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WHY FLY BY NIGHT? INFERENCES FROM TIDALLY-INDUCED MIGRATORY DEPARTURES OF SANDPIPERS

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Abstract.—Semipalmated Sandpipers (*Calidris pusilla*) usually begin long-distance autumnal migratory flights in the evening, although some flocks depart earlier in the day. At a coastal location, morning and early afternoon departures coincided with ascending tides that flooded feeding areas. The hypothesis that the daily timing of migration evolved to maximize the foraging opportunities of migrants predicts tidally-induced departures, whereas specific proposed advantages to nocturnal flight do not. Foraging considerations thus appear to be the primary selective force favoring night flight in this species.

¿POR QUÉ VOLAR DE NOCHE? INFERENCIAS SOBRE SALIDAS DE PLAYEROS INDUCIDAS POR MAREAS

Resumen.—*Calidris pusilla* usualmente comienza sus largos vuelos migratorios de otoño por las noches, aunque algunas bandadas salen temprano en el dia. En una localidad costera, las salidas de mañana y temprano en la tarde coincidieron con el subir de la marea que inundaba áreas de alimentación. La hipótesis de que la migración evoluciona para ajustarse diariamente a maximizar las oportunidades de forrajeo predice salidas inducidas por mareas, mientras ventajas específicas propuestas para vuelos nocturnos no. Consideraciones de forrajeo parecen ser una fuerza selectiva primaria que favorece vuelos nocturnos en esta especie.

Twice a year many migratory birds undergo a profound change in their daily activity rhythms and become active at night. Brewster (1886) tabulated types of birds that migrated by day, night, or both, and suggested that:

> "Timid, sedentary, or feeble-winged birds migrate at night because they are either afraid to venture on long, exposed journeys by daylight, or unable to continue these journeys day after day without losing much time in stopping to search for food. By taking the nights for traveling they can devote the days entirely to feeding and resting in their favorite haunts" (p. 20–21).

Wading birds, he continued,

> "migrate indifferently, and more or less equally, by both night and day. This again was to be expected when we consider that they feed . . . more or less indifferently and freely at all hours, and are not accustomed to seek safety in concealment."

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Brewster's conclusion, from comparative study, that maximizing diurnal foraging time was the selective force determining the timing of migratory flight in many species remains the dominant general hypothesis a century later (Baker 1978, Griffin 1964), but selective advantages to nocturnal flight have also been proposed. Nocturnal migration allows birds to fly under less turbulent and cooler conditions. Flight through smoother air may reduce energy consumption (Bellrose 1967, Nisbet 1955). Flying in cooler air saves water, which might, rather than energy, limit flight range (Berthold 1975, Dorka 1966, Torre-Bueno 1978, Yapp 1956). Finally, evening departures and nocturnal migration allow use of stars, the setting sun, and unique patterns of polarized light at sunset for orientation or navigation (Moore 1987). If these cues are necessary (Moore 1980), the timing of migration would be constrained.

I documented the diurnal pattern of autumnal migratory departures of flocks of shorebirds, primarily Semipalmated Sandpipers (*Calidris pusilla*). Birds were studied at a coastal site, where foraging opportunities were limited for several hours twice each day when tides covered mudflat feeding areas, and at an inland site of comparable latitude where no tidal interruption occurred. If foraging opportunities regulate daily timing of migration, in a proximate or ultimate sense, or both, migratory departures would be expected to coincide with tidal inundation. Observations at the inland site provide a partial control against which behavior at the coast may be evaluated.

METHODS

Presumed migratory departures of Semipalmated Sandpipers were observed near Sibley Lake, North Dakota (46°57'N, 99°43'W), daily between 13 Jul. and 27 Sep. 1978, and on Kent Island, New Brunswick (44°35'N, 60°27'W), in the Bay of Fundy, daily between 11 Jul. and 23 Sep. 1977. Both sites provided relatively discrete patches of foraging habitat for migrant shorebirds. At Kent Island birds changed foraging locations several times each day, as two 12.1 hour cycles of 4.1–5.3 m tides covered and uncovered mudflats.

