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Shorebird Predation on Eggs of Horseshoe Crabs During Spring Stopover on Delaware Bay

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Most species of shorebirds migrate long distances and stop at only a few selected sites (stopovers) to replenish fat deposits that will fuel the remainder of the migratory flight (Myers 1983, Davidson 1984, Senner and Howe 1984, Myers et al. 1987, Piersma 1987). Since great numbers of individuals utilize these stopovers for fattening, it is likely that the collective energy consumption by shorebirds at these stopovers must be large. Delaware Bay located between the states of Delaware and New Jersey in the eastern United States (38°47'N to 39°20'N and 74°50'W to 75°30'W; Clark et al. 1993) is one of these sites in spring. It hosts hundreds of thousands of shorebirds that feed primarily on the eggs of the horseshoe crab (*Limulus polyphemus*; Myers 1986). Birds arrive in synchrony with the horseshoe crabs, which emerge from the sea and lay their eggs in beaches during high tide (Shus-

ter and Botton 1985). As many as 420,000 shorebirds (peak count of all species combined for a 160-km shoreline) have been recorded in a given year (Dunne et al. 1982). A thorough description of Delaware Bay can be found in Clark et al. (1993).

We calculated the total energy consumption by shorebirds during their spring stopover at Delaware Bay by estimating the total energy requirements (energy expenditure and fat deposition), and correcting for the assimilation efficiency of ingested food. Basal metabolic rates (BMR) were calculated using the equations for shorebirds of Kersten and Piersma (1987), which take into account the relatively high BMRs of shorebirds (Castro 1987, Kersten and Piersma 1987, Mathiu et al. 1989). Total energy expenditure was calculated by assuming that the daily energy expenditure is equivalent to 2.5 BMR. This is the average

TABLE 1. Total energy requirements by shorebirds during their spring stopover at Delaware Bay.

Species	Lean mass[a]	BMR[b]	TEE[c]	Energy in fat[d]	Cost of fat[e]	TER (ind)[f]	Popu-lation[g]	TER (pop)[h]	TEC[i]	Eggs inges-ted[j]
Arenaria interpres	101	3.42	4,309	2,646	3,006	7,315	90,360	660.9	1,712	167.0
Calidris canutus	135	4.23	5,329	3,555	4,039	9,368	95,530	894.9	2,318	226.1
C. pusilla	25	1.23	1,549	632	718	2,267	174,233	394.9	1,023	99.8
C. alba	50	2.05	2,583	1,303	1,480	4,063	38,529	156.5	405	39.5
Limnodromus spp.	100	3.39	4,271	2,607	2,962	7,233	2,150	15.5	40	3.9
C. alpina	55	2.19	2,759	1,422	1,615	4,374	2,400	10.5	27	2.6

[a] Grams. Unpublished data.
[b] Basal metabolic rate (kJ/h) after Kersten and Piersma (1987).
[c] Total energy expenditure (kJ) = 21 days (24 h) (2.5 BMR).
[d] Energy in fat (kJ), assuming fat index of 40% (fat/total body mass).
[e] Total cost of fat deposition (kJ) = energy in fat/efficiency of fat deposition.
[f] Total energy requirements per individual (kJ) = TEE + cost of fat.
[g] Population size per species (maximum count; Dunne et al. 1982).
[h] Total energy requirement by each species (kJ $\times$ 10^6). Total for all species is 2,133.2 kJ $\times$ 10^6.
[i] Total energy consumption (kJ $\times$ 10^6), assuming an assimilation efficiency value of 38.6% (Castro et al. 1989a, b). Total for all species is 5,526 kJ $\times$ 10^6.
[j] Metric tons. Total for all species is 538.9 metric tons.

