n = 24$) were used to examine how sanderling populations may be responding to increased disturbance levels on weekends. Total sanderling populations on the study area did not change from weekdays to weekends ($t = 1.06$, $P = 0.298$) nor did the proportion of sanderlings that occurred on AS change from weekdays to weekends ($t = 1.29$, $P = 0.211$). However, a similar paired test of the mean difference between weekday and weekend counts suggest that sanderlings on AS responded to increased weekend activity. Sanderling counts on AS were an average of 58 birds (SE = 23.4; $t = 2.48$, $P = 0.021$) lower on weekends than weekdays; this represents a 21.6% decrease from the mean weekday estimate. Conversely, sanderling populations on AN did not consistently change from weekdays to weekends ($t = 0.08$, $P = 0.933$). Decreases in weekend sanderlings populations on AS tended to be positively associated with increases in human activities on weekends ($r_s = 0.363$, $P = 0.081$). These analyses suggest that some sanderlings were leaving AS on weekends in response to increased human activities, but apparently they did not routinely move to AN.

Nocturnal surveys

A total of 37 nocturnal surveys was conducted in 1992-93 between 16 Oct and 20 Mar. Of 120 sample stations per survey, sanderling occurrence averaged 13.4 (SE = 1.6) on AN and 11.5 (SE = 1.5) on AS at night. During the day, sanderling occurrence averaged 13.9 (SE = 1.4) on AN and 10.0 (SE = 2.0) on AS. Cumulative frequencies of sanderlings at 161-m segments during nocturnal (Figure 12) and diurnal (Figure 13) surveys were well distributed spatially by the end of the winter.

Human disturbance was much lower at night than day. A total of 889 pedestrians, dogs, and vehicles were counted during 37 diurnal surveys. In contrast, only 35 disturbances were counted during 37 nocturnal surveys; 66% of these were pedestrians (Table 10). Spatial distributions of human disturbance were similar at night and day, with most or all occurring on AS (Figures 12, 13). The sum of pedestrians, equestrians, dogs, and vehicles averaged 1.2 per survey (SE = 0.3) on AN during the day and no human disturbance was observed on AN during the night. In contrast, disturbances on AS averaged 22.9 (SE = 4.5) and 0.9 (SE = 0.3) per survey during the day and night, respectively.

After controlling for seasonal (month) variation, sanderling occurrence at 161-m beach segments was associated with the occurrence of human activity during the day (CMH = 8.76, df = 1, P = 0.003) and night (CMH = 6.06, df = 1, P = 0.014). During the day, the presence of any activity decreased the likelihood of sanderlings occurring there by 28% (CH = 0.72, 95% CI = 0.58 - 0.90), whereas the absence of activity increased the likelihood of sanderling occurrence by 10% (CH = 1.10, 95% CI = 1.03 - 1.18). Despite low levels of disturbance at night, the presence of any activity decreased the likelihood of sanderlings occurring there by 83% (CH = 0.17, 95% CI = 0.04 - 0.70); the absence of activity tended to increase the likelihood of sanderling occurrence (CH = 1.37, 95% CI = 1.07 - 1.76).

Sanderlings also tended to occur more frequently at sample stations that were exposed to lower levels of human activities, particularly during diurnal surveys (Figures 12, 13). Spearman correlation analyses suggest that the cumulative frequencies of sanderlings and human activities at 161-m segments were negatively associated during the day (r_s = -0.300, n = 120, P = 0.001) and not associated at night (r_s = -0.027, n = 120, P = 0.768).

To investigate nocturnal shifts in beach use by sanderlings, a paired t-test analysis was used to test the mean difference between the proportion of sanderlings that occurred on AS (rather than AN) during day and night surveys for a given date. On average (n = 37), sanderlings occurred on 9.3% (SE = 4.3, t = -2.15, P = 0.038) more sample stations on AS during nocturnal surveys than during diurnal surveys earlier that same day. This apparent spatial redistribution was more pronounced on weekend surveys ($\bar{x}$ = 10.7, SE = 5.5, n = 17, t = -1.95, P = 0.069) than weekday surveys ($\bar{x}$ = 8.1, SE = 5.6, n = 20, t = -1.23, P = 0.236).

Despite slight shifts in population distribution, there is no evidence that sanderlings behaved differently at night or day. Sanderlings were present at 1,807 of 8,880 samples (120 161-m segments X 74 nocturnal and diurnal surveys); of these, sanderlings flushed on 200 occasions (sanderlings rarely flushed when the night-vision scope was used but often flushed in response to being spot-lit). Of the remaining 1,607 observations during which sanderling behavior was scored, 94.1% showed at least some sanderlings foraging and 11.8% showed at least some sanderlings resting. A 2 X 2 contingency analysis suggests that foraging behavior (or lack of it) was not dependent on whether it was day or night (χ^2 = 0.75, df = 1, P = 0.386).

Discussion

Although seasonal population trends strongly affected the probability of encountering a sanderling on the beach at AINS, it is clear that human disturbance mediated that outcome. The presence of any diurnal human activity within 161-m and 483-m beach segments decreased the likelihood of sanderlings occurring there by 28% and 14%, respectively. Increasing cumulative levels of human activity within those segments was strongly associated with reduced sanderling abundance during the day. Pfister *et al.* (1992) similarly found that sanderling abundance steadily declined with increasing levels of vehicular traffic.

At night, the occurrence of any activity within 161-m beach segments decreased the likelihood of sanderlings occurring there by 83%. However, cumulative levels of human activity were not associated with cumulative sanderling abundance. These data suggest that although current levels of public use at night were not significantly depressing use of the beach by sanderlings, most nocturnal activities appear to disturb sanderlings. Presumably, the light cast by fires, lanterns, and headlights exacerbate the effect of nocturnal activities.

Severe asymmetry in the distribution of sanderling counts on AS and AN can likely be attributed, at least in part, to differences in levels of human disturbance. On average, only 33.4% (SE = 4.7, *n* = 40) of the sanderling population counted during weekday surveys occurred on AS; *i.e.*, twice as many sanderlings occurred on AN. Correspondingly, levels of public use were 25 - 30 times higher on AS than AN regardless of the day of week. High levels of vehicular traffic at Plymouth Beach, Massachusetts, were found to similarly depress sanderling abundance by 50% (Pfister *et al.* 1992). The unexpected closure of AINS during the first winter provided an unreplicated test of this relationship. Whereas cumulative sanderling and human activity counts were only negatively associated prior to the closure (and not after) during the first year, this association persisted throughout the second year.

In response to levels of public use that were three times higher on weekends than weekdays, some sanderlings left AS, but not to AN. These sanderlings were presumably resettling on less disturbed beaches south of AS, particularly on the beaches protected from vehicular access by the Chincoteague National Wildlife Refuge; incidental observations suggested that very high sanderling densities occurred there. The majority of sanderlings, however, remained on AS but apparently compensated for increased disturbance by redistributing themselves. The proportion of sanderlings that occurred on AS was higher at night, particularly on weekends, but did not differ between weekends and weekdays during the day. These data suggest that sanderlings on AS were flocking in larger groups during the day, presumably in areas where disturbance was less, and then dispersing over the mostly undisturbed beach at night to continue foraging. Burger and Gochfeld (1991) similarly argued that sanderlings wintering on Florida beaches foraged at night to avoid diurnal human disturbance.

Pedestrians/equestrians, vehicles, and dogs were weighted equally and each count was treated as a separate disturbance event in these analyses. I could not quantitatively assess which public use activities constituted disturbing stimuli (from the perspective of a sanderling), or those that were more or less disturbing, because my sample size was inadequate. I also could not assess the effect of group size on disturbance because "groups" of pedestrians are often amorphous and ephemeral, and difficult to objectively count during surveys. However, it was apparent that vehicles and pedestrians moving within the swash zone and/or below the berm were more disturbing to sanderlings than those activities which occurred above the berm. Sanderlings often flushed, if for no other reason than to avoid being physically trampled. Additionally, I suspect that small groups ($\leq$ 5) of pedestrians or two vehicles parked within close proximity of each other ($\leq$ 20m) were generally not substantially more disturbing to sanderlings than a single pedestrian or parked vehicle.

AINS was established in 1965 with the mandate that it would be administered "for general purposes of public outdoor recreation, including conservation of natural features contributing to public enjoyment" (PL 89-195). 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". It should be apparent from these survey data that current public use levels on AINS are effectively reducing the quality of beach habitat for sanderlings. The following recommendations are aimed at mitigating or minimizing the effects of human disturbance on sanderling populations (see Morton 1995 for additional discussion):

1) Modify the existing biweeky beach survey so that human activities, as well as avifauna, are counted in 161-m (0.1 mile) segments; separate analyses of the effects of different public uses could be done with adequate sample sizes.

2) Vehicular traffic should remain above the berm (but below the primary dunes) and vehicles should be parked ≥ 30 m (100 ft) from the swash zone regardless of where the berm is.

3) The relatively low levels of human disturbance at night currently offer sanderlings a respite from high diurnal levels of disturbance; however, some constraints on nocturnal use of the beach should be considered should future levels increase.

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Table 7. Summary statistics for weekly surveys of bird populations and human activities on the open beach at Assateague Island National Seashore.

Date	DAY[a]	SAN	DUN	BBP	LARUS	OSP[b]	PED	VEH	DOG	AIR	MAM[c]
112291	0	1264	59	25	1199	0	5	0	2	0	0
112391	1	1469	444	30	441	1	80	1	3	1	0
120691	0	619	1	3	386	0	7	6	0	0	0
120791	1	626	0	0	478	0	26	6	3	1	0
121391	0	2282	3	0	243	0	4	2	0	1	0
121491	1	2364	0	0	344	0	2	2	0	0	0
122091	0	1128	11	0	196	0	8	3	2	0	0
122191	1	1401	9	0	274	0	6	2	2	0	0
122791	0	80	0	0	65	0	11	5	1	0	0
122891	1	435	0	0	324	0	13	4	1	0	0
010392	0	351	0	0	36	0	12	3	2	0	0
011092	0	552	463	0	866	1	0	2	0	0	0
011892	0	176	0	0	288	0	0	4	0	1	0
012592	0	342	0	0	862	0	0	2	0	0	0
020192	0	100	0	0	123	0	0	2	0	0	0
020992	0	90	0	0	292	0	0	1	0	0	0
021692	0	316	43	0	371	0	0	1	0	0	0
022392	0	269	0	0	324	1	0	2	0	0	0
022992	0	133	0	0	58	0	0	3	0	0	0
030892	0	1166	374	0	656	4	0	4	0	1	0
031592	0	1000	0	0	333	8	0	2	0	0	0
032392	0	570	7	0	139	0	4	6	0	0	0
032992	0	648	4	0	734	1	0	2	0	0	0
040392	0	275	2	6	168	31	29	7	1	1	0
100992	0	699	12	26	443	13	28	7	2	0	0
101092	1	772	3	1	825	23	220	39	6	0	0
101692	0	2137	32	0	933	21	49	7	4	0	3
101792	1	1134	9	0	652	2	92	26	3	1	0
102392	0	845	45	9	473	1	27	2	3	0	0
102492	1	804	110	34	559	3	202	33	7	0	0
103092	0	1120	16	18	1549	0	19	10	0	0	0
103192	1	1247	2	3	700	4	8	4	0	0	0
110692	0	901	0	3	326	1	20	5	1	0	0
110792	1	790	2	0	377	0	48	16	2	1	0
111392	0	1529	19	0	162	0	13	7	0	0	0
111492	1	1474	1	1	241	0	68	16	2	0	2
112092	0	846	0	0	255	0	3	4	1	2	0
112192	1	776	1	5	346	1	25	8	3	0	1
112792	0	1303	1	5	58	0	32	16	5	0	0
112892	1	1155	4	0	260	0	60	17	7	0	0
120492	0	1009	0	0	200	0	5	3	0	0	0
120592	1	345	0	0	67	0	0	1	0	0	0
121892	0	673	80	1	798	0	1	1	0	0	0
121992	1	238	0	0	1176	0	23	5	2	0	0
010393	1	280	0	0	82	0	23	1	2	0	0
010493	0	182	0	0	112	0	5	3	0	0	0

011593	0	453	1	0	114	0	4	2	0	0	0
011693	1	254	0	0	65	30	19	4	1	0	0
012493	1	183	0	0	641	0	16	4	3	1	0
012593	0	256	0	0	191	0	4	1	0	0	0
012993	0	59	0	0	47	1	3	0	2	0	0
013093	1	68	0	0	116	0	10	1	0	0	0
020593	0	114	0	0	71	0	4	2	1	1	0
020693	1	50	0	0	27	0	2	0	0	0	0
021493	1	50	1	0	128	0	2	3	0	0	0
021593	0	80	0	0	165	0	21	2	0	0	0
021993	0	81	0	0	172	0	0	0	0	0	0
022093	1	125	0	0	61	1	5	0	0	0	0
030193	0	44	0	1	34	1	0	1	0	0	0
030793	1	184	0	0	287	7	33	0	2	0	0
030893	0	115	1	0	300	0	15	1	0	0	0
031293	0	242	0	0	210	11	2	1	0	0	1
031993	0	90	0	0	129	0	2	0	1	0	0
032093	1	132	0	0	169	0	6	1	0	0	0

DAY = day of week, SAN = sanderlings, DUN = dunlin, BBP = black-bellied plover, LARUS = *Laridae*, OSP = other avian species, PED = pedestrian, VEH = vehicle, DOG = dog, AIR = aircraft, MAM = mammals other than humans.

[a] Day of week: 0 = weekday, 1 = weekend.

[b] Other species include snow goose, red-throated loon, grackle, oystercatcher, piping plover, purple finch, great blue heron, peregrine falcon, killdeer, snowbunting, snowy owl, bufflehead, and cormorant, ruddy turnstone, semipalmated plover, unknown sparrow.

[c] Other mammals include ponies, river otter, red fox.

Table 8. Human activities that occurred between water and dune crest on 24 surveys during Nov 1991 - Apr 1992[a] and 40 surveys during Oct 1992 - Mar 1993.

	1991-92		1992-93	
DISTURBANCE	AN	AS	AN	AS
Pedestrians	6	201	43	1076
Beachcombers/walkers	3	164	40	687
Anglers	0	21	0	270
Backpackers	0	0	0	30
Swimmers	0	4	0	18
Sunbathers	0	0	2	17
Equestrians	0	0	0	21
Surfers	0	4	1	3
NPS personnel	0	6	0	21
Other	3	2	0	9
Dogs	0	17	1	59
Vehicles	3	69	11	243
NPS vehicles	3	54	10	19
Fixed-wing aircrafts	3	1	6	0
Helicopters	2	0	0	0
Other disturbances	0	0	7[b]	0

[a] AINS was closed to public access from 4 Jan - 1 Apr 1992 due to damage by hurricane-induced waves.

[b] Includes wild ponies (5), red fox (1), river otter (1).

Table 9. Mean squares from 2-way ANCOVA models of human activity levels during diurnal surveys of AINS.

		Mean Square[a]	
Source	df	1991-92	1992-93
LOCATION	1	2387.9**	22593.1**
WEEKDAY	1	936.1**	8276.1**
LOCATION X WEEKDAY	1	944.4**	7133.6*
TEMPERATURE	1	3.2	13.8**
WIND SPEED	1	97.1	0.0
ERROR	[b]	134.0	1236.1

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

[b] df = 40, 74, respectively.

Table 10. Diurnal[a] and nocturnal human activities that occurred between water and dune crest on 37 surveys during Oct 1992 - Mar 1993.

	Diurnal		Nocturnal	
ACTIVITY	AN	AS	AN	AS
Pedestrians	35	634	0	23
Dogs	1	44	0	0
Vehicles	7	168	0	12
Fixed-wing aircrafts	6	1	0	0
Helicopters	0	0	0	0
Other disturbances[a]	7	0	8	4

[a] Diurnal and nocturnal surveys were conducted during 1000 - 1400 and 2200 - 0200, respectively.

[b] Other diurnal disturbances included 5 wild ponies, 1 red fox, and 1 river otter; nocturnal disturbances included 7 raccoons and 5 red foxes.

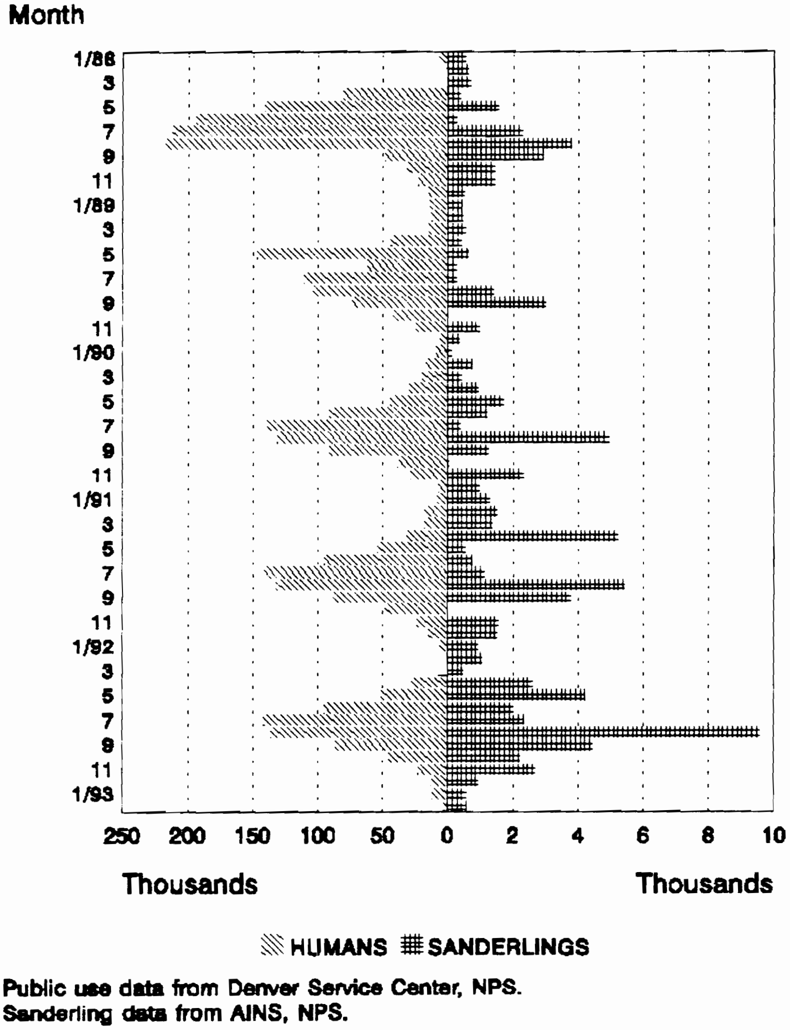


Figure 6. Temporal variation in human and sanderling use of the Maryland portion of Assateague Island National Seashore (1988-93).