A migratory departure was scored when a flock flew upwards and directly away from the study site, and continued ascending until it vanished from view against the sky (cf., Van Tyne and Trautman 1945). Flocks were followed with 9× binoculars or a 15–60× spotting scope. Cases where flocks descended while still in view or flew too low to disappear against the sky were not included. Departures were without exception noisy, with birds calling continuously as they flew.

The time of the departure and the disappearance compass bearing were recorded. Disappearance direction was not considered in judging whether a departure occurred; however, all departures at both locations were to the south or southeast (Lank 1983), the appropriate migratory direction for Semipalmated Sandpipers at that latitude in autumn (Lank 1979, Morrison 1984, Richardson 1979), and most departures occurred on days when winds favored southeasterly flight (Lank 1983). Birds flying southeast of Kent Island may have landed on the southwest shore of Nova Scotia, across the Bay of Fundy, but most of them probably continued on their transoceanic flight to the Lesser Antilles or South America. Grimes (1974), working in West Africa, confirmed with simultaneous radar observations that shorebird departures similar to those I observed were the beginnings of long-distance flights.

Departures could have been seen any time I was in the field. At Sibley Lake, observations were made between 0600–0800 and 1800–2100 on 80%–90% of the days, and on 60–70% of the days at other daylight hours. At Kent Island observations were made between 0600 and 0800 on 20% of the days, and from 40–60% of the days at other daylight hours through 2100. I have not adjusted the observed departure frequencies to reflect hourly variation in observer effort, however, since departures were non-randomly distributed among days, and weighting under a model which assumed randomness among days would distort the pattern more than not doing so.

RESULTS

Times were recorded for 63 departures on 20 different days at Sibley Lake, and those of 55 departures on 16 days at Kent Island. In North Dakota, departures occurred primarily during the hour just prior to sunset, although a few were scattered throughout the day (Fig. 1). At Kent Island, the hourly pattern was more variable, with a mode 2 h before sunset (Fig. 2A). The timing of departures at Kent Island was also non-random with respect to daily tidal cycles (Fig. 2B). Few flocks left at low tide, with the bulk departing as feeding areas were flooded on the ascending tide.

The strong tides of the Bay of Fundy completely inundated sandpiper foraging habitat for 2–3 h each day, and much of the foraging flats around Kent Island were covered for 6–8 h on either side of the highest tides. As the tide rose, many birds flew from earlier-flooded areas and continued foraging at later-flooded sites, but departures also occurred when birds took flight at this time. The dearth of departures 3 h prior to high tide (Fig. 2B) corresponds to a period when birds foraged at an isolated bay that remained unflooded after the rest of the island's mudflats were covered. No departures were observed in the final hour prior to high tide, by which time birds had moved to roost sites or left the island.

The relationships between tidal cycle, sunset, and sandpiper departures over the course of the season at Kent Island are summarized in Figure 3. The clustering of departures on certain days was related to prevailing weather conditions (Lank 1983). All departures early in the day were associated with ascending tides, while departures prior to sunset occurred on descending or low tides. Departures were observed latest in the day when falling or low tides coincided with sunset (31 Jul.; 15, 21, 30 and 31 Aug.). On 15 and 30 Aug. departures occurred during both pre-high tide and sunset departure windows.