value as measured by doubly-labeled water (Castro 1988) for Sanderlings (*Calidris alba*) at different latitudes, and it is the mean value recommended by Drent and Piersma (1990) after reviewing the available literature for shorebirds. Assuming that the average stopover period is about three weeks (Myers 1986, pers. obs.) we obtained the total energy expenditure by multiplying 2.5 BMR by 21 days. The energy stored as fat was calculated by assuming that shorebirds depart Delaware Bay with a fat index of 40% (fat/total body mass), and that the energetic equivalent of fat is 39.5 kJ·g^{-1} (Ricklefs 1974). Because the efficiency of fat deposition in shorebirds is 88% (Kersten and Piersma 1987), the energetic equivalent of the fat deposited was divided by 0.88. The total cost of fat deposition (energetic equivalent plus efficiency of deposition) was then added to the total energy expenditure to obtain the total energy requirements. The total energy requirement for each species was then obtained by multiplying this value by the population of each species, based on aerial census results (maximum counts; Dunne et al. 1982).

Total energy consumption was calculated by dividing the total energy requirements by the assimilation efficiency value of 38.6% (for Sanderlings feeding on horseshoe crab eggs; Castro et al. 1989a). We assume that the value of assimilation efficiency is similar for all species, since assimilation efficiency seems to be primarily a function of food consumed (Castro et al. 1989b). The total mass of eggs ingested is the total energy ingested divided by the caloric equivalent of eggs (wet mass, 10.25 kJ·g^{-1}; Castro et al. 1989a).

Two species (Dunlin [*Calidris canutus*] and Ruddy Turnstone [*Arenaria interpres*]) account for more than 70% of all the energy consumed, even though their populations represent only 38% of the total (Table 1). All species of shorebirds combined require 2,133 $\times$ 10^6 kJ during their spring stopover at Delaware Bay.

Table 1 shows the total energy consumption by species. All shorebirds consume 5,526.2 $\times$ 10^6 kJ, equivalent to approximately 539 metric tons of horseshoe crab eggs.

Because a large female horseshoe crab lays on average 296.4 g of eggs (Shuster and Botton 1985), the total number of females needed to lay the eggs consumed by the shorebirds is approximately 1,820,000, which could be considered a minimum estimate of the female population. Shuster and Botton (1985) calculated a minimum population of 222,000 females during 1977 for Delaware Bay, but suggested that the actual population was probably much larger because this estimate was based on a single spawning event, even though several spawning events are known to occur. Also, their estimate did not take into account crabs that were in shallow waters but not visible. Therefore, this estimate confirms their supposition of a much higher population than 222,000 females. However, these calculations assume that shorebirds feed exclusively on eggs. It is likely that they actually supplement their diet with the ingestion of other food items during their three week stopover (Botton 1984), therefore lowering the consumption of eggs.

Other possible sources of error in our calculations are the assumption that all species depart with a fat index of 40%. This will provide enough energy to fuel a migratory flight of about 4,000 km for most species, sufficient to reach 70°N (Castro and Myers 1989), but the actual amount of fat deposited depends on the final destination, as well as the amount of fat that will remain after the flight. Also, we assume that the increase in body mass is due exclusively to fat deposition, although in several cases significant amounts of protein are also stored (Piersma and Jukema 1990, Piersma and van Brederode 1990).

We analyzed the sensitivity of the estimate of energy consumption when different variables are

changed (Fig. 1). Four variables (population size, BMR, DEE and total fat deposited) were changed up to 50%, with the exception of fat, which was increased only 20% for a total fat content of 50% (fat/total body mass). The model is more sensitive to changes in population size, less sensitive to changes in BMR or DEE, and least sensitive to changes in total fat deposited. Errors in the estimate of population size of up to 50% produce changes in the estimate of total energy consumption well within the same order of magnitude, varying from 280 to 810 metric tons of horseshoe crab eggs. Given the data available to date, therefore, we believe that these results (539 metric tons of horseshoe crab eggs) provide a good approximation of the total energy requirements of shorebirds during spring migration at Delaware Bay. However, if the errors in the sensitivity analysis occur in the same direction, then the accuracy of our estimate would change in a multiplicative fashion.

We did not incorporate estimates of shorebirds' turnover at Delaware Bay because this will not alter the energetic calculations. Even if turnover rates are important, the total number of birds at any given time will remain constant, and the consumption will be the same, regardless of which individuals are actually utilizing the eggs.

