# ENERGY FLOW THROUGH A SOUTH CAROLINA SALT-MARSH SHOREBIRD COMMUNITY

# by Keith L. Bildstein, Roberta L. Christy and Patricia DeCoursey

Although we know much about shorebird foraging behavior and habitat use (see for example Pitelka 1979), we know relatively little about the amount of energy that flows through shorebird communities (see for example Evans et al. 1979, Grant 1981). In an attempt to assess the role of birds in estuarine ecosystem energy flow, we have obtained detailed estimates of the energy demands and impacts of the avian community on a 3000 hectare South Carolina estuary, and are currently analyzing these data (Christy et al. 1981). Here we (i) report on the size and species composition of the shorebird segment of that community and (ii) estimate energy flow through that segment.

The study was conducted on the North Inlet marsh 6 km east of Georgetown, SC (Fig.1). This relatively pristine, high salinity, estuary is typical of the South Carolina coastal plain (Pritchard 1967). The marsh is dominated by Spartina alterniflora and includes oyster reefs, mudflats, sandbars, and tidal pools (Forth 1978).

We approximated the bioenergetics of the marsh's bird community by censusing the community for 2 years and then applying metabolic rate equations to the results of our censuses. This two-stage determination estimated the energy requirements of the community.

Initially we spent 5 months in the field to determine which species were present and where they were. As a result of this preliminary field work, we decided to estimate the populations of a few logistically difficult species and to census directly the remaining species. We used 4 censusing techniques, including 1) aerial surveys, twice-a-month at low tide, of large, conspicuous species, 2) air-boat surveys, at extreme high-tide, of rails, 3) almost daily spot checks throughout the marsh of low-density transient species, and 4) high tide ground counts, twice per month, of communally roosting shorebirds. The last were made on high tides just before and/or after spring tides when almost all shorebirds feeding on the marsh congregated on the few high spots we censused. We chose to survey on these tides because roosts were often flooded on the spring tides and shorebirds roosted on outer beaches then and because many shorebirds remained scattered throughout the marsh on the neap tides.

The results of our surveys were used in a computer simulation model developed to calculate energy demands. The model employs existence metabolism equations developed by Wiens and Dyer (1977), that take into account basal metabolism, thermoregulation and heat accrued incidental to limited motor activity. Input variables for these equations include day length, ambient temperature, bird weight, and whether or not the bird is a passerine. We then added to these requirements the energetic costs of digestion and activity as well as the costs of egg production and chick growth and then determined individual energy requirements (Wiens and Dyer 1977). The results were coupled with our census data which had been modified to produce an approximation of the avian community's density and age structure. Together these data produced an estimate of the total energy demands for the avian community feeding on the North Inlet marsh (for details see Christy et al. 1981).

Ninety-four species of birds were recorded feeding over the marsh during the 2-year period beginning 15 October 1978. A number of additional species were seen along the marsh border. Some of these, especially aerial insectivores, probably fed sporadically on the study site.

Twenty-one species of shorebirds were sighted (Table 1). Although individuals of 17 shorebird species were seen during all 4 seasons, only 5 species of shorebirds bred on or near the study site. More species of shorebirds were most common in the spring than in either summer or fall and only Sanderlings Calidris alba and Lesser Yellowlegs Tringa flavipes were most common in winter. Dowitchers, almost all of which were Limnodromus griseus, comprised 43% of all

Table 1. Seasonal occurrence and relative abundance of shorebirds censused on the North Inlet marsh.

