EDITORIAL

We are inaugurating a series of articles on speculative notions in shorebird biology, of which the following article by David Schneider is the first. Whereas we do not necessarily agree with all the ideas or concepts which may be set out in the articles - nor indeed some of the statements made - we hope that their publication will stimulate debate and dicussion on the topics presented. We invite readers of the Bulletin to respond either through presentation of their own ideas, provocative or otherwise, or through commentary or criticism of subjects under debate - N.A. Editors.

FOOD SUPPLIES AND THE PHENOLOGY OF MIGRATORY SHOREBIRDS: A HYPOTHESIS

by David C. Schneider

The topic of bird migration has a history of speculation that extends back beyond Aristotle, although Belan, in 1517, appears to have been the first person to subject any of these ideas to the indignity of a test (Dorst 1956). The topic apparently escaped Darwin's curiosities, but Wallace (1874) attributed the phenomenon to the agency of natural selection. Once broached, the idea dropped from sight, and subsequent debate focused on the evolutionary history of a trait with no fossil record (cf. Clarke 1912; Wetmore 1927). The idea was resurrected when Lack (1960) made the distinction between proximate causes (how is migration accomplished?) and ultimate or evolutionary causes (why does it occur?). Subsequent work in North America has dealt largely with the orientational mechanisms used by birds to accomplish their migrations (e.g. Emlen 1975; Gwinner 1977).

The absence of American studies on ecological forces shaping migratory patterns is not for lack of hypotheses. There are two types of explanation. The first emphasize the strategic gains from migration, especially those in moving from one abundant food resource to the next. Examples include Cooke's (1910) explanation of the movements of the Golden Plover in North America and Dorst's (1974) illustration of the seasonal coincidence of food abundance and the abundance of the Wood Sandpiper Tringa glareola through its life cycle. Similar explanations have been offered for other vertebrates, for example Plaice (Kuipers 1977).

The second type of explanation emphasizes the tactical constraints and costs associated with migration. Examples include the placement of stopover areas before crossing an ecological barrier (Odum et al. 1961), hawk migration along mountain ridges, and the observation that small trans-Atlantic migrants from North America head out to sea in the fall with the prevailing northwest winds, then shift to a southwesterly course at about the latitude of Bermuda, riding the trade winds to South America. A better understanding of the interaction between the constraints of time and energy and food availability will be needed to gain an understanding of the ultimate causes of bird migration.

Migratory shorebirds are relatively well studied with respect to food supplies, permitting a preliminary look at the role of food supplies in the migratory patterns of this group. I focused on three aspects: (1) the transitory nature of food supplies; (2) the role of birds in causing prey declines; and (3) the degree of association between the phenology of food supplies and the placement and timing of shorebird movements.

Migratory shorebirds are creatures of open habitats - tundra, prairies, salt flats, tidal marshes and flats, and even the sea surface itself. Shorebirds feed primarily on intertidal invertebrates and semi-aquatic insects (Forbush 1925; Bent 1929). The productivity of these groups is highly seasonal at temperate and arctic latitudes (Russell-Hunter 1970; Edmundson and Winberg 1971). Seasonal fluctuations in density are evident in the limited number of studies of tropical intertidal fauna (Green 1968; Smith 1975; Kaufman 1976).

Declines in food abundance, during those seasons when shorebirds are present, have been reported from temperate latitudes ranging from southern California (Quammen 1980) to northern Britain (Goss-Custard 1969). Reports of food depletion within this latitudinal range are frequent (Goss-Custard 1977; O'Connor & Brown 1977; Schneider 1978; Evans et al. 1979). Losses were found in five successive years at a migratory stopover in Massachusetts (Harrington et al. 1976; Harrington & Schneider 1978; Schneider & Harrington 1980).