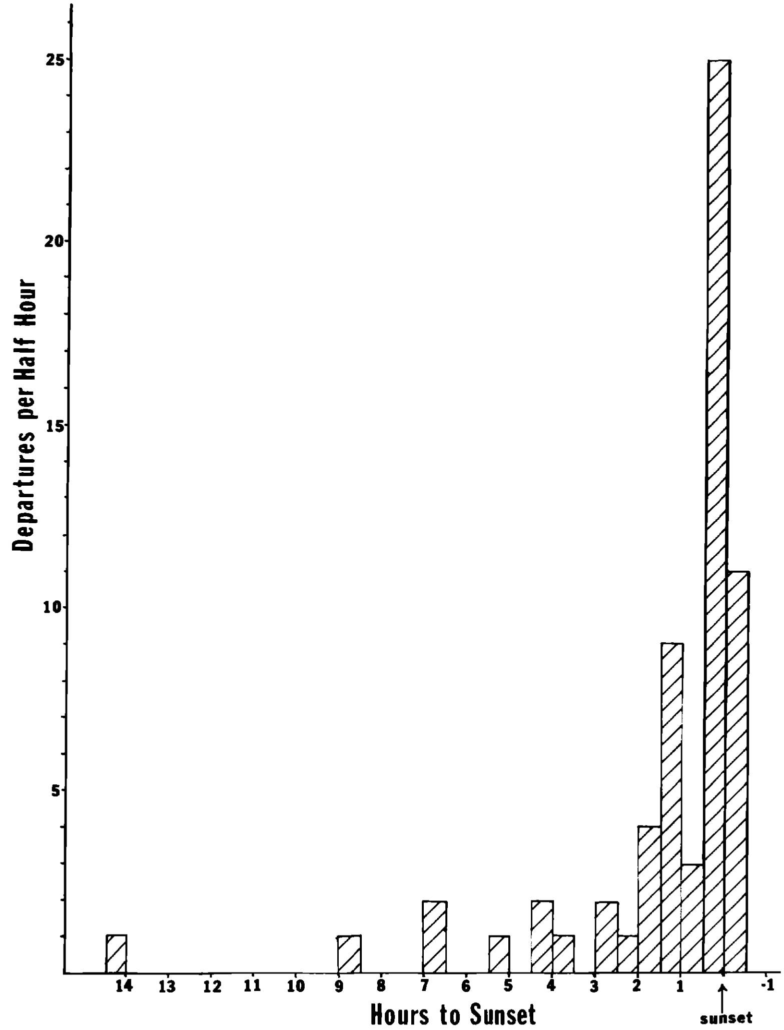

FIGURE 1. The temporal distribution of autumnal migratory departures of sandpipers relative to sunset, at Sibley Lake, North Dakota, 1978.

DISCUSSION

The influence of tide on migratory departures of birds has not been quantified previously (Richardson 1978). In their pioneering radar study on Cape Cod, however, Drury and Keith (1962: p. 473) wrote that the maximum density of shorebird echos "coincides with rising tide, and echo counts rise during the afternoon to a peak one to two hours before sunset." This matches almost exactly the pattern shown in Figure 3.