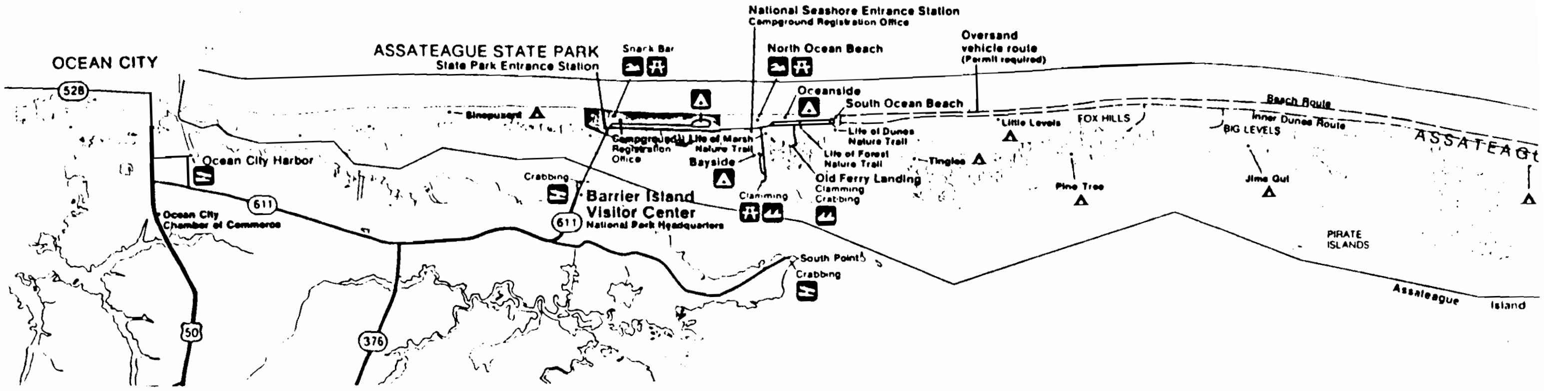


Figure 7. Study area on Assateague Island National Seashore, Maryland.

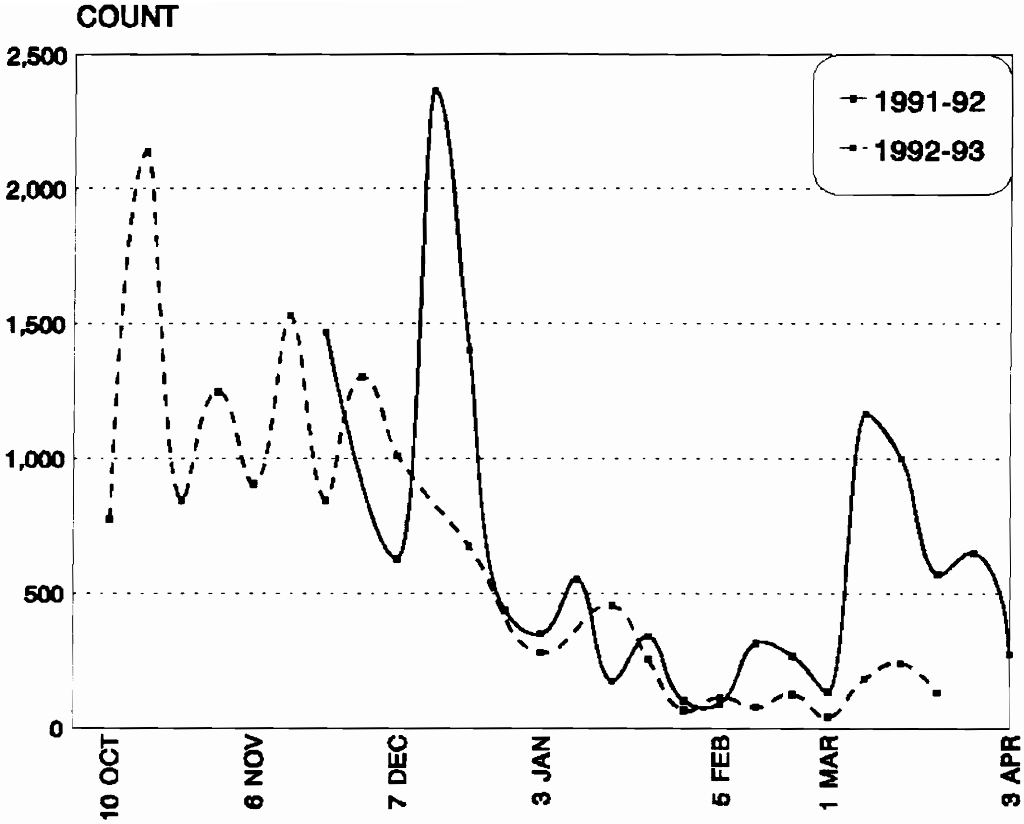
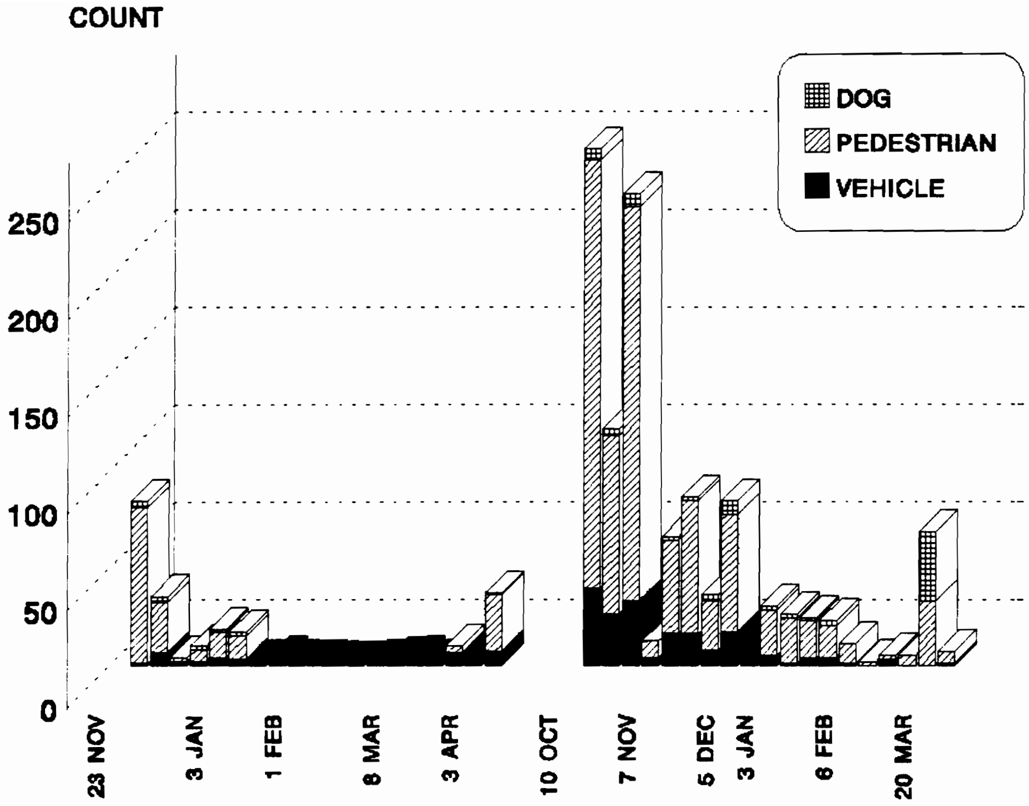
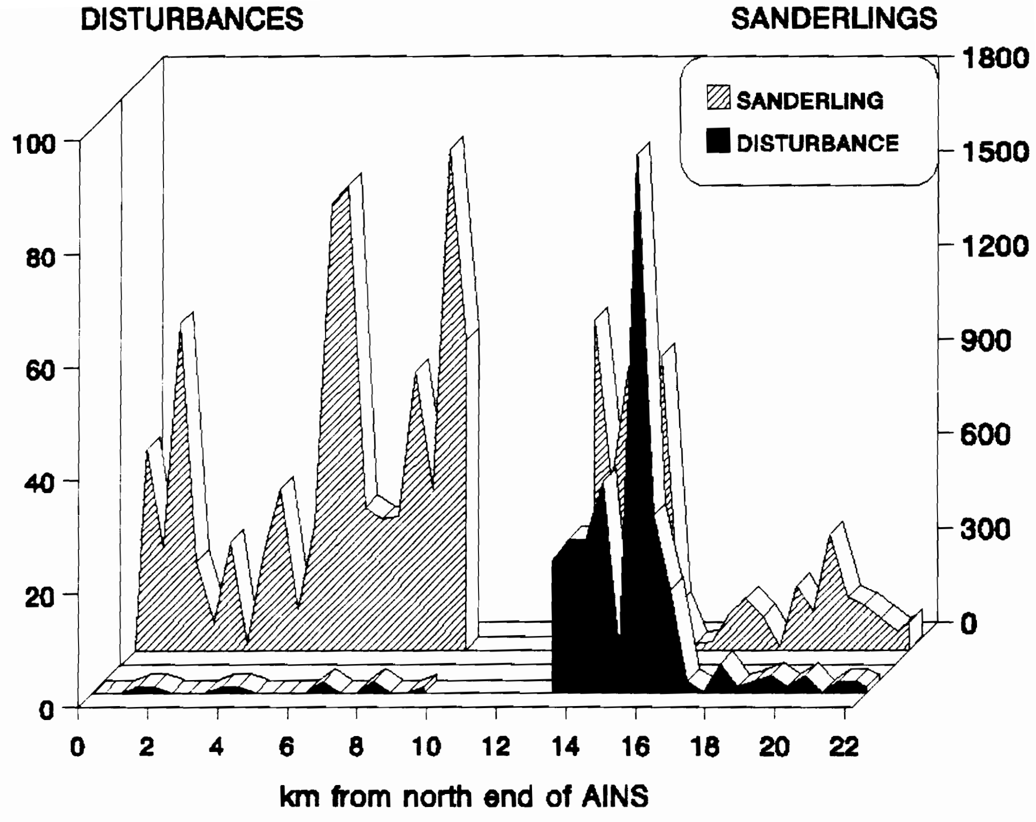


Figure 8. Weekly estimates of sanderling populations on the beach at Assateague Island National Seashore during 1991-92 and 1992-93.



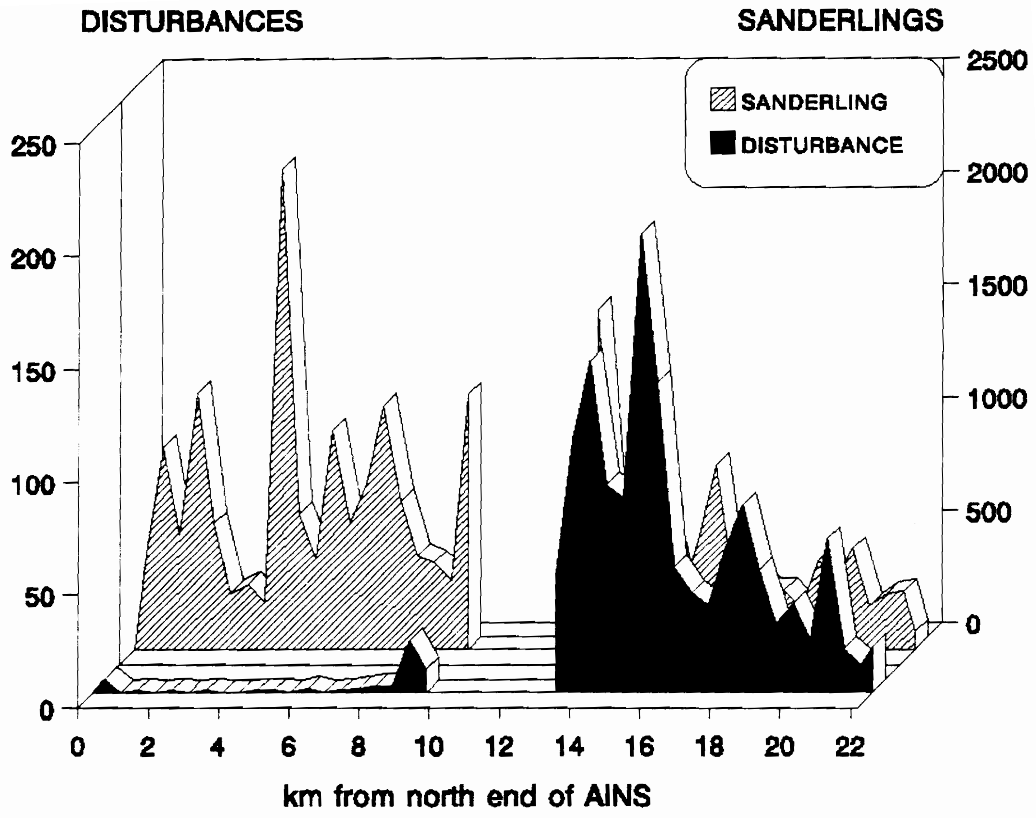
AINS closed to public access during 4 Jan - 1 Apr 1992.

Figure 9. Human activities on weekends during two winters at Assateague Island National Seashore.



Disturbances = pedestrians + equestrians + vehicles + dogs.

Figure 10. Cumulative numbers of human activities and sanderlings by 483-m segments on Assateague Island National Seashore in 1991-92.



Disturbances = pedestrians + equestrians + vehicles + dogs.

Figure 11. Cumulative numbers of human activities and sanderlings by 483-m segments on Assateague Island National Seashore in 1992-93.

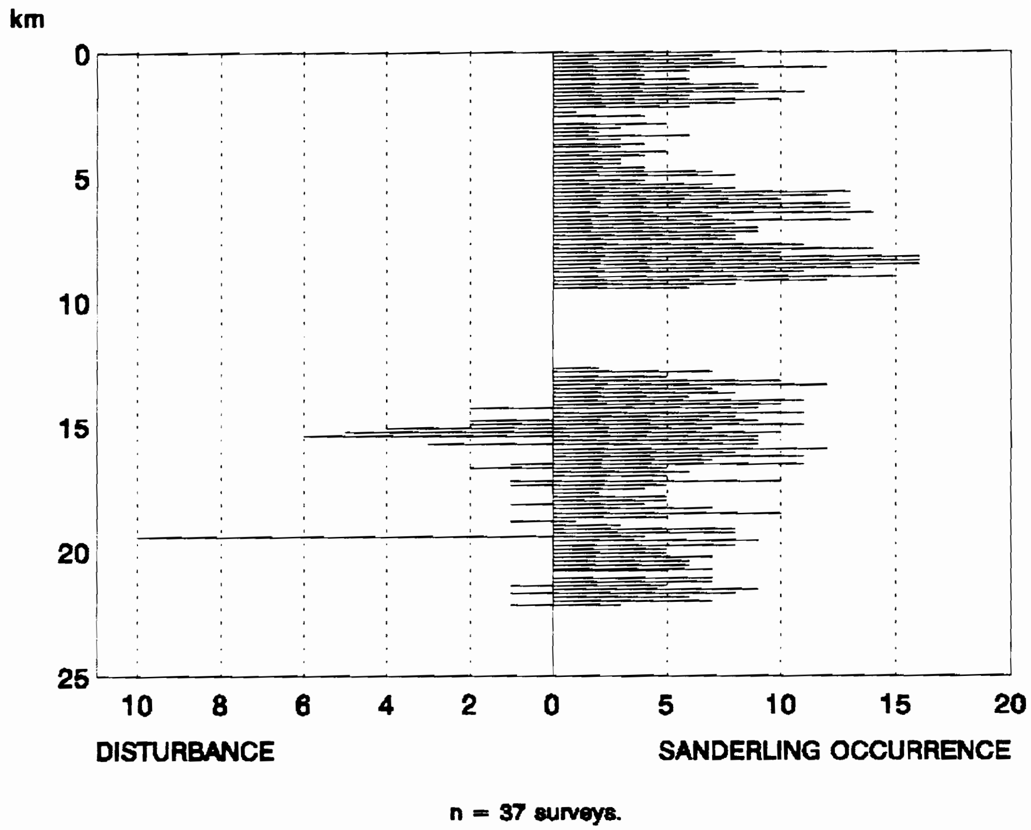


Figure 12. Cumulative nocturnal occurrences of human activities and sanderlings at 161-m increments from the north end of Assateague Island National Seashore in 1992-93.

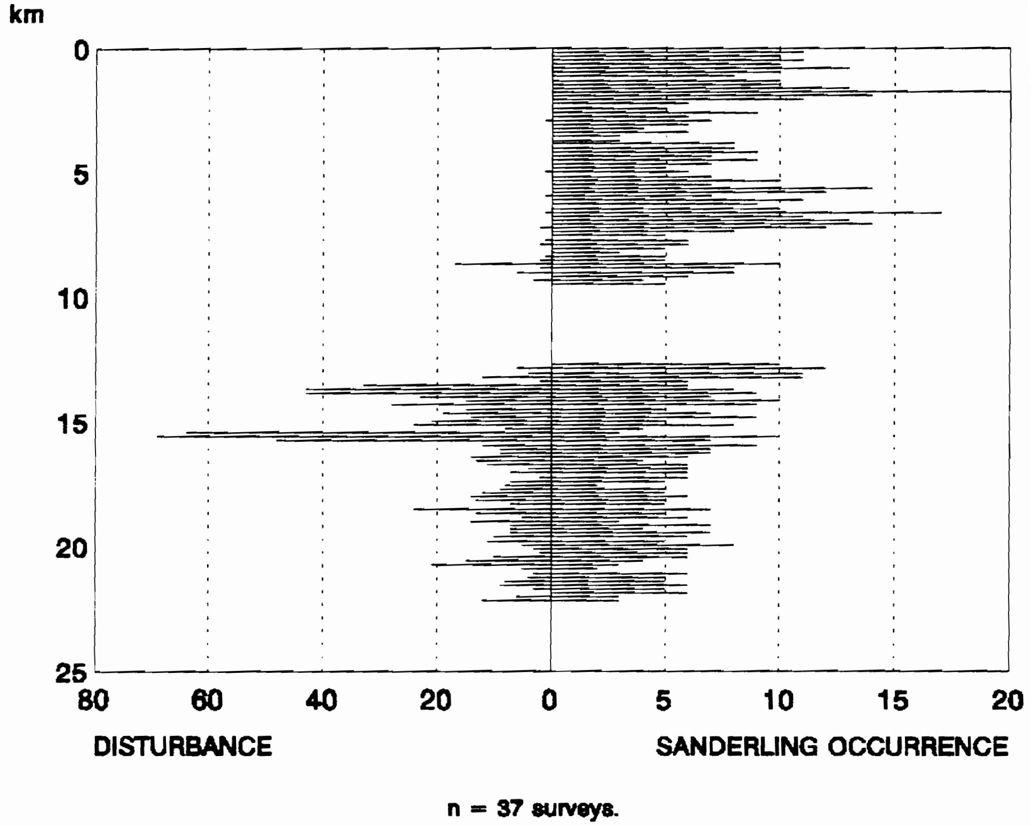


Figure 13. Cumulative diurnal occurrences of human activities and sanderlings at 161-m increments from the north end of Assateague Island National Seashore in 1992-93.