| | Winter[a] | Spring | Summer | Fall |
|---|---|---|---|---|
| American Oystercatcher *Haematopus palliatus* | 2[b] | 4 | 3B | 1 |
| American Avocet *Recurvirostra americana* | NS | NS | 2 | 1 |
| Semipalmated Plover *Charadrius semipalmatus* | 3 | 2 | 1 | 3 |
| Wilson's Plover *C.wilsonia* | NS | 1 | 2B | 3 |
| Killdeer *C.vociferus* | 2 | 3 | 4B | 1 |
| Black-bellied Plover *Pluvialis squatarola* | 2 | 1 | 4 | 3 |
| Whimbrel *Numenius phaeopus* | 3 | 1 | 2 | 3 |
| Marbled Godwit *Limosa fedoa* | NS | NS | 1 | 2 |
| Greater Yellowlegs *Tringa melanoleuca* | 4 | 2 | 1 | 3 |
| Lesser Yellowlegs *T.flavipes* | 1 | 2 | 4 | 3 |
| Willet *Catoptrophorus semipalmatus* | 4 | 1 | 1B | 3 |
| Spotted Sandpiper *Actitis macularia* | 4 | 3 | 1B | 2 |
| Ruddy Turnstone *Arenaria interpres* | 2 | 1 | 3 | 4 |
| Short-billed *Limnodromus griseus* and Long-billed Dowitchers *L.scolopaceus* | 2 | 4 | 1 | 2 |
| Red Knot *Calidris canutus* | NS | 1 | 2 | 2 |
| Sanderling *C.alba* | 1 | 3 | 4 | 2 |
| Semipalmated Sandpiper *C.pusilla* | 3 | 3 | 1 | 1 |
| Western Sandpiper *C.mauri* | 3 | 3 | 1 | 1 |
| Least Sandpiper *C.minutilla* | 3 | 3 | 1 | 1 |
| Dunlin *C.alpina* | 2 | 1 | 4 | 3 |

[a]Winter = 1 Jan – 15 March, Spring = 16 March – 31 May, Summer = 1 June – 30 September, Fall = 1 October – 31 December
[b]1 = season of most abundance, 2 = less abundant than 1, 3 = less abundant than 2, 4 = season of least abundance, NS = not sighted, B = breeds on or near the marsh.

shorebirds sighted. Breeding species, overwhelmingly American Oystercatchers Haematopus palliatus and Willets Catatrophorus semipalmatus, comprised 9% of the annual shorebird population (Table 2). Shorebird numbers peak in the spring and, to a lesser extent, in late summer and early fall, when numerous migrants use the area (Table 3). Somewhat similarly, the size of the entire North Inlet avian community peaks in late summer to early fall and again, to a lesser extent, in the spring. Shorebirds make up 23% of all sightings annually, and are most numerous relative to other species in winter (Fig.2).

Energy flow through the entire avian community averages 9.9 kcal/m²/year, with 2 species, White Ibis Eudocimus albus and Clapper Rails Rallus longirostrus, being responsible for over half of the community's caloric consumption. Avian caloric consumption is greater in the spring than in late summer to early fall, despite the relatively smaller spring population (Fig.2). This is because of both cooler weather in the spring and greater avian biomass, the latter due to average bird weight being substantially higher in the spring. Similarly, shorebird caloric consumption, which averages 1.3 kcal/m²/year, is greatest during spring migration (Table 3). As might be expected from their relative numbers, dowitchers are responsible for 41% of all shorebird caloric consumption. Breeding species, mainly because of the relatively large body sizes of American Oystercatchers and Willets, comprise 23% of shorebird caloric consumption in the summer and 19% of the annual shorebird consumption (Table 2). Even though they make up 23% of all sightings annually, shorebirds comprise only 10% of the avian biomass and only 13% of the community's caloric consumption. Shorebirds contribute least to avian induced energy flow in June (2% of avian caloric consumption) and most in early September (27% of avian caloric consumption; Figure 2). On a seasonal basis, even in winter, when shorebirds are most numerous relative to other species (28% of all birds), they are responsible for only 17% of the avian induced flow (Table 3). Tentative, preliminary comparisons of these data with data concurrently being collected, on other biotic and abiotic sources of energy flow through the marsh ecosystem, indicate that birds contribute little to the overall flow.