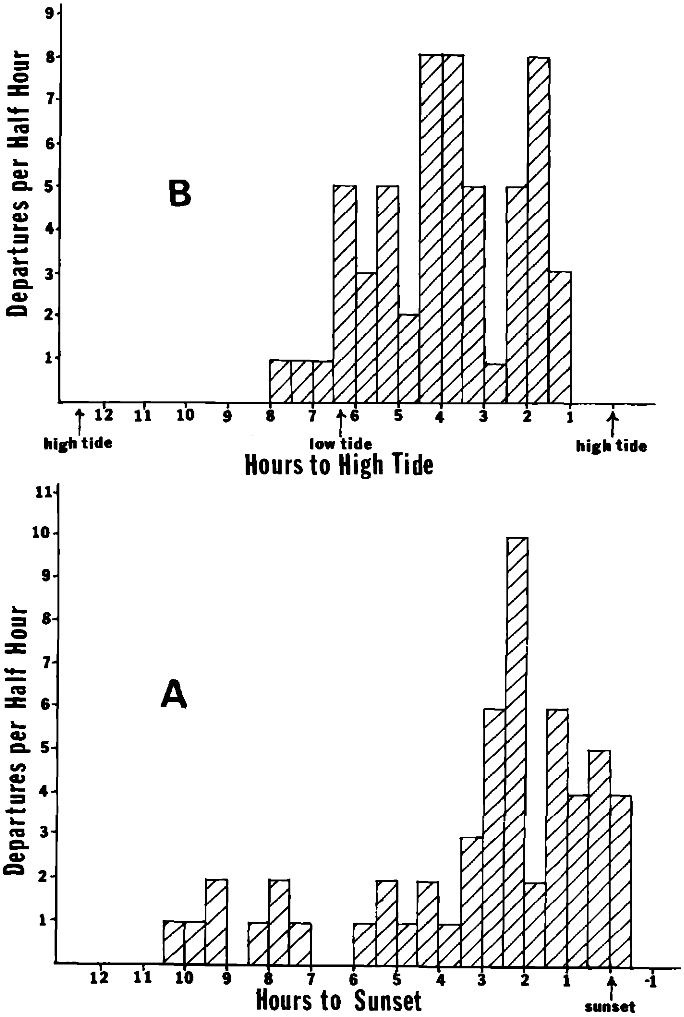

FIGURE 2. The temporal distribution of autumnal migratory departures of sandpipers relative to sunset (A) and tidal cycle (B), at Kent Island, New Brunswick, 1977.

The departure pattern on the coast provides a unique source of data consistent with Brewster's (1886) feeding priority hypothesis to explain why many types of birds migrate at night. The hypothesis involves two related, but separate propositions. The first is that birds migrate when their feeding efficiency would be relatively low. The second is that flying at night allows birds to conclude long flights when they can forage more efficiently, as opposed to landing with depleted stores when food was less available. Little can be said for Kent Island sandpipers with regard to

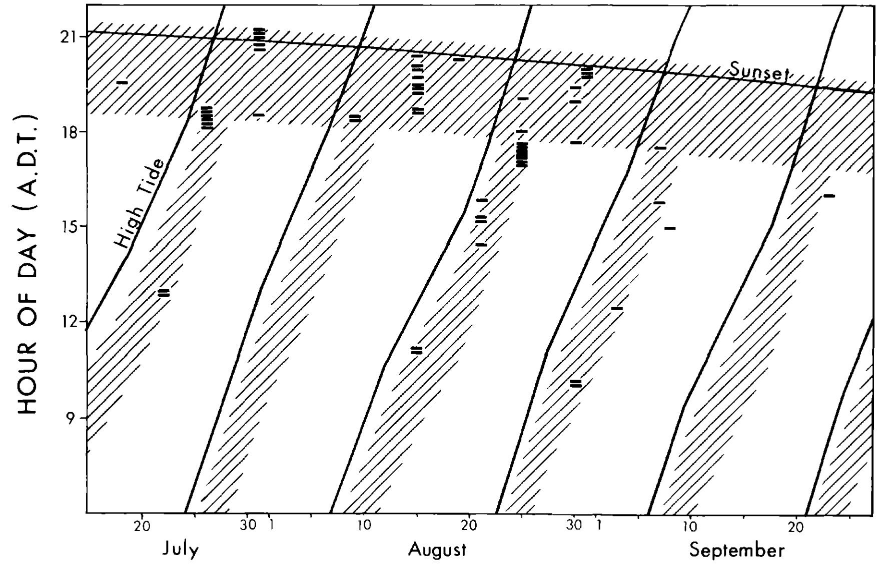

FIGURE 3. The timing of migratory departures of sandpipers from Kent Island, New Brunswick, relative to date, hour, sunset and tidal cycles. Each departure is marked with a short, horizontal black line. For graphical clarity, departures occurring within a short period of time are evenly spaced. Solid lines indicate the time of sunset or high tide as they changed each day throughout the season. Shaded areas are post-hoc daily "departure windows": ca. 3 h during the late ascending tide and 2 h around sunset.

this second point, since estimates of transoceanic shorebird flight times, and probably the flights themselves, range from 40–70 h (Stoddard et al. 1983).

Tidally-induced departures are consistent with the first presumption of the feeding priority hypothesis. Birds left when food became unavailable, just as occurs for many species at night. At Kent Island, sandpipers faced a 2–4-h period when food was in fact less available to them than during low tides during the night. The observations suggest that a lack of food availability overrode the potential advantages of evening departures mentioned in the introduction, even when sandpipers were beginning long-distance flights. Neither changes in turbulence or heat stress, nor the use of crepuscular cues, predict tidally-induced diurnal departures. Long-distance migrants may avoid dehydration by flying at altitudes sufficient to allow cooling without evaporative heat loss (Torre-Bueno 1978). Since sandpipers departing during the day were well-oriented (Lank 1983), sunset cues are apparently not necessary in this species. Given the diversity of orientational information used by different species (Keeton 1980) and even variability among individuals within species (Moore 1985), the use of crepuscular or nocturnal cues is probably a secondary adaptation to an unusual activity cycle ultimately driven by a diurnal feeding priority.