CHAPTER 4

Effects of Human Disturbance on Nonbreeding Sanderlings at Assateague Island National Seashore

Introduction

Data from the International Shorebird Survey indicate that North American populations of sanderlings (*Calidris alba*) have monotonically decreased 80% between 1972 - 1983 (Howe *et al.* 1989). Myers (1989) has 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 9-month 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 (Pfister *et al.* 1992) and wintering areas (Burger and Gochfeld 1991).

I 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, I specifically addressed 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?

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 7). 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 Jul or Aug, with numbers exceeding 100,000 during either month (Figure 14). Even in Jan, which is usually the month of least visitation, visitors averaged 9,563 (SE = 1,341.8) from 1988 - 1993. A recent public use survey suggested that 11.3% of trips to AINS originate during

Nov - Mar (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 11). 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 Apr - May and a larger autumn pulse in Jul - Aug (Figure 15). Biweekly beach surveys conducted by NPS personnel show that sanderling populations in Nov - Mar varied from 30 - 2700 during 1987 - 1992. Minimum counts during Jan, 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, I 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. I 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 Oct and Nov 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, I 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. I 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. I used analysis of covariance (ANCOVA) to determine the effect of human activities on sanderling density. I 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.

I 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 13). 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 Nov, Dec, and Jan during both winters, but were lower in Feb 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; $\chi^2 = 0.46$, 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 14). The distribution of slope types was similar on both beaches ($\chi^2 = 0.213$, 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 ($\chi^2 = 55.78$, df = 1, $P < 0.001$) and widths ≤ 100 m ($\chi^2 = 106.77$, df = 1, $P < 0.001$) occurred more frequently on AS than AN.

Distributions of slope type ($\chi^2 = 34.99$, df = 2, $P < 0.001$) and beach width ($\chi^2 = 22.20$, 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 ($\chi^2 = 0.61$, 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$\cdot$h^{-1} (95% CI = 0.54 - 0.69), although rates as high as 41 events$\cdot$h^{-1} were recorded on one weekend in Oct 1992. Vehicles and pedestrians accounted for most human activities, averaging 0.41$\cdot$h^{-1} (95% CI = 0.36 - 0.46) and 0.19$\cdot$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 15). Similarly, geometric mean activity rates during the winter were almost 6 times higher on AS than AN (t-test, P = 0.0001; Table 15). 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 ($P \leq 0.002$). Human activity averaged 0.20 events•h^{-1} on AN and 1.16 events•h^{-1} on AS (Table 15). 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 16) 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 Nov ($\bar{x} = 0.94$, 95% CI = 0.70 - 1.22) and lowest in Feb ($\bar{x} = 0.37$, 95% CI = 0.22 - 0.54), although rates did not differ among Jan, Feb, and Mar ($P \geq 0.185$). 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 Feb 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 (χ^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 15). Sanderlings occurred on 60% of plots on AN, but only on 52% of plots on AS (χ^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 14).

Use of AINS by sanderlings varied temporally over the winter. A 2-way ANOVA (Table 16) 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 Nov, decreased in Dec, and was least in Jan - Mar. 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 (Jan - Mar) 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 17). 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 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 15). 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 15).

Separate 2-way ANOVAs (Table 16) 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 Oct, decreased to 0.20 (95% CI = 0.09 - 0.31) in Feb, and increased to 1.14 (95% CI = 0.77 - 1.59) in Mar. *Emerita* population phenology was not identical during both years ($P = 0.0001$). *Emerita* populations in 1991-92 declined precipitously during the third week in Dec and began increasing during the first week in Mar; in contrast, populations in 1992-93 declined during the third week in Nov and showed no evidence of increasing by Apr.

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, I was concerned about the effect of observer activity on sanderling activity, particularly if some or all of the sanderlings flushed. To minimize possible observer effects, I 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 ($\chi^2 = 1.80$, 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 ($\chi^2 = 136.2$, df = 1, $P < 0.001$)

and on the plot at any time during the observation period ($\chi^2 = 79.5$, 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 16).

Contingency analyses suggest that sanderlings clearly flushed more frequently in response to a pedestrian than vehicle ($\chi^2 = 4.50$, df = 1, $P = 0.034$), particulary when the disturbance source was approaching at the water's edge ($\chi^2 = 23.00$, 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 17) 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 Oct, declined slightly in Nov and Dec, were minimal during Jan and Feb, and began to increase in late Mar and early Apr.

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 18) but were now negatively correlated with human activity rate (r^s = -0.16, *P* = 0.074; Figure 19). 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 12): 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 18). 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 18). 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 19). 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 20). 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 20).

However, this same analysis applied only to plots on which sanderlings occurred (*n* = 312) did not show human activity as a significant effect (Table 20). 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 21). 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.

I 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 21). 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 22). 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 23). 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 24). 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 23). 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 (Table 25) 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 26).

Monthly means of HEE suggested a distinct bimodal distribution of energy expenditure over the winter season (Figure 22). 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 22). In addition, mean HEE for sanderlings on disturbed plots coincided with HEE averaged for all plots after Nov, 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 Oct was substantially elevated because of high disturbance levels (Figure 22).

Energy expenditure differed for sanderlings that used different areas of AINS during the nonbreeding season. Mean HEE was 9.0 kJ•h^{-1} for sanderlings on AS and 6.0 kJ•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 27). On average, sanderlings spent 38% more time foraging (Table 27) on AS, an area which averaged 42% fewer invertebrates than AN (Table 15). Paradoxically, foraging time and invertebrate abundance were positively correlated for those plots on which sanderlings occurred (Table 23). This suggests that sanderlings were not increasing their foraging time on AS due to fewer invertebrates; rather, sanderlings were extending their feeding time despite 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

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, I 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, I 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, I 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. I 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, pedestrian traffic 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 18). My 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 16). 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.

I 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 I 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 21). 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 23, 24). Behavior scored as **pause** probably included more subtle forms of vigilance. Behavior scored as **feed** probably included more subtle forms of agitation; I frequently observed caged sanderlings peck at the cage floor when they were exposed to disturbing stimuli (Chapter 2).

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 22). 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 26) 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.

I 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 (Chapter 1). Balance trials with captive sanderlings suggest that EM does, in fact, increase in response to low-level chronic disturbance, albeit slightly (Chapter 2). 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). I 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 23), but disturbed sanderlings averaged 152% more time in flight than undisturbed sanderlings (Table 24).

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 15). At least during diurnal hours, sanderlings on AN rested more and fed less, expending 50% less energy than those on AS (Table 27).

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 (Chapter 3). 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 has resulted in an average energy expenditure that would not be significantly different had sanderlings existed in an undisturbed environment (Figure 22). 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 11. Public participation in selected recreational activities on the Maryland portion of AINS during 1985-86[a].

Activity	Secondary (%)	Primary (%)	$\bar{x}$ h 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
Picnick	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 12. 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	$\Sigma \cdot 200\ m^{-1}$	0 - 882
sanderlings	C	$\bar{x} \cdot 200\ m^{-1}$	0 - 602.5
Laridae (per scan)	C	$\Sigma \cdot 200\ m^{-1}$	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 13. 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 14. 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 15. 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 16. 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 17. 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 18. 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 19. 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_0: r = 0.

Table 20. 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.

		Mean Square[a]	
Source	df	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 21. 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 22. 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 23. 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 24. 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 25. Mean squares from 2-way ANOVA model of the effects of human disturbance and prey occurrences on hourly energy expenditure by sanderlings on 312 200-m plots.

Source	df	Mean square[a]
DISTURBANCE	1	884.23*
PREY	1	3677.51**
ERROR	309	74140.93

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

Table 26. 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 $n = 273$	DISTURBED[b] $n = 39$
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.

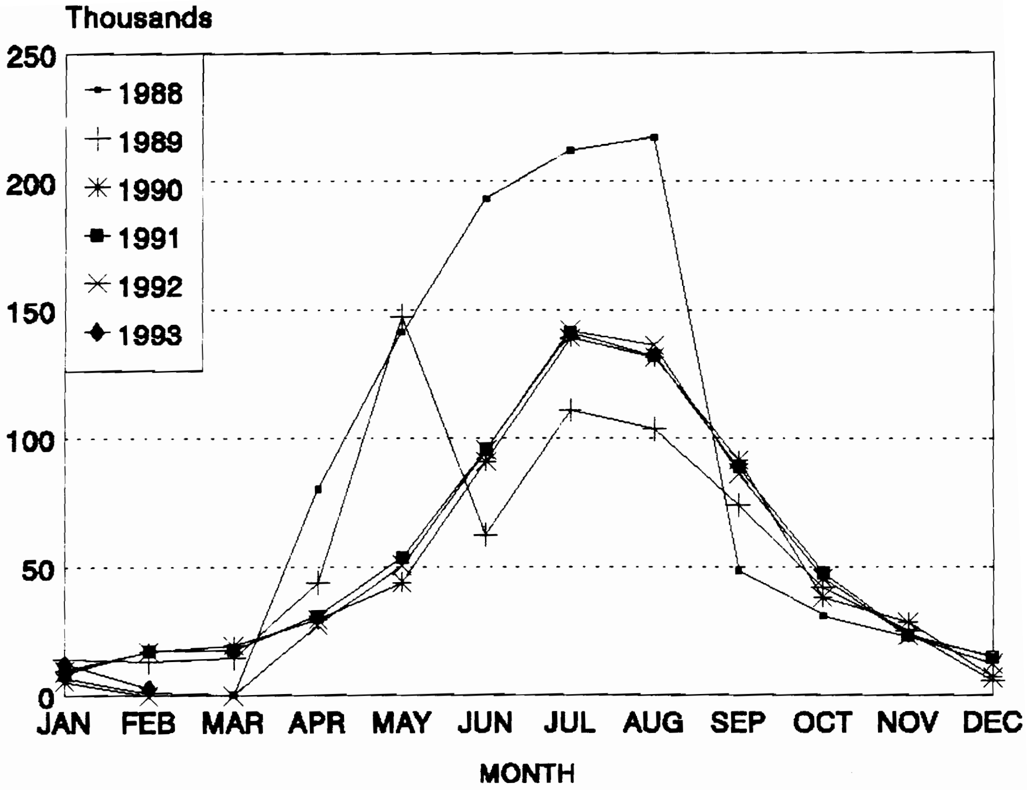
Table 27. Arithmetic means and standard errors (weighted by count) of percent time spent in different behaviors and energy expenditure ($kJ \cdot h^{-1}$) by sanderlings using AN and AS.

BEHAVIOR[a]	AN	AS	*P*[b]
	n = 168	*n* = 144	
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.

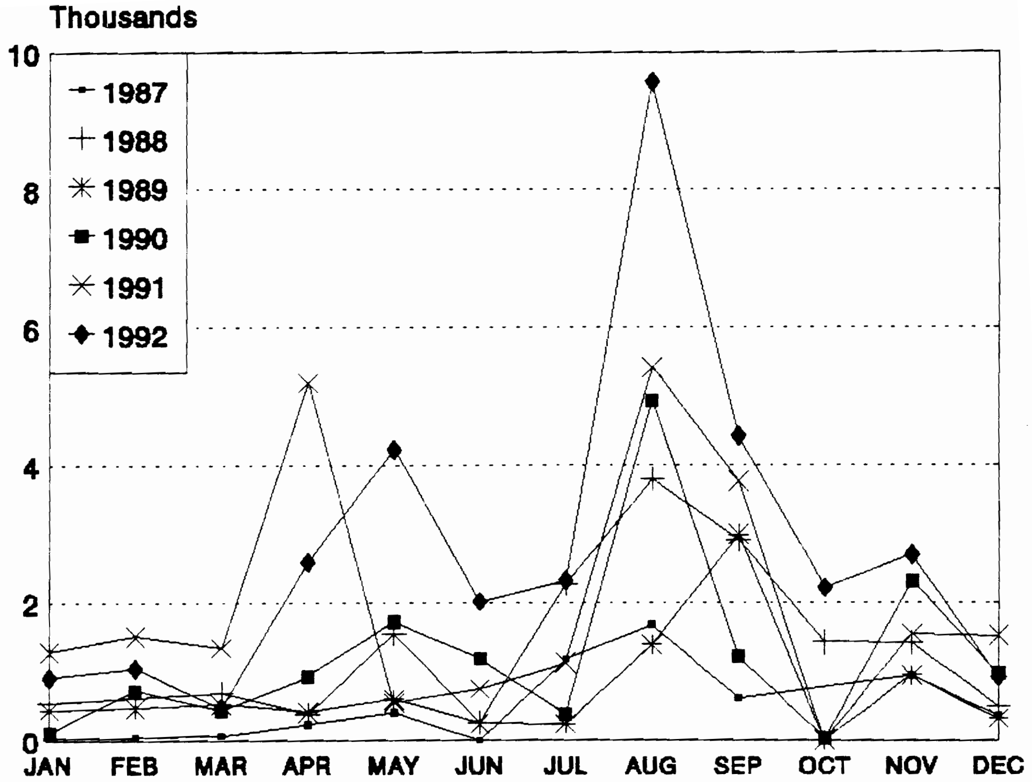
[b] Probability that F > F (ANOVA) based on least square means and standard errors. MANOVA test for no LOCATION effect on overall time budget: Wilks' $\lambda = 0.800$, df = 7,304, F = 10.87, $P = 0.0001$.

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



Statistics from Denver Service Center, NPS.

Figure 14. Number of visitors to the Maryland portion of Assateague Island National Seashore (1988-93).



NPS unpubl. data; maximum counts used when > 1 survey per month.

Figure 15. Seasonal trends in sanderling populations on Assateague Island National Seashore (1987-92).

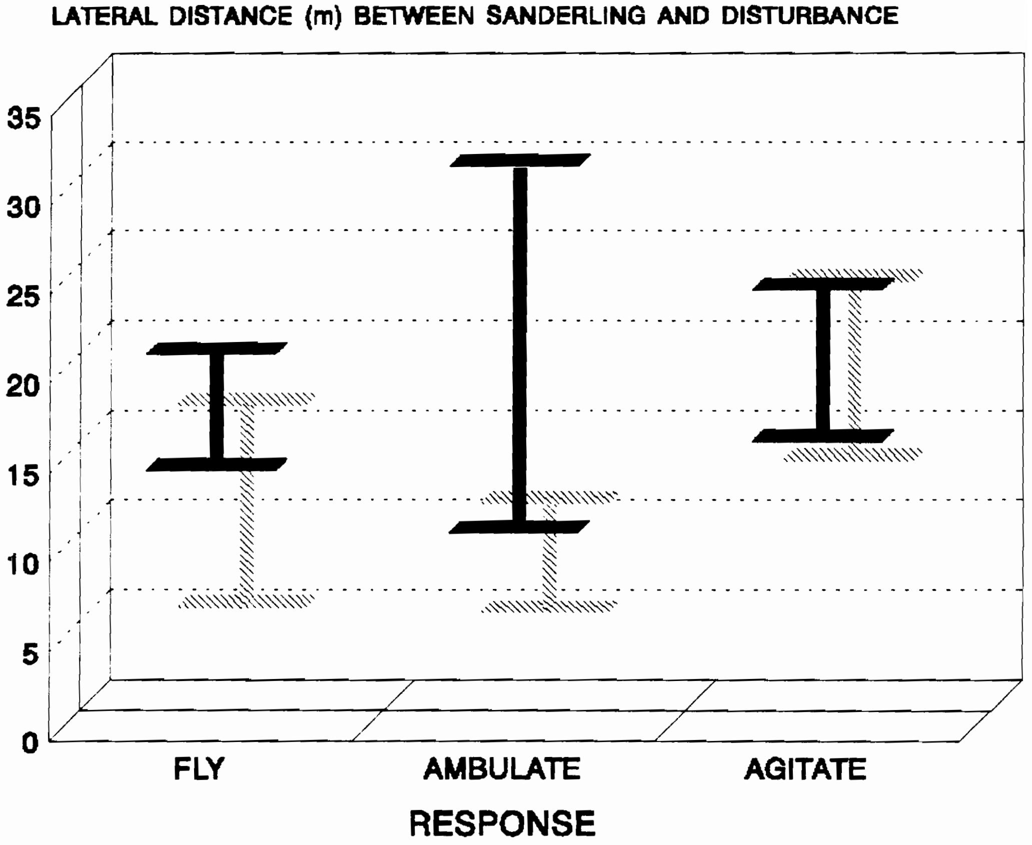
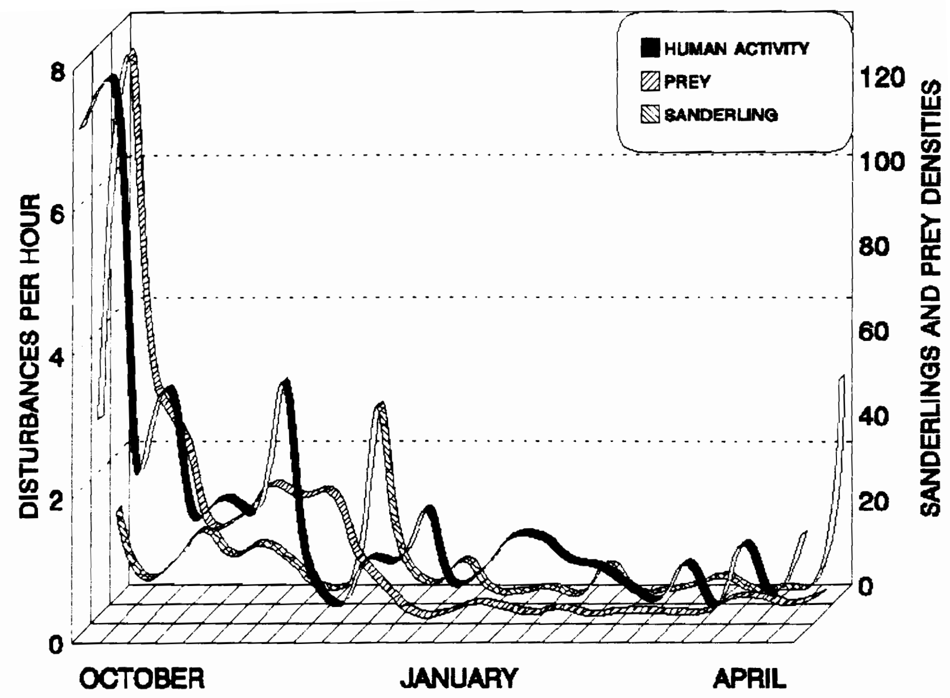
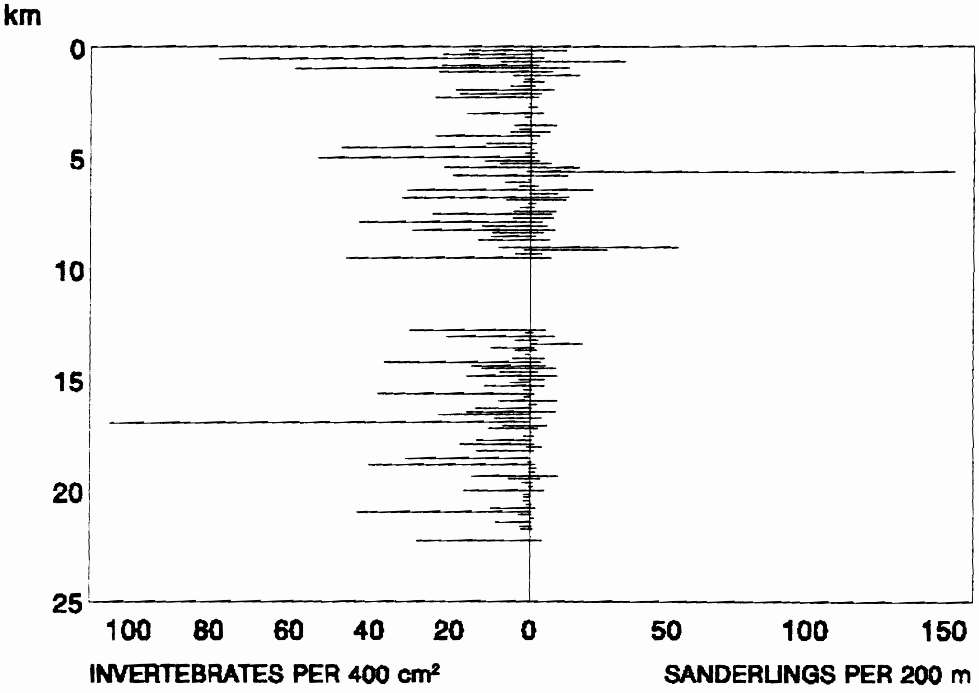


Figure 16. Mean distances (95% CI) at which sanderlings respond to an approaching vehicle (striped) or pedestrian (solid).