So much for our data. Do these data really tell us anything? First, although energy flow through the shorebird community may appear low (1.3 kcal/m²/year) when averaged over the entire 3,000 hectare marsh, shorebird use of the marsh is far from random, and certain portions, i.e. tidal pools, mudflats and oyster bars, are used quite heavily. Shorebird induced energy flow in these areas of intense use is probably quite important locally.

Second, our study is an attempt to estimate only the direct trophic effects of avian consumers (i.e. calorific consumption) in the North Inlet marsh. While avian consumers may be ecologically unimportant in terms of this direct contribution to ecosystem energy flow, this does not necessarily relegate them to a minor role in ecosystem function: they may play a very important indirect regulatory role (see for example Wiens and Dyer 1977). Consider, for example, Northern Harriers Circus cyaneus wintering on the North Inlet marsh. Almost all species of birds wintering on the marsh are, at least sometimes, flushed by harriers. Detailed observations of Boat-tailed Grackle Quiscalus mexicanus responses to harriers indicate that grackle feeding behavior is disrupted for approximately 10 min following a harrier flyover. This is the case even when the harrier does not pursue the disturbed flock. At present we are attempting to determine how these shifts in behavior affect energy flow through the avian community. The possibility exists that this indirect, disruptive effect approaches the direct trophic effect of harriers on the marsh. These observations, as well as those of Myers (1980) who described dramatic shifts in the social behavior of foraging Sanderlings with the appearance of a Merlin Falco columbarius, clearly illustrate that avian consumers can affect their prey bases indirectly (i.e. behaviorally) as well as directly (i.e. via consumption).

All of this points out that simulation models are but a first step in understanding the role of birds in estuaries. As yet, we cannot even be certain of how far we are from our ultimate goal, because of the uncertain magnitude of indirect effects. How quickly we proceed depends not only on assessing both direct and indirect effects but also on our ability to establish a common currency that can combine them in a meaningful, quantitative fashion.

Table 2. Five dominant types of shorebirds on the North Inlet marsh.

| | Number of individuals | Biomass | Caloric Consumption | |
|---|---|---|---|---|
| Winter | DOW[a] (42)[b] | DOW (36) | DOW (44) | |
| | DUN (18) | AOY (25) | BBP (44) | |
| | BBP (11) | BBP (19) | AOY (13) | |
| | SAN (10) | DUN (8) | DUN (12) | |
| | YEL (6) | YEL (5) | YEL (6) | [a]DOW = Dowitcher spp., DUN = Dunlin, |
| Spring | DOW (29) | DOW (26) | DOW (25) | YEL = Greater and Lesser Yellowlegs, |
| | DUN (24) | BBP (19) | BBP (16) | BBP = Black-bellied Plover, |
| | BBP (11) | DUN (11) | DUN (16) | AOY = American Oystercatchers, |
| | SAN (8) | AOY (11) | WIL (9) | SAN = least, Semipalmated and Western Sandpipers, |
| | YEL (7) | WIL (10) | YEL (7) | WIL = Willet, SPP = Semipalmated Plover. |
| Summer | DOW (55) | DOW (51) | DOW (52) | [b]Percent of shorebird community. |
| | SAN (17) | AOY (17) | WIL (11) | |
| | SPP (9) | WIL (11) | AOY (11) | |
| | WIL (6) | BBP (5) | SAN (8) | |
| | AOY (3) | SPP (5) | SPP (6) | |
| Fall | DOW (43) | DOW (37) | DOW (45) | |
| | SAN (20) | AOY (32) | AOY (18) | |
| | DUN (11) | BBP (12) | BBP (10) | |
| | BBP (7) | DUN (5) | DUN (8) | |
| | AOY (6) | SAN (4) | SAN (6) | |
| Annual Mean | DOW (43) | DOW (38) | DOW (41) | |
| | SAN (14) | AOY (21) | AOY (12) | |
| | DUN (13) | BBP (13) | BBP (12) | |
| | BBP (7) | WIL (7) | DUN (9) | |
| | SPP (6) | DUN (6) | WIL (6) | |