The total energy flow at beaches in Delaware Bay during these three weeks can be calculated by assuming that the total beach length at Delaware Bay (New Jersey and Delaware sides) is 160 km (Dunne et al. 1982) and that the average beach width where the egg spawning occurs is 10 m (Shuster and Botton 1985), for a total area of 1.6×10^6 m^{-2}. The energy flow, therefore, is:

$$(5{,}530.3 \times 10^6 \text{ kJ}) \cdot (1.6 \times 10^{-6} \text{m}^{-2}) \cdot (21 \text{ day}^{-1})$$

$$= 164 \text{ kJ} \cdot \text{m}^{-2} \cdot \text{day}^{-1}.$$

This is much greater than values previously reported for shorebirds throughout the annual cycle (e.g. 0.01 kJ·m^{-2}·day^{-1} in South Carolina [Bildstein et al. 1982]; 0.21 kJ·m^{-2}·day^{-1} in the Wadden Sea [Smit 1981]; 0.23 kJ·m^{-2}·day^{-1} in South Africa [Puttick 1980]; 5.14 kJ·m^{-2}·day^{-1} in South Carolina [Grant 1981]). We believe that the high value of energy flow we obtained is the result of the peculiarity of this resource (horseshoe crab eggs), which is spatially and temporally concentrated in Delaware Bay, and attracts great numbers of shorebirds.

This high energy consumption and energy flow clearly shows the importance of Delaware Bay to migrating shorebirds, and implies that shorebird spring stopover might be a crucial and very important segment of the annual cycle of both birds and horseshoe crabs. It also demonstrates that the conservation of this and other stopovers is critical for a conservation plan for migratory shorebirds (Myers et al. 1987).

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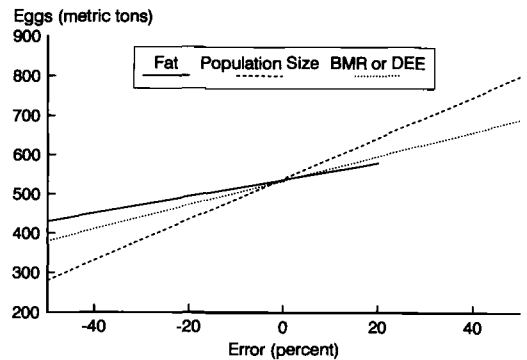

Fig. 1. Sensitivity analysis estimate of energy consumption by shorebirds at Delaware Bay. Energy consumed (expressed in metric tons of horseshoe crab eggs) plotted as function of possible errors (in %) in estimates of population size, BMR or DEE, and total fat deposited.

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Natal Dispersal and First Breeding Age in Monk Parakeets

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Between 1983 and 1988 an intensive study on population dynamics and behavior of the Monk Parakeet (*Myiopsitta monachus*) was carried out by the Centro de Zoología Aplicada, University of Córdoba. The Monk Parakeet is unique among parrots in building its own nest of sticks. Often the nest is integrated into a compound nest (Forshaw 1978) or lodge; these deserve attention because collaboration in nest building represents an important form of helping (Brown 1987).

Reduced natal dispersal and delayed breeding also are considered important determinants of helping by favoring the accumulation of a surplus of nonbreeding individuals (Brown 1978). Natal dispersal and age at first breeding is of particular interest in Monk Parakeets because the species shows at least some characteristics that suggest it is a communal breeder. Indications of an incipient degree of allofeeding also have been found in the Monk Parakeet by Martella (1985) and Emlen (in press). Our paper concerns adult movement, natal dispersal and age at first breeding and their implications in the evolution of communal breeding.

Methods.—Fieldwork was carried out between 1983 and 1988. The study area was about 600 ha of natural and cultivated pasture with patches of forest located near the town of Jesús María, Province of Córdoba, Argentina (31°05′S, 64°11′W).

Adults and young were censused three times a year: before the breeding season (September), after this season (March), and in winter (June). Total population counts were obtained by trapping birds from the nests at night using a specially designed funnel net (Martella et al. 1987) placed below each nest entrance, supplemented by direct observations during the day.