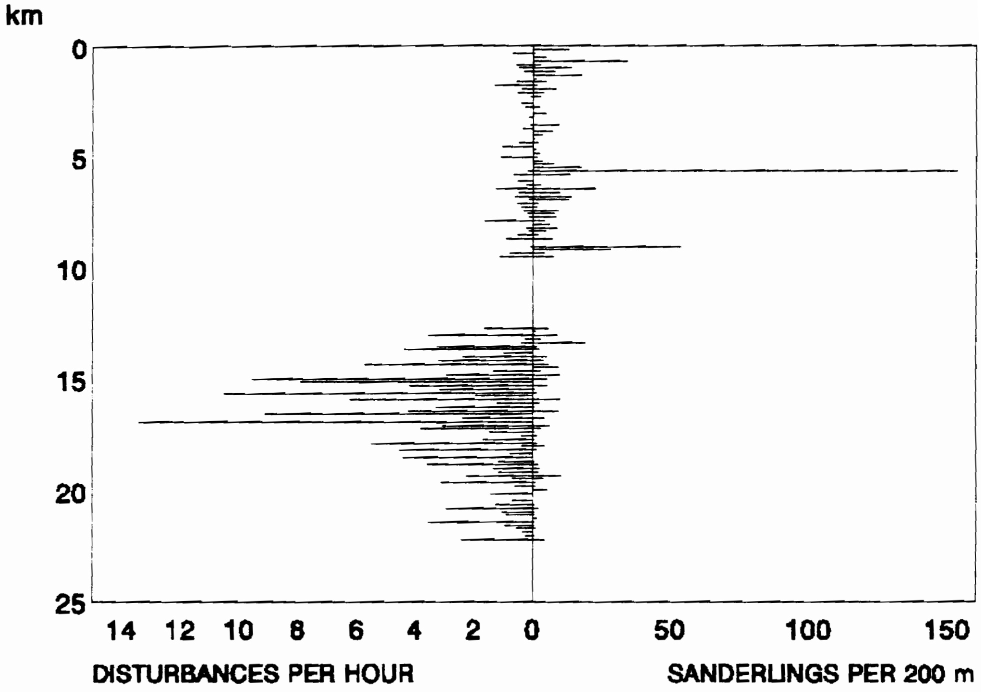
Sanderling count = mean of 6 scans per plot.
Prey estimate = *Donax* + *Emerita* + polychaete + amphipod.
Human activity = pedestrians + equestrians + vehicles + dogs.

Figure 17. Sanderling, invertebrate prey and human disturbance on 200-m beach plots averaged by week.



n = 552 plots averaged over 120 increments.
Sanderling count = mean of 6 scans per plot.
Invertebrates = *Donax* + *Emerita* + polychaetes + amphipods.

Figure 18. 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 19. Mean sanderling density and disturbance rate at 161-m increments from the north end of Assateague Island National Seashore.

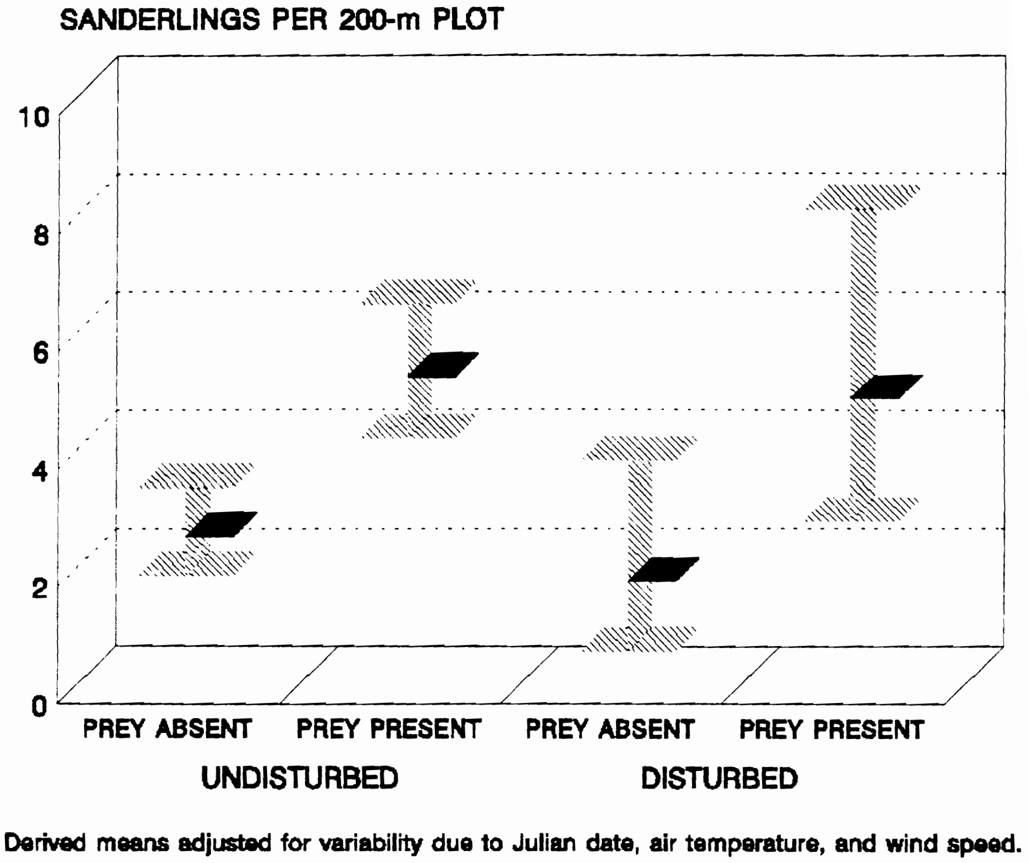


Figure 20. Least square means (± 1 SE) of sanderling abundance within 312 200-m plots on which human activity and invertebrate prey are present or absent.

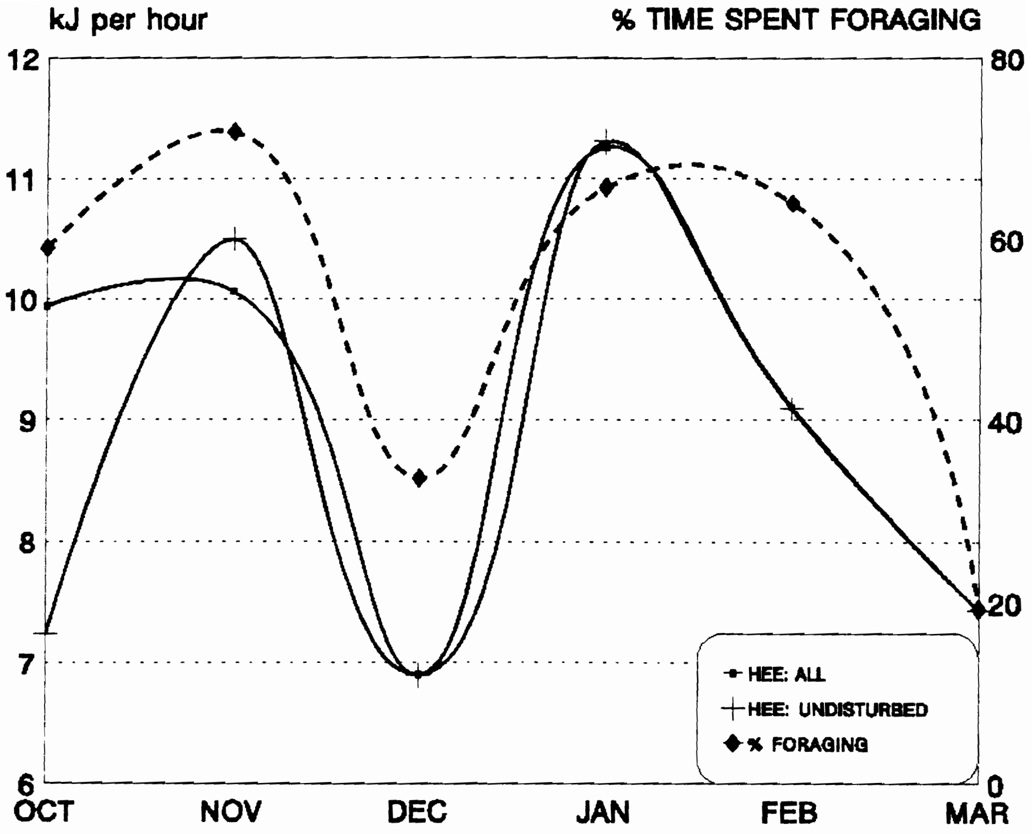


Figure 21. Monthly averages of percent time spent foraging and hourly energy expenditure by sanderlings on all plots (*n* = 312) and undisturbed plots only (*n* = 273).

APPENDIX A

Maintenance of Nonbreeding Dunlins and Sanderlings in Captivity

Introduction

Researchers have held wild-caught shorebirds (*Charadrii*) for short-term behavioral (Myers *et al.* 1980, Swennen *et al.* 1989) and nutritional (Castro *et al.* 1989, Klaassen *et al.* 1990) studies. Plovers (*Charadriidae*) and oystercatchers (*Haematopus*) have been held for extended periods (Kersten and Piersma 1987), and two species of plovers have been reared in captivity (Malone and Proctor 1966, Page *et al.* 1989). However, with the possible exception of Serventy *et al.* (1962), there is no literature on relatively long-term maintenance of sandpipers (*Scolopacidae*) in captivity.

As part of a larger study of the energetics of wintering sandpipers, both dunlins (*Calidris alpina*) and sanderlings (*Calidris alba*) were brought into captivity for experimental purposes. In 1990, several nonbreeding dunlins were captured and maintained for > 13 mos, but with some mortality and body mass loss. During this time, Lesley A. Colby and I developed holding facilities and investigated the palatability and metabolizability of several commercially available feeds. In 1993, using techniques developed for dunlins, several nonbreeding sanderlings were captured and maintained for < 2 mos with no mortality or body mass loss. This paper documents the methods we used to maintain wild-caught nonbreeding dunlins and sanderlings in captivity. This information is intended primarily for researchers and, to a lesser extent, for rehabilitators.

Methods and Results

Capture

Dunlins and sanderlings were mistnetted (Bleitz Wildlife Foundation, 38-mm mesh, 12.8m X 2.1 m) at Chincoteague National Wildlife Refuge, Virginia. These birds were captured under Scientific Collecting Permits PRT-748997 (U.S. Fish and Wildlife Service) and SCP9056 (Virginia Dept. Game and Inland Fisheries). Birds were aged by plumage (Prater *et al.* 1977), identified with aluminum leg bands, and transported for 8 hrs in cardboard poultry boxes to the vivarium at Virginia Polytechnic Institute and State University (VPISU). Initial capture weights were recorded with an Avinet™ 100-g spring scale to the nearest 0.5 g; subsequent weights were recorded with an electronic balance (± 0.01 g).

Twenty-seven dunlins were captured during Oct - Nov 1990 and transported to the vivarium within 3 d of capture. All birds were in residence at the vivarium by 20 Nov. Mean capture weights of 13 adult and 14 immature dunlins were 55.1 g (SE = 1.4) and 52.3 g (SE = 2.5), respectively. Between capture and transfer, dunlins were provided with drinking water and meal worms *ad libitum* while maintained in poultry boxes. However, birds appeared stressed and did not eat well. One adult and 2 immatures died within 3 d of transfer, and 1 adult was euthanized after 5 d because of a damaged leg.

Twenty-four sanderlings were captured during Jan 1993. Mean capture weights of adult and immature sanderlings were 55.1 g (*n* = 20, SE = 1.4) and 54.6 g (*n* = 4, SE = 3.8), respectively. Rather than immediate transfer to the vivarium, sanderlings were collectively held captive outdoors ≤ 13 d in a 2 X 0.5 X 0.75 m cage until enough birds were caught. The cage was a raised metal frame covered with 2-cm^2 vinyl-covered hardware cloth on the sides and plastic garden netting on the top. Two-thirds of the cage floor was covered with sand and the other third was a fiberglass tray with continuously-flowing water. Sanderlings were fed Zeigler™ (Gardners, PA) salmon starter No. 3 (2 mm) *ad libitum*, supplemented with meal worms and minced clams (*Mercenaria mercenaria*). Sanderlings were collectively transferred to the VPISU vivarium on 22 Jan. Mean body mass on the day before transfer ($\bar{x}$ = 55.0 g, SE = 0.8) was identical to mean capture weights ($\bar{x}$ = 55.0 g, SE = 1.3), despite an extended holding time.

Maintenance of dunlins

Dunlins were maintained in quarantine and relative isolation on a 10L:14D photoperiod (0730 - 1730) at 20° C; maximum and minimum temperatures were recorded daily. Two to 4 birds were kept in 61 X 61 X 41 cm stainless steel rabbit cages with solid sides; grated doors were covered with 2-cm^2 vinyl-covered hardware cloth to prevent escape. Grated cage floors were covered with Shepherd™ cageboard (a stiff, textured paper product) and changed daily. Bathing water in 33 X 23 X 5 cm teflon-coated aluminum pans was provided daily. Oyster shell fragments and drinking water with dissolved Nekton™ vitamin supplement were provided *ad libitum* in two clay crocks. Salmon grower (BioSponge™, Sheridan, WY), Purina™ pheasant starter, Purina™ flamingo complete, meal worms, wax worms, frozen brine shrimp, sliced chicken livers, and canned salmon roe were investigated as possible feeds. Based largely on apparent palatibility, and ease of storage and feeding, 2-mm granulated salmon grower was chosen as the *ad libitum* maintenance feed. This feed is 45% protein, 16% fat, and 3% crude fiber, and had estimated ME values of 15.4 $kJ \cdot g^{-1}$ (B. Kenny, per. comm.). Nekton MSA™ amino acid and calcium supplement was supplied with the salmon grower.

Dunlins experienced some "head scalping" during transport and early in captivity. After acclimation (perhaps conditioning), this ceased to be a problem. However, bleeding wrists continued to be problematic, particularly for a few individuals. Wings, particularly along the carpals, were damaged by hitting the sides of the cage during attempted flight. Two adults and 1 immature showed signs of "wing droop" within 4 weeks of capture and 1 immature showed signs after 16 weeks. Dunlins with wing droop often dragged the tips of their wings (primaries 9 and 10) behind them, rather than folding them over their retrices.

One adult with wing droop died on 30 Jan when blood was drawn for genetic analysis. Another adult (41.5 g) and 1 immature (25 g) eventually died on 15 Apr and 10 June, respectively, from apparent starvation, despite having maintained body mass during several weeks of captivity. Although causes of death are unknown, necropsy of the latter dunlin showed an enlarged liver. For comparative purposes, mean body masses reported hereafter represent the 9 adult and 11 immature dunlins that were successfully maintained in captivity for the duration of experiments.

Mean body masses of adults ($\bar{x}$ = 59.9 g, SE = 1.7, *n* = 9) and immatures ($\bar{x}$ = 61.9 g, SE = 2.0, *n* = 11) peaked at similar values on 31 Dec, > 2 mos after capture, but tended to decline thereafter (Figure 22). Causes of this phenomenon are unknown. Salmon grower was the sole nutrient source between 14 Feb - 8 Apr. On 8 Apr, diet was again supplemented with meal worms because of concerns about declining body mass. Results were equivocal; mean body mass continued to decrease until 5 May ($\bar{x}$ = 50.9 g, SE = 0.8, *n* = 20), but increased for several weeks thereafter (Figure 22).

Between 18 April and 14 May, the light period was gradually increased from 10 h to 14.5 h (0600 - 2030). Coincidentally, evidence of molting was first noted two days later on 20 April. This observation suggests that dunlins either would have undergone at least a partial molt despite a fixed photoperiod, or were primed to respond rapidly to a change in photoperiod. By 14 May, at least nine birds showed distinct markings of the black belly patch exhibited during breeding.