## NUMBER OF BIRDS
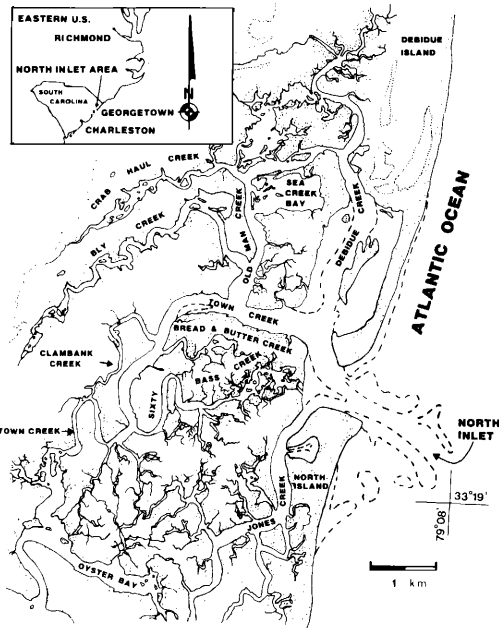


## DAILY CALORIC CONSUMPTION (kcal x 10⁶)

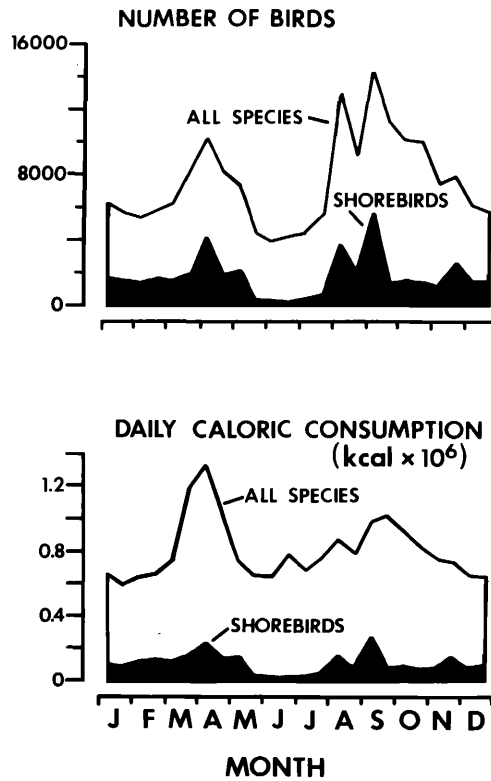Figure 1. Map of the 3000 hectare North Inlet marsh.

Figure 2. Seasonal fluctuations in the number of birds and in avian induced energy flow on the North Inlet marsh. Shorebird contributions are indicated in black.

Table 3. Seasonal and annual summaries of shorebird numbers, biomass, and caloric consumption.

|  | Number of individuals | Biomass (kg wet weight) | Caloric Consumption (kcal x 10³/day) |
|---|---|---|---|
| Winter | 1605(28)[a] | 212(12) | 117(17) |
| Spring | 2082(27) | 263(10) | 140(14) |
| Summer | 1759(21) | 216(9) | 90(11) |
| Fall | 1605(20) | 212(11) | 103(14) |
| Annual Mean | 1765(23) | 224(10) | 109(13) |

[a]Percent of avian community

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# TERRITORIALITY OF WHIMBRELS *NUMENIUS PHAEOPUS HUDSONICUS* WINTERING IN PANAMA

## by Elizabeth P. Mallory

Several workers have concluded that behavioral and ecological differences between closely related and/or ecologically similar shorebirds on the wintering grounds have evolved to minimize competition among migratory species, or between migratory and resident species (Ashmole 1970; Baker & Baker 1973). Marked geographic isolation has been found among ecologically similar migrants, or migrants and residents (Myers 1980a), and this pattern probably evolved as a response to competitive pressures in the past.