The frequency of these reports, immediately south of the breeding range of most species, stands in contrast to the situation on Nearctic breeding grounds. At Barrow Point, in Alaska, breeding begins in June but fly availability does not decrease until late July (MacLean & Pitelka 1971). The only reported case of food depletion on the breeding grounds is that of Bengtsen et al. (1976). This case is unusual in that the prey were lumbricids, rather than the anthropods that make up the bulk of the diet in breeding shorebirds. Food depletion was not found at two tropical wintering localities: Panama (Schneider, in prep) and Peru (Duffy et al. 1981).

The role of birds in reducing food supplies has been investigated by a variety of techniques. Evans et al. (1979) showed that the caloric demand by shorebirds was sufficient to make a large contribution to observed declines. Bengtsen et al. (1976) and Schneider (1978) showed that declines did not occur in areas protected from shorebird predation. At least three techniques have been developed to separate the effects of bird predation from the effects of other predators. A canopy of wide mesh wire reduced foraging activity by shorebirds and produced significant treatment effects (greater density inside than outside the canopy, relative to differences at the start of the experiment) at a site in Peru (Duffy et al. 1981). However, canopies do not necessarily exclude all birds, and thus are suspect as experiments unless observed frequently. Bloom (1980) developed a cage with sides that rise under water, excluding birds at low tide while allowing predator access at high tide. Quammen (1980) used floating cages in two southern California bays to show that shorebirds made a significant contribution to prey losses at some sites. Quammen used sham cages to control for the effects of siltation and changes in current strength on invertebrate densities.

Detailed studies of the seasonal abundance of shorebirds relative to the seasonal abundance of foods are lacking. A figure presented by Dorst (1974, p.649) suggests a strong correlation between the phenology of the Wood Sandpiper and its food supplies. Quammen (1980) did find increases in the density of invertebrates in a tidal flat during spring, when shorebirds reached a peak in abundance.

The relation between prey and predator phenology appears to be stronger at the scale of months than at the scale of weeks. For example, shorebirds breed during the short arctic summer, but at the scale of weeks it is evident that the adults of many species depart before any major decrease in food availability (Pitelka 1959). At a wintering ground in Panama, shorebirds reached a peak in abundance during the dry season (January to mid-April), a period of rapid growth of intertidal invertebrate populations. However, shorebirds departed in April, before any major drop in the average density of intertidal animals (Schneider, in prep).

At least three sets of factors would tend to reduce the correlation between shorebird phenology and food supplies at the scale of weeks: weather patterns, cross-seasonal interactions, and spatial or temporal variability pf prey. Weather patterns introduce some variability at the scale of days, since the arrival and departure of large numbers of birds coincide with passage of weather fronts (cf. review by Richardson 1978). At a migratory stopover in Massachusetts the exact dates of arrival, peak numbers, and departure changed from year to year, but the week to ten-day periods during which these events took place were remarkably stable from year to year (Harrington & Schneider 1978

The timing of departure may also be affected by cross-seasonal interactions (Myers 1981), including the availability of food at a subsequent location along the migratory route (Schneider & Harrington, in prep). Discrepancies between the timing of departure and the timing of decrease in food supplies are especially likely in predators whose success depends upon widely separated sources of food.

Spatial variability of food supplies at any one location may also condition the phenology of shorebirds. If shorebirds face some constraint on their food intake, such as low average prey densities or limited periods of tidal exposure, then the abundance of high density patches may be more important than the average density of food within an area (Schneider & Harrington 1980). Seasonal changes in patchiness may be at least as important to shorebirds as seasonal changes in average prey density.

Year-to-year variability in either abundance or patchiness may also be important in shaping the phenology of migratory shorebirds. During an investigation of the abundance of shorebird prey, MacLean & Pitelka (1971) found that emergence of flies occurred before, rather than during, the period of maximum average temperature at Barrow, Alaska. Subsequentl Myers & Pitelka (1979) suggested that this is due to the increased probability of freezing temperatures after late July, despite higher average temperatures. Similar considerations of year-to-year predictability may apply to the birds that feed on these insects, especially if the period of maximum average insect numbers is not a period of low year-to-year predictability in numbers.