On 17 May, dunlins were transferred to facilities at Patuxent Wildlife Research Center in Laurel, MD. Birds were maintained in quarantine on a 15L:9D photoperiod (0600 - 2100), but ambient temperatures were poorly controlled. Birds continued to be provided daily with crushed oyster shells, Nekton™ vitamin supplement, bathing water, and salmon grower *ad libitum*, supplemented with 1 - 4 meal worms per bird. As before, floor papers were changed daily; however, smooth-sided butcher paper was used initially.

Dunlins were considered to generally be in good condition by the resident veterinarian (G. Olsen), although one bird was treated with Baytril™ (0.03 mls per injection at 22.7 $mg \cdot ml^{-1}$, twice daily for 5 d) for an inflamed carpus. Feather molt continued in all birds although none ever fully developed the black belly patch. Birds continued to increase body mass through 16 June ($\bar{x}$ = 60.7 g, SE = 1.9), but showed a precipitous mass loss thereafter (Figure 22). Coincidentally, toe nails were clipped for the first time on 2 July. Floor paper also was changed about this time to one with a rougher texture because some birds were developing a "bumblefoot-like" syndrome where tissue around the toes was inflamed and appeared splayed, but was not infected. Although these actions appeared to alleviate foot problems, body mass continued to decline. Mean body mass was 50.7 g (SE = 0.9) on 1 Aug, the day before they were transferred back to the VPISU vivarium for additional experimentation. All 20 dunlins were euthanized by thoracic compression in Dec 1991, >13 mos after capture.

Maintenance of sanderlings

Sanderlings were maintained at the VPISU vivarium in the same facilities used for dunlins except that only one bird was assigned per cage. Birds were provided with Zeigler™ salmon starter No. 3, oyster shell fragments, drinking water, and bathing water *ad libitum*. We chose not to provide vitamin or amino acid supplement because birds were expected to be maintained in captivity for a relatively short time.

Total body electrical conductivity (TOBEC) was measured in live sanderlings with an EM-SCAN SA-1 Small Animal Body Composition Analyzer™ whenever they were weighed. Because the electrical conductivity of lipids is only 4 - 5% that of nonlipid tissues (Pethig 1979; cited in Walsberg 1988), measures of TOBEC effectively index wet lean mass. An index of lean body mass (I_{LM}) was calculated as

$$I_{LM} = S - E/R$$

where S = average of 4 chamber measurements with sample, E = average of 4 empty chamber measurements, and R = average of 2 calibration measurements (Walsberg 1988, Morton *et al.* 1991). At the conclusion of subsequent experiments, sanderlings were euthanized, body composition was determined by proximate analysis, and the relationship between TOBEC and lean mass was investigated. See Chapter 2 and Appendix 2 for further details on methodology.

Mean sanderling body mass did not significantly change after transfer to the VPISU vivarium ($r = 0.44$, $P = 0.381$, $n = 6$) and was never less than that recorded at time of capture (Figure 4). Mean body mass on 2 Mar, the day they were euthanized, was 56.4 g (SE = 1.9, $n = 24$). During this same period, mean I_{LM} values decreased after sanderlings were transferred to the vivarium (Figure 4; $r = -0.995$, $P < 0.001$, $n = 6$), from 47.7 units (SE = 1.0) to 39.5 units (SE = 0.9). Simple linear regression analysis suggests that dry lean mass decreased 0.187 g for every 1-unit decrease in I_{LM} ($R^2 = 0.72$, $P < 0.001$) or ≈ 1.5 g over 40 d. These data suggest that sanderlings experienced muscular atrophy (presumably flight muscles) in this caged environment, although there was no obvious decrease in body mass.

Feed and feed intake

The metabolizability of 6 commercial feeds by dunlins and sanderlings was investigated. Nutritional content of feeds varied from 12.1 - 50.0% crude protein, 2.7 - 16% fat, and 1.0 - 6.8% fiber (Table 28). Nutritional content of the four Purina™ feeds was determined from grab samples whereas that of the two salmon feeds were values reported by their manufacturers. Dunlins were fed all Purina™ feeds and the Biosponge™ salmon grower whereas sanderlings were fed only Ziegler™ salmon starter.

Metabolizable energy was determined in a series of 3-d and 4-d food balance trials. During trials, the grated floor was replaced with plexiglas or linoleum and known amounts of feed were provided daily. Uningested feed and egested feces were collected daily, freeze-dried ≥ 12 h, and weighed to obtain dry mass. Grab samples of dried feed and feces were combusted in a Parr™ adiabatic bomb calorimeter to determine energy content. Metabolizable energy was the difference between energy contents of consumed feed and egested feces, expressed as $kJ \cdot g^{-1}$ dry feed and percent (kJ metabolized $\cdot$ kJ ingested$^{-1} \cdot 100$).

The relative efficiency with which dunlins metabolized feeds varied from 54.4 - 69.8% and tended to increase with protein rather than fat content (Table 28). Dunlins obtained the most energy per g dry feed ingested from salmon grower, which had higher protein, fat, and energy content and lower fiber content than the other feeds tested. Salmon feeds were metabolized by dunlins and sanderlings equally well (Table 1), despite different manufacturers and some variability in reported nutritional content.

Although ambient room temperatures were relatively constant at the VPISU vivarium, small changes in maximum and minimum temperatures affected intake of salmon grower by dunlins. During a 42-d monitoring period, mean maximum temperature was 21.8° C (SE = 0.2) and ranged 20 - 25°; mean minimum temperature was 19.1° C (SE = 0.2) and ranged 16 - 22°. A multiple regression model (PROC REG; SAS Institute 1985) suggests that minimum and maximum temperatures accounted for 23% of the variation in wet feed intake (df = 2,39, *P* = 0.006). Minimum and maximum temperatures were positively and negatively correlated with daily food intake, respectively, despite being within the thermoneutral zone. The depression of feed intake during high diurnal temperatures is well known, but the elevated intake due to low temperatures the previous night is less so (but see Kendeigh *et al.* 1969).

Discussion

Despite the problems described here, most dunlins and sanderlings appeared to acclimate well to both commercial salmon feed and the caged environment. Of 23 dunlins that survived the initial (<5 d) capture and transfer stress, only 3 birds died over a period of 13 mos. Dunlins generally retained good plumage condition, maintained body mass (albeit with high variability), and showed signs of normal alternate breeding molt. No sanderlings died during transfer or the 2 mos they were held captive, and they remained in excellent condition. The bleeding wrist, splayed toes, and wing droop syndromes that we observed in a few dunlin were not observed in sanderlings.

Because sanderlings flock during the nonbreeding season, maintaining them singly in cages may have reduced the propensity to flush and thereby reduced incidences of bleeding wrists and damaged carpals. However, I think it more likely that interspecific differences in escape behavior explained the lack of sanderling wing damage. In the wild, dunlins probe for invertebrates on exposed tidal flats and tend to flush in response to disturbance. In contrast, sanderlings actively probe for invertebrates in the sand between waves and often run from disturbance. Although both sandpiper species tolerated captivity surprisingly well, sanderlings may be behaviorally more suited for research in a caged environment.

The splayed toes that were observed in some dunlins would likely have occurred in sanderlings had they been held in captivity longer. However, I believe that the smooth-sided butcher paper that was used for a short time exacerbated the problem, and the fact that toenails had to be clipped for the first time while using this paper was not coincidental. Wax paper, newspapers, or plastic-coated materials would likely have had a similar detrimental effect. For relatively short periods (2 - 6 mos), the cageboard that was used most of the time would be adequate flooring in a caged environment. A surface with more texture should be found for longer periods.

Wing droop was an unexpected phenomenon. Sanderlings should have exhibited it had it been simply due to flight muscle atrophy. I believe that it was due to permanent muscle damage (*i.e.*, capture myopathy) that may have occurred during capture. Bollinger *et al.* (1989) showed that the concentration of creatine kinase, an indicator of muscle damage, was higher in wild mallards (*Anas platyrynchos*) that were caught by methods which restrained birds for longer periods. Mistnetting works as a capture technique by effectively restraining birds (see Keyes and Grue 1982 for a review of mistnetting), sometimes for extended periods if several individuals are simultaneously captured. Most of the dunlins were captured in groups, whereas most of the sanderlings were caught singly. Had sanderlings been caught otherwise, I suspect that incidences of wing droop might have been observed.

The cause(s) of the bimodal distribution of dunlin body mass between Nov 1990 and Aug 1991 was not apparent (Figure 23). Body mass peaked on 31 Dec and 16 June. Although decreasing body mass may be attributed to nutritional deficiencies or captivity-induced muscle atrophy, neither adequately explains the early summer increase in body mass. It seems more likely that varying body mass of dunlins simply reflects an endogenous seasonal cycle. The midwinter peak in lipid reserves of several shorebird species in the wild is recognized (Pienkowski *et al.* 1984:45) and at least two species of captive waterfowl lost weight and reduced food intake after midwinter despite being fed *ad libitum* (Hepp 1986, Perry *et al.* 1986). The timing of the early summer peak coincides with the compressed breeding cycle of high arctic-nesting shorebirds such as dunlin and sanderling. Researchers conducting nutritional or energetic studies on captive shorebirds over extended periods may need to adjust their experimental designs to account for these endogenously-regulated variations in body mass.

High-protein salmon feed, supplemented with vitamins and oyster shells, appears to be an adequate maintenance diet for nonbreeding dunlins and sanderlings. Metabolizable energy content of salmon feed and the relative efficiency (*i.e.*, assimilation efficiency) with which it was metabolized compares favorably with natural foods. Sanderlings at 25°C metabolized 18.8 $kJ \cdot g^{-1}$ of meal worms (*Tenebrio* sp.) and 8.3 $kJ \cdot g^{-1}$ of horseshoe crab (*Limulus polyphemus*) eggs; metabolic efficiency was 76% and 38.6%, respectively (Castro *et al.* 1989).

I do not consider the holding facilities developed here appropriate for either long-term studies or for raising shorebirds in captivity. These cages are recommended for maintaining sandpipers over relatively short periods, generally < 2 mos. Researchers or rehabilitators who intend to return their subjects to the wild should be aware that birds, at least sanderlings, may begin losing lean mass almost immediately in a caged environment. Longer periods could be accomodated if birds were held between experiments in larger cages (to permit short flight) with better bathing facilities, such as the interim holding facility that was described for sanderlings.

Chincoteague National Wildlife Refuge provided housing and permission to capture shorebirds. G. Maxey, L. S. Morton, and W. Wilmoth helped mistnet birds. D. E. Gemmell and the staff at the VPISU vivarium provided cheerful and expert care of all birds. K. Wright graciously provided samples of Purina™ feeds for testing purposes. A. Robinson determined energy content of feed and fecal samples for sanderlings. Use of tradenames does not imply product endorsement.

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Table 28. Mean nutritional and energetic content of 6 commercial feeds[a] consumed by wild-caught dunlins and sanderlings.

	DUNLIN					SANDERLING
	Purina™ Pheasant Maintenance	Purina™ Pheasant Starter	Purina™ Waterfowl Starter	Purina™ Amphibian	Biosponge™ Salmon Grower	Zeigler™ Salmon Starter
Protein (%)	12.1	30.3	19.7	48.3	45.0	50.0
Fat (%)	2.7	2.7	3.5	12.1	16.0	15.4
Fiber (%)	6.8	6.0	6.7	3.6	3.0	1.0
Gross energy (kJ•g^{-1})	18.0	18.6	16.7	21.4	22.3	22.6
Metabolizable energy (kJ•g^{-1})	9.8	12.5	10.3	14.4	15.5	15.7
Metabolizable energy (%)	54.4	67.3	61.7	67.2	69.8	69.5

[a] Purina Mills, Inc., Mazuri™, St. Louis, MO; Zeigler™ Bros., Inc., Gardners, PA; BioSponge™, Sheridan, WY.

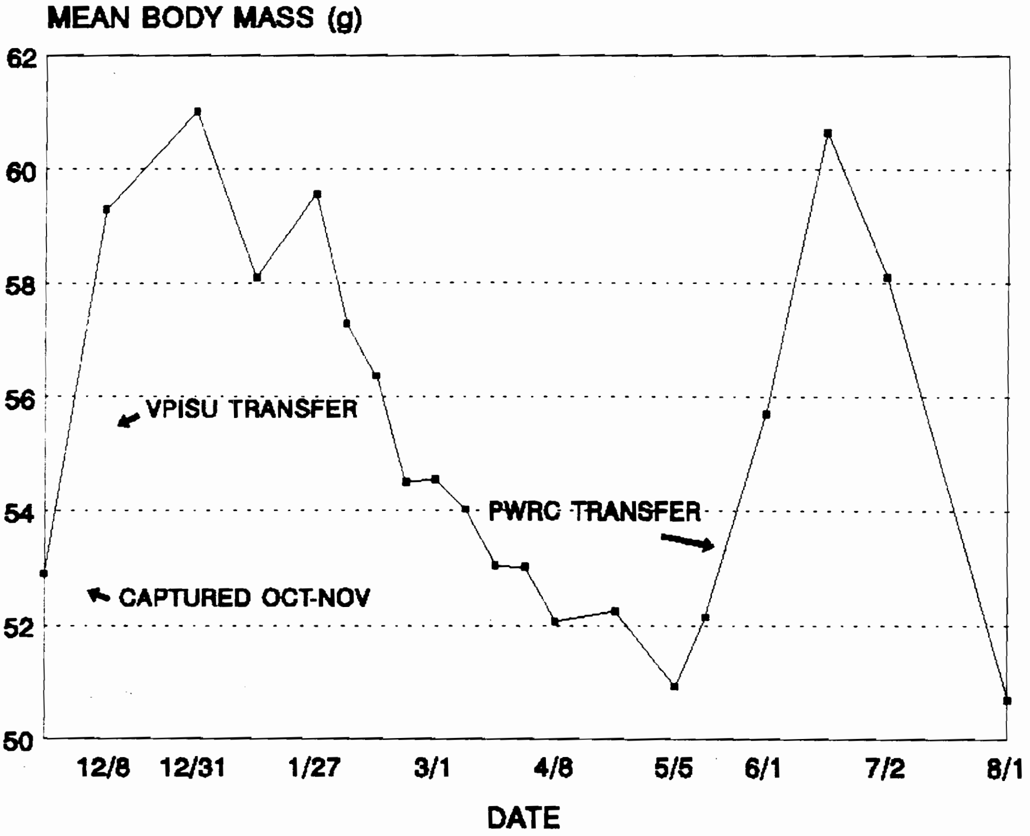

Figure 22. Mean body mass of 20 dunlins maintained in captivity.

APPENDIX B

Estimating Total Body Lipids From Measures of Lean Mass

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Introduction

Physiological conditions of wild birds generally is considered to be a function of total body lipids relative to body size. Lipid has twice the caloric density of protein (Ricklefs 1974) and only 0.2 - 0.3 g lipid/g nonlipid tissue are needed to maintain functional homeostasis in birds (Odum *et al.* 1964). Lipid levels can be measured accurately by ether extraction of the homogenized carcass, but this requires sacrificing the bird. Alternatively, body mass alone or body mass expressed in some allometric relationship with external structural measurements (to account for individual differences in body size) can be used as an index of lipid levels in live birds (see Johnson *et al.* 1985 and references therein).

Total body electrical conductivity (TOBEC) recently has been used to index lean body mass of several wild avian species (Walsberg 1988, Castro *et al.* 1990).

Because the electrical conductivity of lipids is only 4 - 5% that of nonlipid tissues (Pethig 1979; cited in Walsberg 1988), currently used commercial devices primarily measure lean mass. Regression analyses have shown that 95 - 99% of the variation in TOBEC values are attributed to changes in lean body mass (Walsberg 1988, Castro *et al.* 1990); predicted lean body mass can then be subtracted from total body mass to estimate lipid mass. Because the technique is simple, noninvasive (as opposed to lipid extraction methodologies), and appears to be more accurate than conventional indices for measuring physiological condition of live birds, it significantly expands the possibilities of conducting nutritional studies under field situations.

While studying the applications of TOBEC, we found that R^2 values for lean mass regression may misrepresent the precision with which lipid mass can be estimated. Lipid and lean mass sum to body mass by definition. It has been implicitly assumed in the literature that prediction of one component should permit prediction (with the same confidence) of the other. In this paper, however, we use body composition data from dead American woodcocks (*Philohela minor*) to show that although the absolute value of the error associated with predicting lean mass is identical to that associated with calculating lipid mass (*i.e.*, from predicted lean mass), the relative error is much greater for the latter. Furthermore, body mass and TOBEC values regressed on lipid mass directly predict lipid mass better than subtracting predicted lean mass from body mass. The fact that TOBEC is lower in dead birds than live birds is irrelevant because the problem we identify in this note is fundamentally statistical and not methodological.

Methods

Fourteen woodcocks were collected in December 1988 and January 1989 on the Eastern Shore National Wildlife Refuge, Virginia. Specimens were double-bagged in plastic and frozen. After completely thawing, woodcocks were sexed and aged by plumage characteristics (Larson and Tabor 1980) and weighed to the nearest gram.

TOBEC was measured with an EM-SCAN™ SA-1 Small Animal Body Composition Analyzer using the procedures outlined in Walsberg (1988). Each woodcock was placed on its dorsum with spine straight, aligned along the long axis of the chamber. An index of lean body mass (I_{LM}) was calculated as

$$I_{LM} = (S - E) / R; \tag{1}$$

where S = average of four chamber measurements with sample, E = average of four empty chamber measurements, and R = average of two calibration measurements (Walsberg 1988, Castro *et al.* 1990).

The carcass was plucked, and bill, tarsi, and contents of esophagus, proventriculus, and viscera were discarded. The carcass was then sectioned, freeze-dried for ≥48 hr, ground in a commercial Waring blender, and freeze-dried again for 24 hr to obtain dry carcass mass. Lipids in one 7 - 10 g sample from each carcass homogenate were extracted for ≥ 12 h using ethyl ether in a Soxhlet apparatus after oven-drying samples at 55°C for 12 h. Lean mass (LM) was the difference between whole body and lipid masses.

Lean and lipid masses were regressed on log-transformed I_{LM} (Castro *et al.* 1990) using simple linear regression techniques (PROC REG, SAS Institute 1985). Relative error was expressed as $|\hat{y} - y|$ divided by y. Body mass (BM) and log I_{LM} were subsequently regressed on lipid mass using multiple regression techniques (PROC REG, SAS Institute 1985). Lipid mass predicted from the multiple regression model was denoted by LI_{hat}, whereas lipid mass estimated from the difference between BM and LM_{hat} was denoted by LI_{hat}*. Significance was defined as $P \leq 0.05$ for all statistical inference.

Results and Discussion

Our sample of woodcocks included 10 juvenile males and 4 juvenile females; *n* = 14 for all subsequent analyses. Mean body mass was 163 g (SE = 8.5) and ranged 106 - 215 g. Mean lipid mass was 13.2g (SE = 1.6), ranged 1.0 - 21.6g, and represented 7.8% (SE = 0.9) of whole body mass.

Lean mass regressed on I_{LM} yielded the following equation:

$$\log I_{LM} = 4.6572 + 0.0087\ LM_{hat}. \tag{2}$$

The R^2 value for this regression model was 0.725 ($P = 0.0001$). In contrast, the regression between lipid mass and log I_{LM} yielded an R^2 of 0.317 ($P = 0.036$). Lean mass was subsequently predicted from the inverted regression equation shown above (Eq. 2):

$$LM_{hat} = -532.85 + 114.42(\log I_{LM}). \tag{3}$$

As expected, Eq. 3 predicted lean mass well; the mean difference in lean mass between predicted and laboratory values was 11.8 g (SE = 3.1), which is within 8.9% (SE = 2.9) of laboratory values. Similarly, estimates of lipid mass derived from predicted values of lean mass (Ll_{hat}* = BM - LM_{hat}) differed 11.8 g (SE = 3.1) from laboratory values; however, this translates to estimates that are only within 362% (SE = 236) of laboratory values.

It is apparent from these data that the absolute error (11.8 g) associated with LM_{hat} is identical to the error associated with $LI_{hat}*$. However, because lipids always represent a smaller proportion of avian body mass than nonlipid tissue (Griminger 1976), the proportional error will be correspondingly larger for estimates of the lipid fraction than the nonlipid fraction. This disparity is reflected empirically in the very different coefficients of determination for regressions of lipid and lean mass on log I_{LM}.

The difference can be further explored theoretically by examining the sources of error for parameters estimation and by considering an alternative multiple regression model for predicting lipid mass. The model implied by subtracting LM_{hat} from BM is a two-stage model. The first stage of the model is derived from Eq. 3:

$$LM = \gamma_0 + \gamma_1(\log I_{LM}). \qquad (4)$$

The regression parameters are estimated from the simple linear regression between LM and log I_{LM} (Eq. 2), and from the inverted regression (Eq. 3). The second stage of the model is given as the following:

$$LI* = BM - LM \qquad (5)$$

Combining the two stages result in the following model:

$$LI^* = BM - \gamma_0 + \gamma_1(\log I_{LM}). \tag{6}$$

This model has a fixed slope for BM of 1.0 and the parameters γ_0 and γ_1 are estimated from the association between LM and log I_{LM}; this is not an efficient way to estimate lipid mass.

In contrast, body mass and log I_{LM} can be used to predict lipid mass (LI_{hat}) in the following general multiple regression model:

$$LI = \beta_0 + \beta_1(BM) + \beta_2(\log I_{LM}). \tag{7}$$

The power of BM and log I_{LM} to predict lipid mass is indicated by the reduction of the sum of squares for lipid mass. The sum of squares error,

$$SSE = \Sigma(LI - LI_{hat}^*)^2, \tag{8}$$

relative to the sum of squares for lipid mass gives the proportion of variation unexplained by the model used to predict lipid mass. For the two-stage model, however, SSE is equal to the sum of squares error for lean mass because

$$SSE^* = \Sigma(LI - LI_{hat}^*)^2 = \Sigma(LM - LM_{hat})^2, \tag{9}$$

and because $LI = BM - LM$ and $LI_{hat}^* = BM - LM_{hat}$. The problem with the two-stage model is that if lean mass has a high SSE then it is possible that the SSE for lipid mass is actually larger than the total sum of squares for the model! This situation could occur when lean mass is poorly estimated or when lean mass has a much larger variance than lipid mass (even though LM may be well estimated).

As the estimated coefficient of determination using SSE is not appropriate in this application (i.e., it could be negative), another approach would be to compare the squared correlation between LI and LI_{hat}^* with the coefficient of determination for the multiple regression model (Kleinbaum *et al.* 1988:330). The two-stage model yielded $r = 0.416$ ($P = 0.139$) or $R^2 = 0.173$. In contrast, the multiple regression model yielded an R_2 of 0.692 ($P = 0.002$); partial correlation coefficients for BM and log I_{LM} were 0.549 ($P = 0.004$) and 0.115 ($P = 0.257$), respectively. The higher coefficient of determination represents a 300% increase in association between lipid mass and the explanatory variables.

Multiple regression models also are more flexible than the two-stage approach because they allow the addition of covariates. For example, with the addition of sex into the above model (Eq. 7), the R^2 increased to 0.828 ($P = 0.0004$) and sex explained 44% of the variation in lipid mass ($P = 0.018$).

The multiple regression model cofirms several points made both empirically and theoretically in the previous discussion. Because the variation in lipid mass is primarily reflected in body mass and not lean mass, body mass should be incorporated into the regression model rather than being used externally to the model to calculate lipid mass from predicted lean mass. Secondly, although body mass and log I^{LM} are highly correlated with each other ($r = 0.83$, $P = 0.0002$), these variables do not contain completely redundant information (see Hamilton 1987); in this case, the inclusion of log I^{LM} explained 11% more of the variance in lipid mass alone. Thirdly, TOBEC values do not explicitly measure lean mass and need not be used to calculate lean mass directly; rather, TOBEC values can be used to correct for individual differences in body size using multiple regression techniques in much the same way as more conventional lipid indices have been calculated in the past (*e.g.*, Whyte and Bolen 1984, Ringelman and Szymczak 1985).

Our intent is not to disparage the use of TOBEC or other measures of lean body mass (*e.g.*, Connell *et al.* 1960, Child and Marshall 1970, Pasco and Rutishauser 1985). To the contrary, we believe that TOBEC does estimate body lipids in live birds better than most conventional condition indices, albeit only slightly. However, the current practice of reporting R^2 values for regression models of lean mass on TOBEC grossly overestimates the precision with which body lipids are being estimated. We suggest that investigators using measures of lean mass, such as TOBEC, should apply cross-validation techniques (Kleinbaum *et al.* 1988:330) or confidence intervals (Castro *et al.* 1990) to investigate the appropriateness of equations for predicting lipid mass. Furthermore, we suggest using TOBEC within multiple regression models to prdict lipid mass, rather than using TOBEC to predict lean mass.

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APPENDIX C

Management of Human Disturbance and its Effects on Waterfowl

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Introduction

Human disturbance of waterfowl and other wildlife is an increasingly recognized environmental problem, particularly among wildlife professionals. Managers of 16 National Wildlife Refuges (NWRs) in northeastern U.S. perceived lowered productivity, aberrant behavior, reduced use of preferred habitat, reduced use of refuge lands, and mortality to be consequences of human disturbance; furthermore, the reduction or elimination of 65% of situations involving waterfowl-human interaction was considered at least moderately important to management objectives (Purdy *et al.* 1987). Yet, in a recent review of 211 publications that included discussions of waterfowl-human interactions (Dahlgren and Korschgen 1992), only

8% were of studies conducted in the U.S. and had titles that explicity referred to human disturbance. This absence of scientific literature has created a situation in which the effects of human disturbance may be acknowledged but poorly managed or, alternatively, may be dismissed as inconsequential by land managers.

Managing human disturbance is not technically difficult. It requires on the part of the land manager an appreciation of disturbance as a complex phenomenon, a basic understanding of how disturbance affects waterfowl, and a willingness to prohibit or regulate some human activities that may negatively impact waterfowl populations. The following sections define human disturbance, describe how it is studied, and discuss some of the deleterious effects of disturbance on waterfowl. Several management strategies are then discussed and the program at Chincoteague NWR is used to illustrate a comprehensive approach to managing human disturbance.

What is human disturbance?

Human disturbance of waterfowl and other wildlife may be defined as any intentional or unintentional anthropogenic action that elicits a metabolic or behavioral response. Disturbance generally does not include actions that involve a tactile stimulus, but rather the visual, olfactive, or aural threat of one. For example, an off-road vehicle that destroys a mallard nest is not a disturbance (it is a source of mortality), but vehicular noise that flushes a nesting hen is considered a disturbance.

Numerous sources of human disturbance have been identified in the literature. The relative importance of different disturbances to waterfowl, at least from the perspective of researchers, can be inferred from the number of times a disturbance is identified in published literature (Dahlgren and Korschgen 1992). Based on this index, pedestrians, aircrafts, boats, anglers, hunters, recreational activities in general, and researchers themselves are important disturbance sources (Table 29; also see Boyle and Samson 1983, Gladwin *et al.* 1988, York 1994).

However, managers should take a cautious approach to categorizing some human activities as disturbances. What may be disturbing to humans may not necessarily be so to some wildlife, and the reverse may be true as well. For example, Watson (1988) presumed dogs were a source of disturbance to nesting dotterels, yet dogs may be used as attractants in Dutch *endecoy* traps for waterfowl. Similarly, aircraft are required to fly above minimum altitudes during fall staging of lesser snow geese in the Arctic NWR, yet staging black brant showed increased response to helicopters with increasing altitude (Ward *et al.* 1988).

Avian perception of an event as *disturbing* is partly a function of inherent characteristics of the stimulus itself. These characteristics include the type, duration, magnitude, and frequency of a stimulus. Disturbance types have been categorized in several ways. Belanger and Bedard (1989, 1990) and Morton *et al.* (1989*a*) distinguished natural from human-induced disturbances. Some investigators have separated human disturbances by their actual source (traffic, pedestrian, aircraft, hunting activity; Fraser *et al.* 1985, Belanger and Bedard 1989) while others have distinguished levels of human activity (Stalmaster and Newman 1978, Anderson and Keith 1980, Watson 1988); this latter classification is more a measure of the *magnitude* of disturbance. Within this framework, disturbance sources can be further discriminated. For example, aircraft noise (*i.e.*, decibels, percent attentuation) has been quantified as functions of aircraft type, lateral distance, and altitude (Ward *et al.* 1988, Derksen *et al.* 1989). Certainly classification of disturbance can be carried to any resolution depending on management or research objectives.

Other factors such as landscape, experience, temporal variability, predisturbance behavior, and weather also may mediate avian perception of an event as *disturbing*. These factors are discussed below.

How is human disturbance studied?

Seven approaches to studying the effects of human disturbance on waterfowl and other wildlife have been identified in the literature:

1) Flush response (flight time, flush distance, flush threshold) can be intentionally or incidentally induced in the field (Owens 1977, Ward *et al.* 1988, Klein 1993).

2) Behavioral and energetic changes in the field can be measured with time budgets (Morton *et al.* 1989*a*, Belanger and Bedard 1990).

3) Population redistribution or displacement can be demonstrated in the field with observational (Korschgen *et al.* 1985, Keller 1991) or telemetry (Austin and Humburg 1992) methods.

4) Physiological responses can be assessed with heart-rate telemetry in both field (MacArthur *et al.* 1982) and laboratory (Wooley and Owen 1977, Ball and Amlaner 1980).

5) Simulation models (Frederick *et al.* 1987), Habitat Suitability Index models (Chapman and Howard 1984), and statistical models (Montopoli and Anderson 1991) can be used to assess the effects of disturbance (and management thereof) on waterfowl and other wildlife populations.

6) Inferences can be drawn from other laboratory and experimental approaches not specifically targeted to examine human disturbance as used in this context, including animal damage control (Thompson *et al.*

1968) or hazing (Boag and Lewin 1980, Craven and Ellis 1982), commercial poultry (Murphy and Duncan 1978), animal behavior (Bronson 1968, Mueller and Parker 1980), and handling stress (Meier *et al.* 1973).

7) The effects of research activity on breeding birds (particularly colonial nesters) and subsequent nest depredation is a controversial issue in the ornithological literature (Duffy 1979, MacInnes 1980, Strang 1980).

Much of the published literature has focused on documenting that disturbance occurs rather than examining the mechanistic causes of disturbance. Many of these studies pose a problem in that investigators may erroneously conclude that human disturbance *per se* has no effect on the examined parameters (*e.g.*, Watson 1988, Frederick and Collopy 1989), whereas there are alternative explanations. For example, the "disturbance" source applied in a study may not be *perceived* as a stressor by the study animal. Even if the disturbance is appropriate, it may not be applied at a level sufficient to promote a behavioral response. An investigator can conclude that a specific type or level of human activity is not a disturbance but, by definition, cannot conclude that human disturbance has no effect.

Similarly, inverse associations between densities of nest or roost sites and human development may simply demonstrate preferences rather than species tolerance limits. 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.

It is not overly important that land managers understand how human disturbance is studied. However, they should be aware that disturbance can be a complex phenomenon to study. Managers should be cautious about generalizing the results of studies conducted elsewhere, with different species, or during different seasons to waterfowl-human interactions on their own areas.

What are the effects of human disturbance on waterfowl?

The single most cited effect of human disturbance on waterfowl and other avifauna is the flush response and its consequences. Flying is energetically costly behavior. A black duck consumes 10.4 times more energy in flight than at rest (Wooley and Owen 1978)! The flush response is mediated by several biological and psychological factors that are often time- and site-specific including:

- Species-specific tolerances. For example, eight waterfowl species varied their responses to different levels of water-based recreational activity on a Welsh lake (Tuite *et al*. 1983), and pink-footed geese responded to helicopters sooner than barnacle geese (Mosbech and Glahder 1991).

- Temporal differences. For example, entire flocks of staging snow geese flushed more readily in response to disturbance during spring than fall (Figure 23; Belanger and Bedard 1989).

- Predisturbance behavior. For example, bald eagles on the ground almost always flew when approached and generally at much greater distances than eagles in trees (Knight and Knight 1984), and staging black brant were more responsive to aircraft overflights when they were resting at high tide (Ward *et al.* 1987).

- Landscape. For example, wintering white-fronted (Norris and Wilson 1988) and pink-footed (Madsen 1985*b*) geese congregated in larger flocks and flew shorter distances when disturbed in larger agricultural fields.

- Experience of individuals. For example, older Canada goose broods were more tolerant of repeated disturbance than younger ones (Eberhart *et al.* 1989), but older bald eagles flushed sooner than young eagles in response to an approaching human (Stalmaster and Newman 1978).

This last point may be an important determinant of waterfowl response to disturbance. The flight response of a goose flock to disturbance may be largely determined by the individual behavior of its most nervous members (Owens 1977, Belanger and Bedard 1989). A larger flock with more sentinels is not only more likely to identify a potential disturbance sooner than a smaller flock, it also is more likely to have members with a wider range of individual tolerances to disturbance. This may explain why larger flocks of Atlantic brant (Figure 24), graylag geese, and pink-footed geese tend to flush at greater distances from disturbance than smaller flocks (Owens 1977, Madsen 1985*a*).

Waterfowl also must cease whatever other behavior they were engaged in prior to being disturbed. For black duck pairs in early spring, this may mean interruption of courtship and/or nesting activity (Stotts and Davis 1960). For nesting hens, this means an unattended nest with increased probability of egg depredation (Choate 1967), nest abandonment (Balat 1969) and/or interruption of incubation (Bouffard 1983). For molting canvasbacks and redheads, this means interference with habitat selection and possible use of suboptimal lakes during the flightless period (Bergman 1973). For a migrating bird, this may mean interference with normal flight patterns and increased susceptibility to accidental death (Blokpoel and Hatch 1976), predation, or being shot (Bartelt 1987). For family groups of Canada geese, this may mean disrupted bonding and early brood breakup (Bartelt 1987). For wintering or migrating waterfowl, this may mean cessation of feeding and/or resting activities (Paulus 1984, Korschgen *et al.* 1985, Morton *et al.* 1989*a*, Belanger and Bedard 1990, Laskowski *et al.* 1993).

This last point may be critical for refuging waterfowl. Even if flight time per disturbance is short, the additional time snow geese spend resettling between landing and continuation of feeding may become lengthy even at low disturbance rates (Figure 25; Belanger and Bedard 1990). Additionally, wintering black ducks experienced reduced energy intake while doubling energy expenditure during observed disturbances at Chincoteague NWR (Morton *et al.* 1989*a*). The cumulative effect of reduced energy intake and feeding time may be prohibitive for refuging waterfowl. Modelling of the energetics of snow geese staging at Arctic NWR suggest that reduced feeding time and energy intake have greater effects on daily fat gain than increased energy expenditure due to flight (Brackney 1987).

Although flight in response to acute disturbance is most obvious to human observers, there are costs associated with nonflight responses at chronic levels. Any behavioral deviation from rest can be energetically expensive. Wintering black ducks, for example, responded to disturbance by spending more time in alert and escape behaviors and less time resting and feeding, even when they failed to flush (Morton *et al.* 1989*a*). An alert black duck, or one that is walking or swimming, consumes 1.8, 1.4, and 1.8 times, respectively, more energy than a bird at rest (Wooley and Owen 1978).

Furthermore, lack of a behavioral response does not mean lack of a metabolic or physiological response. Ball and Amlaner (1980) demonstrated that an alert but caged Herring gull shows a consistent heart-rate response to an approaching human. Similarly, MacArthur *et al.* (1982) found that mountain sheep had elevated heart rates when disturbed by aircraft despite showing no evidence of behavioral response. Although there is some question as to the relationship between heart rate and metabolic rate (Wooley and Owen 1978), it is clear that wildlife are responding with a heightened state of vigilance even when there is no apparent behavioral response.

In general, disturbance increases maintenance costs by increasing energy expenditure and decreasing energy intake. Morton (1992) suggested that waterfowl 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.

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.

Regardless of how land managers choose to view human disturbance, it should be apparent that disturbance can have multiple effects on waterfowl, some of which are subtle. Waterfowl adjacent to a dike or road may be physiologically stressed without showing behavioral responses and, furthermore, may not be representative of the species as a whole. Klein (1989) found that some individual waterbirds and mottled ducks at "Ding" Darling NWR were consistently tolerant of people while others flushed immediately. These findings suggest that land managers should interpret their own observations of waterfowl-human interactions cautiously.

Effects of disturbance due to hunting activity

The effects of disturbance induced by hunters and hunting activity warrants attention as a separate issue. The response of waterfowl to human disturbance is intimately related to their experience with hunters and hunting. Matthews (1982) points out that "if ducks and geese were not hunted, the effects of other man-made disturbances would be much less severe; it is Man (*sic*) that makes wildfowl wild". Land managers know this to be true. Waterfowl in refuges and city parks often feed from human hands. Conversely, wintering brant flushed at distances > 500 m on tidal flats that were frequented by hunters, but could be approached within 150 m on unhunted flats (Owens 1977). The fact that staging snow geese resume feeding much sooner after disturbance in spring than in fall (Belanger and Bedard 1989) suggests a more subtle effect of autumn hunting.