Having distinguished between large scale (monthly) and fine scale (weekly) patterns in migratory timing, I predict that three patterns will explain most of the large scale movements of shorebirds in the New World. These are:
1. The poleward movement of warmer weather, resulting in a freezing of aquatic and semi-aquatic habitats and in a vernal or summer bloom of invertebrates.
2. A similarly poleward moving bloom of benthic marine invertebrates, lagging behind the terrestrial bloom. The timing of this bloom in eastern North America can be seen in Table 1.
3. The location of tropical upwellings, and the seasonal winds that carry aquatic detritus onshore to intertidal benthic communities.

These patterns yield several predictions. One is that the poleward movement of most species will be by a more gradual drift than the return, which will be "clumped" at the point where post-breeding shorebirds encounter the poleward moving bloom. Thus, in North America, one would predict a less aggregated distribution of shorebirds during northward movement in the spring, and a more aggregated distribution during southward movement after breeding. A similar prediction may be made for those species that move into the temperate latitudes of South America during the austral summer. Another prediction is that birds will tend to shift from terrestrial to marine habitats toward the end of the summer, due to the lag in marine productivity, whether the birds are in the northern or the southern hemisphere.

A final prediction is that shorebirds in the tropics will be concentrated in areas where productivity is enhanced by local upwellings. The major tropical upwellings in the New World are along the coast near Surinam and Venezuela (Schott 1931a, 1932b), Peru and northern Chile (Gunter 1936a, b) and the Gulf of Panama (Schott 1931b, 1935). Shorebirds do show seasonal movements in the tropics, based on phenological data presented by Spaans (1978). One would predict that the phenology of shorebirds at tropical locations, as at any other, will reflect the relation of prey to the seasonal production and movement of organic material to intertidal areas.

Phenological studies represent a first step in testing the hypothesis that shorebird migration is driven by global patterns in the productivity of invertebrates, through the agency of natural selection on traits such as timing, direction, and length of migration. Direct confirmation of this hypothesis requires demonstration that these traits have a heritable component, and that individual birds that deviate from the mean value for these traits suffer a lowered survivorship.

Table 1. Months of peak abundance of benthic infauna along the Atlantic coast.

Location	Habitat	Peak abundance	Source
Georgia	shallow subtidal	Jan-Feb	Frankenberg (1971) Thalassia Jugosl. 7:49
Georgetown, S.C.	intertidal sand	Dec-April	Holland and Polgar (1971) Mar. Biol. 37: 341
Pamlico River, N.C.	shallow subtidal	March-April	Tenore (1972) Ecol. Monogr. 42: 51
Newport River, N.C.	intertidal mud	March-April	Commito (1976) Ph.D. diss., Duke University
Assateague Island, Va.	intertidal flats	June	Woodin (1978) Ecol 59: 274
York River, Va.	shallow subtidal	June-July	Virstein (1977) Ecol. 58: 1199
Rehobeth Bay, Del.	shallow subtidal	May-June	Watling (1975) J. exp. mar. Biol. Ecol. 19: 27S
Long Island Sound, Conn.	shallow subtidal	late May	Myers (1977) J. mar. res. 35: 609
Long Island Sound, Conn.	subtidal	May-June	McCall (1977) J. mar. res. 35: 221
Barnstable Harbor, Mass.	intertidal flats	June-July	Whitlatch (1977) Biol. Bull. 152: 275

The hypothesis that shorebird migration is driven by spatial-temporal patterns in food productivity has some important implications for the conservation and well-being of these populations. If shorebirds are meeting the demand for a relatively continuous food supply by an evolutionary adjustment of their itineraries to the seasonal production of food supplies, then the survival of migratory species may depend upon a sufficient number of habitats to carry shorebirds through their life cycle. Field tests of this hypothesis become interesting in the context of the management of migratory populations, as well as in the context of the theory of migration.

Acknowledgements

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