In addition to sensitizing waterfowl to human activity, disturbance-induced flight can increase hunting mortality. Bartelt (1979) used log-linear modeling to show that disturbance levels influenced the likelihood of radio-marked Canada geese being shot at Horicon NWR more than hunting pressure! Similarly, Frederick *et al.* (1987) developed a simulation model for fall-migrating lesser snow geese on DeSoto NWR. Sensitivity analyses suggest that hunter-induced disturbance of feeding geese (which reduced energy gains and subsequently hastened emigration) affected waterfowl use-days more than direct hunting mortality.

To minimize their exposure to hunters and hunter activity, waterfowl may shift their use of habitats. Morton *et al.* (1989*a*, 1989*b*) argued that disturbance levels (including hunting activity) outside Chincoteague NWR were high enough to force wintering black ducks into a pattern of nocturnal feeding within surrounding saltmarsh and diurnal resting within refuge impoundments. Paulus (1984) similarly suggested that wintering gadwalls responded to hunting activity in wetlands outside Rockefeller Refuge by using refuge impoundments.

The intent of this section is not to disparage waterfowl hunting. After all, many individuals and agencies manage land with the objective of increasing waterfowl hunting opportunities. Furthermore, many so-called nonconsumptive recreational activities are ultimately consumptive (Wilkes 1977). Rather, managers of public and private lands who are aware of the interactions between disturbance and hunting mortality, and between hunting activity and waterfowl response to disturbance, can incorporate them into the decision-making process. Ebbinge (1991) argued that just as poisoning from lead shot ingestion and crippling are indirect effects of hunting, so is habitat loss due to hunting activity.

Management Strategies

Several strategies can be used to manage human disturbance and its effects on waterfowl. Complete denial of human access (closure) is the most drastic measure, but it may be warranted under certain conditions. Disruptive activities can be prohibited and public access can be restricted. Buffer zones can be designated to protect important waterfowl habitats or screens can be used to diminish the sights and sounds of human activity. These strategies tend to work by manipulating the spatial and temporal distribution of human activities (zoning) and depend, to some extent, on aggressive law enforcement to be effective.

Alternatively, food availability or quality can be enhanced to mitigate for the energetic costs of disturbance-induced stress. Public education may be used to sensitize wildlife-oriented user groups to the effects of their behaviors on waterfowl. Most importantly, the costs of human disturbance need to be acknowledged and incorporated in the decision-making process of NWRs, wildlife management areas, parks, other public lands, and private sanctuaries. These strategies are discussed in more detail below.

Prohibition of human access

Waterfowl may be protected from human disturbance by prohibiting human access. Although Linduska (1982) described lands owned by the NWR System, National Audubon Society, states, private gun clubs, Ducks Unlimited, and individuals as sanctuaries, little of it actually represents the inviolate refuge called for by Kahl (1991). Many of these public and private lands are maintained for various human uses. However, there is good justification for designating some lands or portions of some lands as refuges from human intrusion. Fog (1982), for example, attributed re-establishment of a common eider colony on a Danish island to prohibition of human entry.

Migrating waterfowl also may benefit from complete exclusion of human activity. Fredrickson and Reid (1988) described a situation in which a mallard, feeding in habitats with disturbance, takes 40% longer to regain body fat after an 8-hr flight than one feeding in habitats with no disturbance. Despite the fact that this is a hypothetical scenario, there is circumstantial evidence that some waterfowl species may be predisposed to avoid disturbance because of restrictive time and energy budgets. Mayhew (1988) showed that the longer a waterfowl species took to meet minimum daily energy requirements, the more likely it was to be found wintering on British refuges (Figure 26).

Although refuge size will vary with management objectives, Belanger and Bedard (1990) recommend that feeding areas protected from human intrusion be at least 200 ha so that geese, when flushed, will re-settle within the area rather than return to their roosting site. Additionally, managers of public lands should explain the purpose of prohibiting human access to some areas through education programs. Gigliotti (1991) argued that designating protected areas promotes the myth that humans are separate from their environment, which ultimately reduces people's feelings of personal responsibility. Education programs associated with refuges should attempt to circumvent this possible outcome.

Prohibition of certain human activities

Most management programs regulate disturbance by prohibiting some human activities that conflict with other management objectives. Off-road vehicles (ORVs) are prohibited or restricted on many Atlantic beaches because they disturb breeding piping plovers, nesting colonial seabirds, and migrating shorebirds. Hunting, fishing, clamming, and harvesting of other natural products are often prohibited because these activities are perceived as consumptive, although their disturbance component may be at least as critical to waterfowl populations. Boating, water skiing, and jet-skiis may be prohibited because of direct impacts on submerged aquatic vegetation and water quality, and indirect impacts on island-nesting birds and resting and feeding waterfowl. Roller-blading, jogging, wind-surfing, and bicycling are increasingly being scrutinized because they are often perceived as health-oriented rather than wildlife-oriented recreational activities. Dogs, whether leashed or not, are often prohibited because disposal of their waste is problematic or because their behavior towards wildlife and people other than their owners is unpredictable.

For management purposes, Pomerantz *et al.* (1988) suggested that human activities should ultimately be viewed in the context of their impacts on wildlife and not on a superficial classification of use (such as consumptive *vs* nonconsumptive). As an example, they describe a scenario in which surf fishermen appear to disturb nesting piping plovers on a National Wildlife Refuge and the easy (but erroneous) solution would be to prohibit surf-fishing. Upon closer examination, nest disturbance is actually caused by surf fishermen driving to and from the beach, by pets and nonfishing companions of fishermen exploring the beach, and by fishermen picknicking on the beach. The offending publics are then off-road tourers, beachcombers, pets, and picknickers (not anglers), and the impacting activities are driving on beaches, exploring on foot, unrestrained pets, and picknicking. Angling itself is not impacting plovers and may be continued, with certain restrictions, as a compatible public use of the refuge.

Just as the consumptive-nonconsumptive dichotomy may be inappropriate for managing disturbance, so may be the classification of activities as wildlife- or nonwildlife-oriented. Klein (1993) found that approaching birds on foot was the most disruptive of usual visitor activities at "Ding" Darling NWR. The most offending public was wildlife photographers who were more likely to approach birds, to stop more frequently, and to get out of cars more often than nature observers, anglers, crabbers, and nonwildlife-oriented fitness and drive-through user groups. Similarly, Matthews (1982) argued that on small bodies of water, managers may be forced into a "birds or boats" ultimatum regarding use of powerboats (regardless of why powerboats are being used).

Many refuge managers permit special uses such as researching, banding, and photographing. Despite their scientific and educational intent, these activities should be reviewed with the welfare of bird populations in mind (Buckley and

Buckley 1976). On the other hand, managers should not be overly restrictive. Researchers sometimes need a free hand to obtain data of high quality and many that study birds are already sensitive to their effects on nest predation (Duffy 1979, MacInnes 1980, Strang 1980). Besides, compared to scientific collecting, 6,000 times more birds are killed by hunters in the U.S., 4,000 times more are killed by collisions with windows, 2,900 times more are killed by automobiles, and 100 times more are killed by pest-control operations (Walsberg 1993). Perhaps the best solution is for managers to inform special-use permittees about species of concern, sensitive habitats, and certain behaviors that are disturbing to waterfowl and other wildlife. Certainly this user group should be receptive to environmental education and voluntary compliance; if not, permits can be contingent on appropriate behavior.

Restriction of public access

Another approach to zoning is to restrict public access rather than prohibit certain human activities. Buckley and Buckley (1976) listed several techniques for limiting public access on land including sign posting, fencing, restricting boat landing facilities, prohibiting pets (and therefore their owners), and providing towers and boardwalks in lieu of direct access. Over water, Kahl (1991) suggested including establishment of waterfowl protection areas that prohibit disturbance, and no-wake or nonmotorized boating zones. User fees, permits requiring specific qualifications, limiting the number of visitors present (*e.g.*, parking restrictions), and intentionally making it difficult to travel are also ways of regulating public access (Klein 1989). Chincoteague NWR provides an example of the latter technique: bicycles and motorized vehicles are prohibited on certain roads to discourage people from accessing more remote areas of the refuge.

An excellent mechanism for restricting access in high public-use areas is to provide visitors with alternative transportation such as shuttles and tram tours. These services confine the viewing public to fewer vehicles. Visitors can be enticed to use trams by prohibiting personal vehicles from accessing parts of the refuge that the tram tours. Additionally, Klein (1989) suggested using tram tours as an opportunity for environmental education (including information on human disturbance). Use of shuttle services, rather than personal vehicles, can be encouraged by restricting parking spaces or the number of vehicles allowed entry, by prohibiting vehicles altogether, or be assessing higher entry fees for people entering refuges in vehicles than aboard shuttles.

Buffer strips and screens

Areas of high waterfowl use, remote areas, or other special areas can be protected from human disturbance with buffer zones and screens. A buffer zone is simply a collar of land or water that is intended to increase the distance between human activities and waterfowl. Screens, usually vegetative or an earthen dike, obscure the sight and sound of human activities from waterfowl. Both buffers and screens are usually placed around the area to be protected. Habitat Suitability Index models that incorporate disturbance as a component use this approach (*e.g.*, Chapman and Howard 1984). However, both can be placed around areas of concentrated human activity. For example, vegetative screens, fencing, and buffer zones are used by the Vermont Department of Fish and Wildlife to mitigate disturbance-induced impacts of housing developments on deer wintering areas (K. Royar; pers. comm.). Visitor centers or parking lots could be similarly buffered or screened on public lands.

Two studies suggest that buffer zones for field-feeding geese should be at least 100 - 250 m. Madsen (1985*b*) reported that fields with widths < 500 m (radius = 250 m) were not used by pink-footed geese in Denmark due to adjacent traffic volume. In contrast, Keller (1991) did not find pink-footed or greylag geese in Scottish fields with centers < 100 m from roads. Erwin (1989) similarly recommended distances of 100 - 300 m for sign-posting around established seabird colonies in Virginia and North Carolina. Over water, Matthews (1982) recommended that boat traffic (particularly power boats) be prohibited from entering within 300 m of waterfowl refuges.

Many refuges restrict aircraft to certain altitudes which effectively creates a buffer zone above waterfowl. Belanger and Bedard (1989) recommended restricting aircraft to > 500 m above refuging snow geese and Owens (1977) called for the same restriction over brant in estuaries. Most managers have neither the authority nor the enforcement capability to regulate air space other than with altitude restrictions at best (Dewey and Mead 1994). However, they should be aware that waterfowl vary their responses to different aircraft at different altitudes, lateral distances, and speeds (Ward *et al.* 1988). For example, Owens (1977) found that aircraft at altitudes < 500 m and distances < 1500 m away could flush brant; helicopters were worse than fixed-wings, and low speed aircraft were worse than high speed aircraft. Aircraft noise may ultimately be more disturbing to waterfowl than the sight of one; brant appear to respond to a threshold sound exposure level of 65 dBA regardless of aircraft type, lateral distance, and altitude (Ward *et al.* 1988).

Vegetation and earthen dikes can be used to screen human activities from waterfowl (Matthews 1982). In the mid-Atlantic states, perhaps efforts to control *Phragmites* should not extend to areas immediately adjacent to roads, trails, and other points of access. Artificial islands (for loafing and nesting waterfowl) could be placed so that as much surface water as possible is blocked from view at nearby access points. For field-feeding waterfowl such as geese, a buffer zone may work better than a screen. Madsen (1985*b*) found that use of large fields (> 600 m from road) by pink-footed geese was reduced when more than one view was obstructed; similarly, goose utilization (*i.e.*, dropping density) increased with distance from windbreaks. Waterfowl on land probably feel threatened by close vegetation that may provide cover for avian or mammalian predators.

Increase food availability or quality

The impacts of human disturbance on waterfowl also may be mitigated by increasing food availability or quality. Waterfowl may be able to compensate for disturbance-induced stress by increased foraging opportunities in high quality habitats. Any traditional enhancement technique may be considered for increasing food such as plantings, crop leasing, or moist soil management. Supplemental feeding also may be an appropriate technique for increasing food availability, particularly on private sanctuaries (Dennis and Chandler 1974). Regardless of the approach, managers should entice waterfowl to use managed habitats by restricting public access or by restricting their food enhancement efforts to areas with low disturbance rates.

Public education

One of the most effective means for inducing voluntary reduction of human disturbance is through public education programs. Most people who participate in wildlife-oriented activities are presumably doing so because they enjoy and appreciate their experiences with wildlife. Although most users may be unaware that their actions can cumulatively be so detrimental to wildlife, certainly this is an audience receptive to environmental education. Klein (1993), for example, found that people who spoke with roving staff at "Ding" Darling NWR were less likely to disturb wildlife than other recreational users. She 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.

Similarly, Matthews (1982) suggested encouraging good "etiquette" among naturalists, birdwatchers, and wildlife photographers. These user groups may be unaware that their vehicles can sometimes be less disturbing to wildlife than they are or that they may get closer to wildlife by staying in their vehicles than by approaching on foot. Casual photographers often use inexpensive cameras with relatively short lenses that require minimal distances between themselves and waterfowl; long lenses ($\geq$ 200 mm) could be promoted as both an investment in better photographs and higher waterfowl populations. Individuals who do approach waterfowl, such as photographers, should be taught that they can often get closer (without flushing birds) by approaching downwind from waterfowl, by refraining from getting between waterfowl and water, or by wearing neutral-colored clothing. Handling and feeding waterfowl should always be discouraged.

Educators can use lectures, videos, leaflets, exhibits, signs, information in permits and brochures for ORVs, and press releases about nesting birds to inform publics about human disturbance (Buckley and Buckley 1976). User groups may be more receptive to education in outdoor rather than indoor settings. Klein (1993) reported that people who visited the information center at "Ding" Darling NWR were as likely to disturb wildlife as those who did not; however, those visited by roving staff outdoors were less inclined to disturb wildlife.

Public observation blinds, combined with education efforts, may prove to be an excellent management technique on public lands. The Wildfowl Trust in the United Kingdom uses a system in which small blinds are constructed at intervals along screened corridors (Matthews 1982). The best way to screen the approach is to throw up parallel earthen banks 2 m high; the banks screen the sight and sound of people and the water-filled borrow ditches are used by waterfowl. Tall emergent vegetation may alternatively be used to screen approaches. Wood or fiberglass blinds are constructed on a rot-proof base; adjustable seats and viewing slots that are shielded by hinged shutters are provided. Just as hunters, ORV owners, or researchers often must receive instruction or certification to use public lands, use of blinds could be contingent on completion of a short seminar or video that sensitizes people to their potential for disturbing wildlife.

Matthews (1982) also described auditorium-like blinds that can accomodate more than 100 persons. These are equipped with inward-sloping glass windows, chairs, carpet, and heating. Although these may sound excessive to American managers, large refuges may be able to justify their construction for educational purposes in much the same way that public zoos and aquariums have. Educators would have an opportunity to expose relatively large numbers of the public to free-living wildlife in a forum conducive to discussions on species identification, life history, management, and waterfowl-human interactions.

Decision-making process

Human disturbance needs to be recognized explicitly, not implicity, in discussions of waterfowl management. Failure to do so may lead to situations in which the compatibility of human activities with the conservation mission of many public lands are legally challenged (Curtin 1993). In the most publicized test of the doctrine of compatibility, the Defenders of Wildlife forced Ruby Lake NWR in 1978 to restrict outboard motors and prohibit waterskiing because these activities were impacting waterfowl production (Bouffard 1982).

Perhaps the most effective way of reducing or eliminating waterfowl-human interactions is to integrate disturbance as an issue in the decision-making process. Waterfowl management plans for small land areas should contain a section that specifically addresses human disturbance. Managers of large public facilities, such as NWRs, should consider developing a separate plan for managing human disturbance. Management plans for public use are not likely to address waterfowl-human conflicts adequately because the intent of these programs is generally to promote public use. Waterfowl and public use plans should at least be well integrated; although solutions to waterfowl-human conflicts will often involve public use issues, the problem is fundamentally biological and one that requires a thorough understanding of waterfowl ecology. Reinforcing regulatory compliance through an active law enforcement program and voluntary compliance through education programs cannot be overemphasized.

Modelling also may be appropriate for large refuges with a combination of high waterfowl and visitor populations. Frederick *et al.* (1987) developed a FORTRAN simulation model for fall-migrating lesser snow geese on DeSoto NWR. Components of this model included population level, time and energy budgets, food density and distribution, food-searching flight characteristics, migration rates, and the effects of weather, hunting pressure, and land management practices within the system. Hunter-induced disturbance was modelled by specifying the mean length of time that geese remain undisturbed after landing; effects of varying this parameter on waterfowl use-days could then be assessed in sensitivity analyses. Similar models could be developed for other refuges that incorporate disturbance from other human activities.

In situations where few data are available, the *ad hoc* approach used by Montopoli and Anderson (1991) to model bald eagle-human interactions on the Snake River may be a unique solution. Rather than using empirical data, eight experts in eagle behavior were asked to score an eagle's expected response to 63 scenarios involving numbers of nonmotorized boats or rafts, bank users, undeveloped pull-outs, developed pull-outs, and concentrated use areas. These collective judgments were used to build a logistic regression model that was subsequently validated with empirical data collected on a 45-km stretch of the Snake River. This model is currently used by managers of Bridger-Teton National Forest and Grand Teton National Park to assess the cumulative effects of land development and associated activities. With validation, this may be an excellent interim approach to managing wildlife-human interactions until adequate and appropriate empirical data exist.

The management techniques described here manipulate the spatial distribution of human activities. Managers should be aware that these techniques have a temporal component. Complete closures, activity prohibition, access restriction, buffers, and food enhancement can be implemented seasonally, monthly, weekly, or daily. Decisions about temporal management are dependent on species-specific phenology and human visitation patterns.

The management program at Chincoteague NWR provides a prototypic example of manipulating spatial and temporal components of human disturbance. Chincoteague NWR encompasses nearly 14,000 acres, most of which are on the Virginia portion of Assateague Island, and includes 2,600 acres of impounded wetlands. Chincoteague NWR provides wintering and nesting habitats for more than 300 bird species, including large populations of wintering greater snow geese and American black ducks. It is the third most highly visited NWR, drawing more than 1 million visitors annually, many of which are enroute to its beach frontage on the Atlantic Ocean. The following strategies are used at Chincoteague NWR to reduce this enormous potential for waterfowl-human interactions:

- Entrance gate. The only access to the refuge is controlled by a timed gate that permits entry between dawn and dusk.

- Wildlife loop. Although travel by foot and bicycle on this 3.4 mile loop is unrestricted during the day, motorized vehicles are only allowed from 1500 to dusk.

- Beach Road. Parking is not permitted along the only vehicle access to the beach. Borrow ditches between the impoundments and road serve as an unintentional but effective deterrent to human access. Parking at the ocean beach parking lots is managed by a "one-car-out, one-car-in" entry system when available parking is filled.

- Service Road. Travel is restricted to foot traffic on this 7.5 mile road that accesses more remote northern parts of the refuge. Bicycles and motorized vehicles are prohibited, effectively discouraging most recreational users.

- Toms Cove Hook and the Wild Beach. The southern 2.5 miles of Toms

Cove Hook and several miles of beach in the north are closed to human access from early spring - late summer to protect tern and piping plover breeding activities.

- ORV zone. A total of 48 ORVs are allowed at any one time on a 4-mile beach zone on Toms Cove Hook during the winter. During the rest of the year, the southern 2.5 miles of this zone are closed and only 18 ORVs are allowed at any one time on the remaining 1.5 miles. During a recent special closure of part of the ORV zone because of unexpected plover nesting activity, volunteers staffed a station to allow the nest to be observed by visitors, to provide information about plover-human interactions, and to enforce the closure.

- Recreational activities. Horseback riding is restricted, boating access is restricted, and boating within impoundments is prohibited. Overnight surf-fishing is allowed by permit only; otherwise, camping is prohibited. Fishing, crabbing, and clamming are allowed in salt water areas and in one impoundment immediately adjacent to Beach Road. Nonhunting publics are restricted to roads, paved trails, boardwalks, tidal flats, or beaches. The archery season for deer has been recently shortened because it coincides with autumn use of the refuge by migrating waterfowl. Dogs are prohibited, even in vehicles.

- Osprey and Safari tours. Land tours and boat cruises are operated on the refuge by concessionaires. The latter visits remote areas of the refuge that otherwise have restricted access.

- Master Plan. The recent EIS for the Master Plan (USFWS 1992*a*) integrates selected human and wildlife uses of the refuge. Figure 27 illustrates one way of incorporating human disturbance into the decision-making process.

Some managers may not have the data necessary (or the mandate) to manage human disturbance on their lands as comprehensively as at Chincoteague NWR. Although the scientific literature on disturbance is increasing, managers may need interim measures. Perhaps managers can target a species known to be sensitive to disturbance (*i.e.*, an indicator species) or a species of special concern (because of management objectives) for study or management. Although management strategies for a single species may not fully protect other waterfowl from disturbance, these two approaches will likely err on the conservative side.

A progressive approach to managing waterfowl-human interactions is strongly advocated. Despite 1.3 million waterfowl hunters in 1986, the waterfowl hunting public has been declining since 1971 (Flather and Hoekstra 1989). However, there were 109.6 million Americans 16 years old or older who participated in primary nonconsumptive wildlife-oriented activities in 1985, a 32% increase since 1980

(Flather and Hoekstra 1989). Consumptive and nonconsumptive wildlife-oriented activities totaled 1,083 million use-days nationwide in 1991 (USFWS 1992*b*). These statistics suggest an enormous and immediate potential for disturbing waterfowl and other wildlife. With diminishing wetlands, expanding human populations, and increasing participation in wildlife-oriented activities, background levels of human disturbance can only increase.

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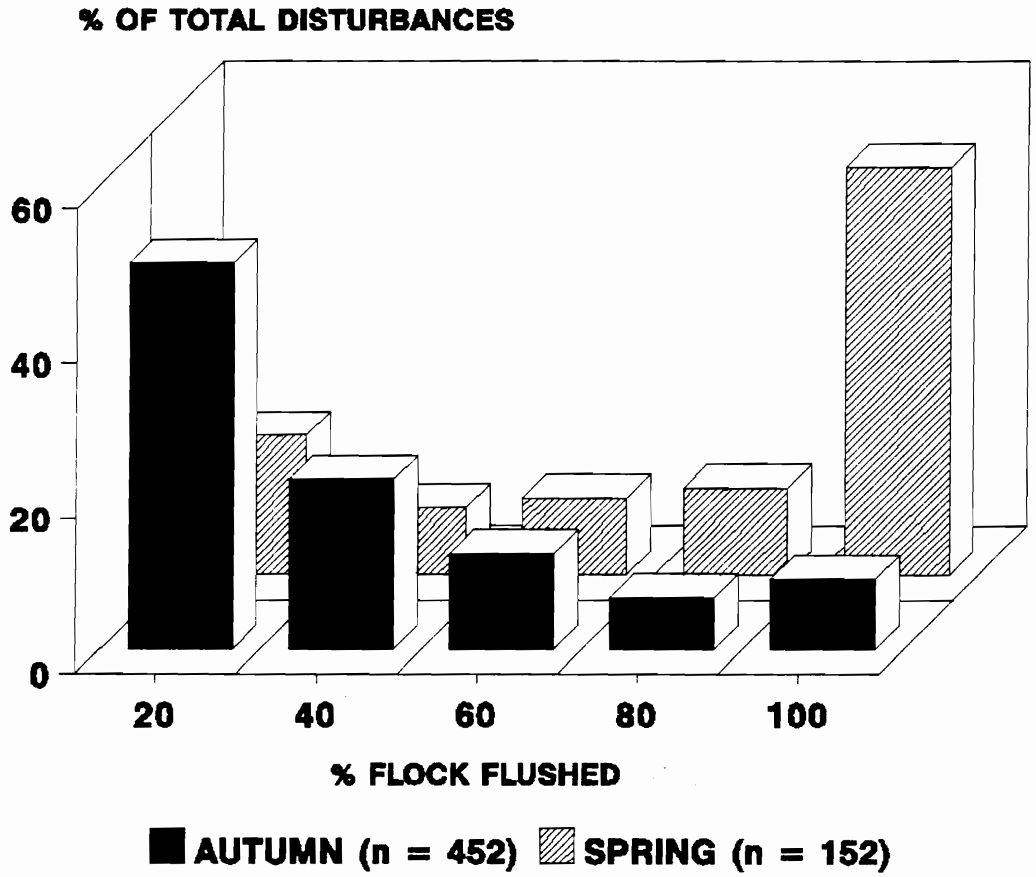

Figure 23. Seasonal difference in flush response of staging snow geese (Belanger and Bedard 1989).

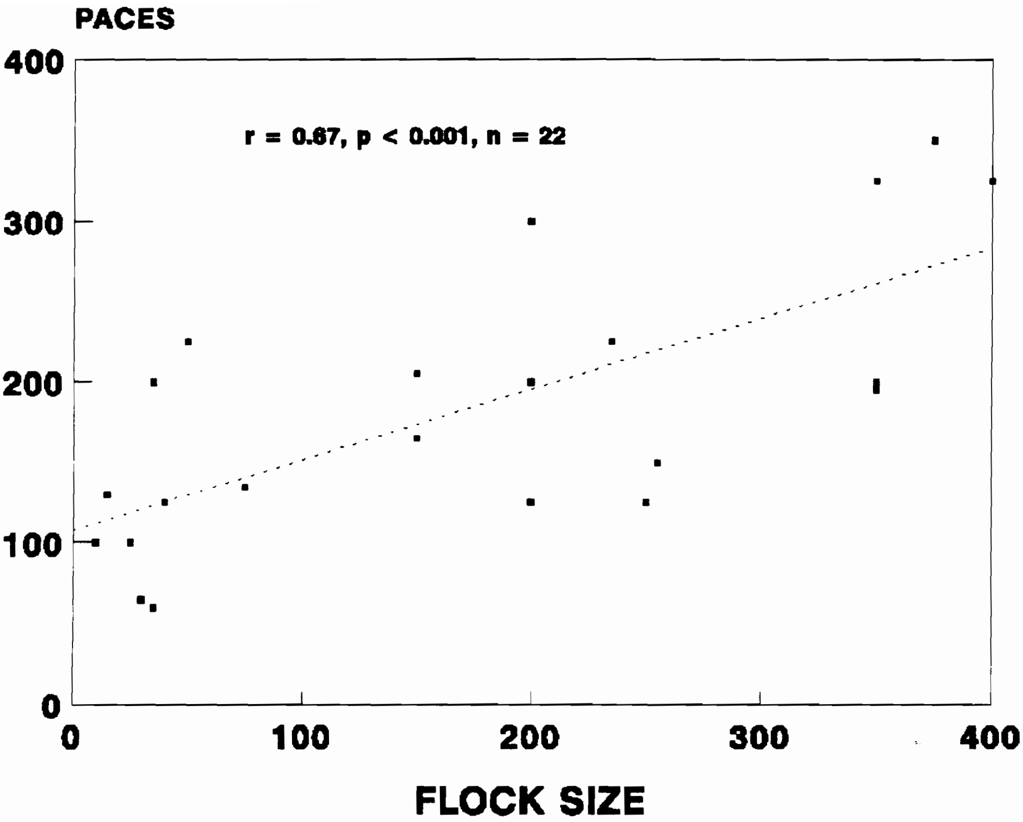

Figure 24. Effect of flock size on flush distance of wintering brant (Owens 1977).

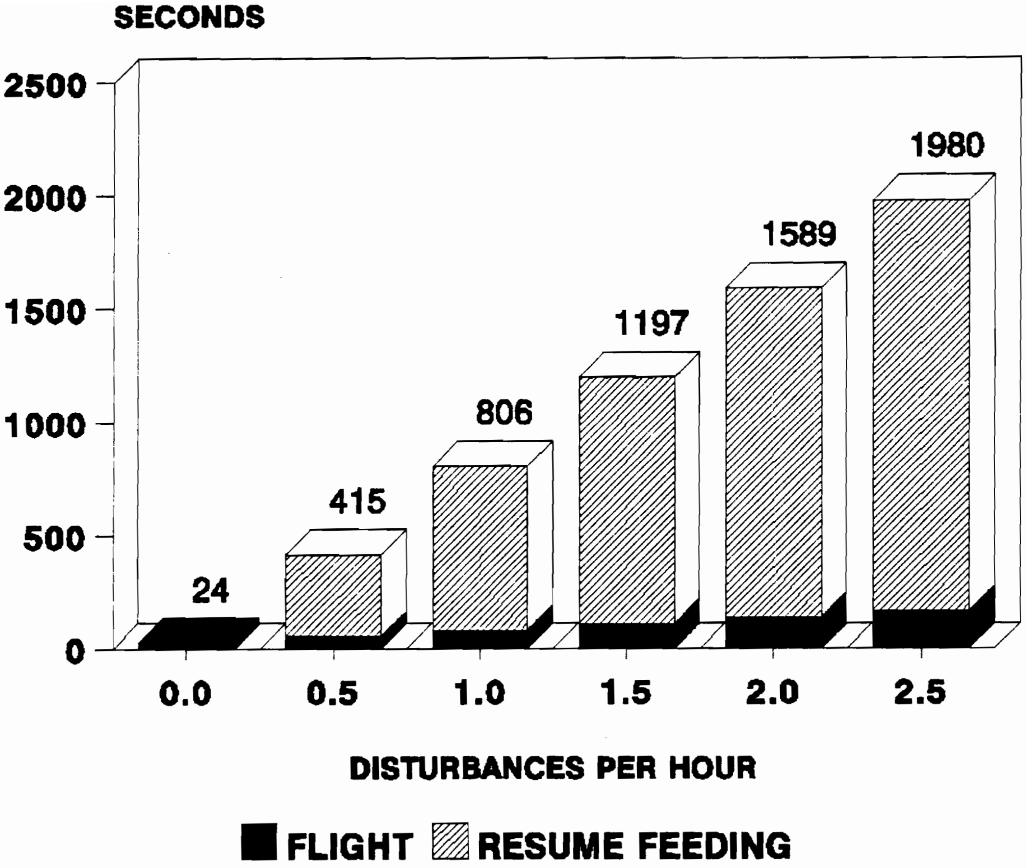

Figure 25. Cumulative foraging time lost by staging geese at different disturbance rates (Belanger and Bedard 1990).

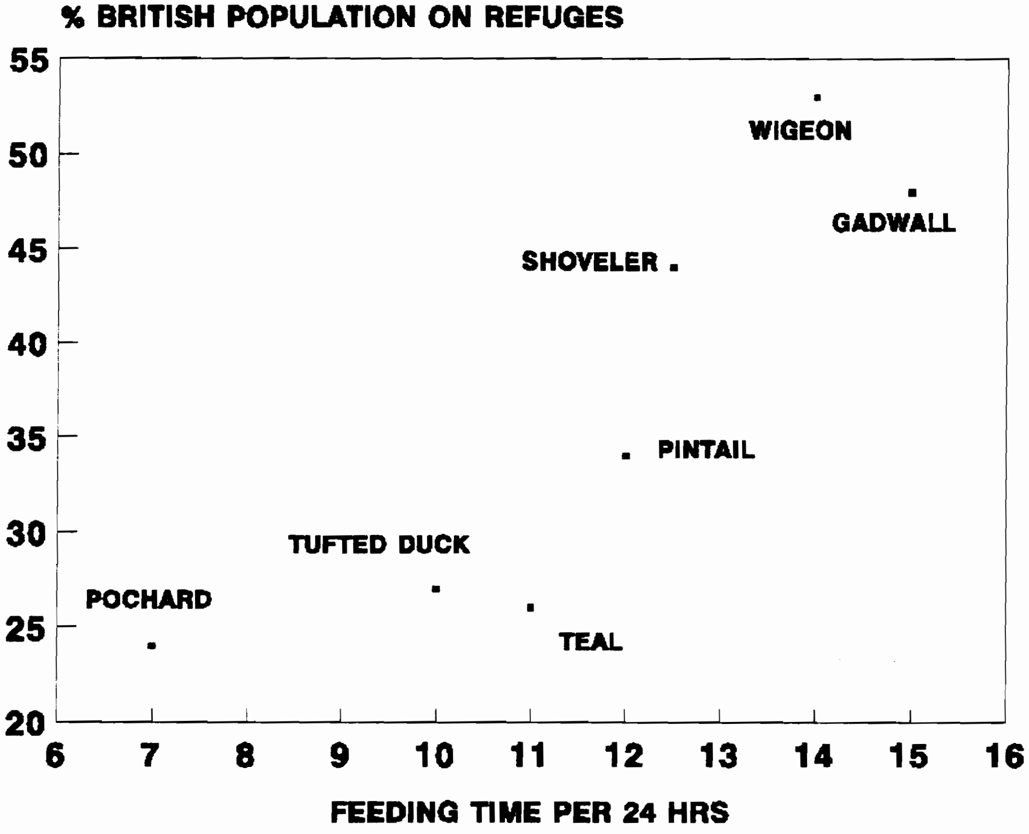

Figure 26. Waterfowl use of British refuges in relation to feeding time (Mayhew 1988).

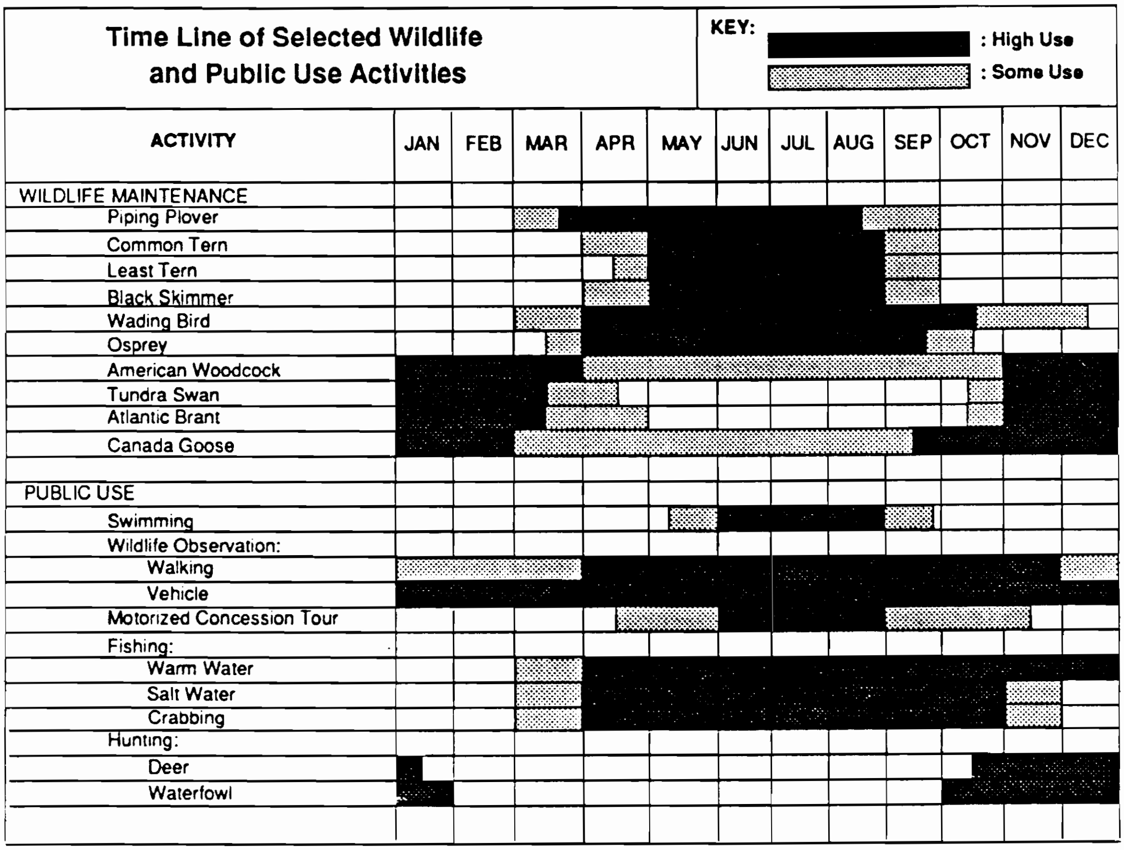

Figure 27. Time frame of selected wildlife and public uses of Chincoteague National Wildlife Refuge (USFWS 1992*a*).

VITA

John M. Morton was born on 1 June 1957 in Madison, Wisconsin. After attending public schools both there and Hawaii, he graduated from Madison Memorial High School in 1975. He graduated with a Bachelor of Science degree in Wildlife Ecology from the University of Wisconsin at Madison in 1980. He completed a Master of Science degree in Wildlife Science from Virginia Polytechnic Institute and State University in 1987. He completed his requirements for a doctoral degree in Wildlife Science in 1996.

His formal education was interrupted frequently by employment with several agencies, including the U.S. Fish and Wildlife Service, Vermont Department of Fish and Wildlife, and Wisconsin Department of Natural Resources, in locations scattered from Alaska to Ecuador, and Virginia to Guam. He currently studies endangered species on Guam as a wildlife biologist with the Pacific Islands EcoRegion of the U.S. Fish and Wildlife Service. He married Leslie D. Sweeney in 1992.