Inland, where tides are absent, sandpipers showed a sharp peak of departures during the hour before sunset (Fig. 1). The few exceptions were associated with particular meteorological conditions (Lank 1983). Increased migration of shorebirds around sunset has been quantified by radar studies at numerous coastal locations, including the Maritimes (e.g., Drury and Keith 1962, Evans 1968, Grimes 1974, Lack 1963, Richardson 1979), but comparable inland data are lacking. The coastal radar estimates of "large-echo" traffic rates are much less peaked than the Kent Island departure pattern (Fig. 2A), reflecting a pooling of migrants that begin their flights at different distances from the radar site.

Brewster stated that shorebirds foraged and migrated "more or less indifferently" both by day and night. Since sandpipers showed a preference for nocturnal migration, however, the feeding priority hypothesis is supported only if sandpipers feed less efficiently, or face greater predation risk, at night. In tidal situations, shorebirds often forage at night, including Semipalmated Sandpipers (Gratto et al. 1984, personal observation). No data on the relative efficiency of diurnal versus nocturnal foraging are available for Semipalmated Sandpipers. Sanderlings (*Calidris alba*) can assess prey density through probing alone (Gerritsen and Meiboom 1986), and increased nocturnal activity of prey species could make night foraging more efficient than diural foraging (e.g., Grey Plovers [*Pluvialis squatarola*] feeding on nocturnally active polychaete worms [Dugan 1981]). However, data from wintering populations show that shorebirds forage at night only when they are unable to meet their metabolic needs during the day (Pienkowski et al. 1984), implying that nocturnal foraging is less preferred. Decreased foraging opportunity is thus a common environmental feature of both tidal and sunset migratory departure windows (Fig. 3), and maximization of feeding opportunities is supported as a selective factor favoring nocturnal migratory flight.

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LITERATURE CITED

BAKER, R. R. 1978. The evolutionary ecology of animal migration. Holmes and Meier, New York.

BELLROSE, F. C. 1967. Radar in orientation research. Proc. Int. Ornithol. Congr. 14:281–308.

BERTHOLD, P. 1975. Migration: control and metabolic physiology. Pp. 77–128, *in* D. S. Farner, J. R. King, and K. C. Parkes, eds. Avian biology, v. 5. Academic Press, New York.

BREWSTER, W. 1886. Bird migration. Mem. Nuttall Ornithol. Club 1. Nuttall Ornithological Club, Cambridge, Massachusetts.

DORKA, V. 1966. Das jahres und tageszietliche Zugmuster von Kurz und Langstreckenziehern nach Beobachtungen auf den Alpenpassen Cou/Bretolet (Wallis). Ornithol. Beob. 63:165–223.

DRURY, W. H., JR., AND J. A. KEITH. 1962. Radar studies of songbird migration in coastal New England. Ibis 104:449–489.

DUGAN, P. J. 1981. The importance of nocturnal foraging in shorebirds: a consequence of increased invertebrate prey activity. Pp. 251–260, *in* N. V. Jones and W. J. Wolff, eds. Feeding and survival strategies of estuarine organisms. Plenum Press, New York and London.

EVANS, P. R. 1968. Autumn movements and orientation of waders in northeast England. J. Zool. 150:319–369.

GERRITSEN, A. F. C., AND A. MEIBOOM. 1986. The role of touch in prey estimation by *Calidris alba.* Neth. J. Zool. 36:530–562.

GRATTO, G. W., M. L. H. THOMAS, AND C. L. GRATTO. 1984. Some aspects of the foraging ecology of migrant juvenile sandpipers in the outer Bay of Fundy. Can. J. Zool. 62:1889–1892.

GRIFFIN, D. R. 1964. Bird migration. Doubleday, New York.

GRIMES, L. G. 1974. Radar tracts of palearctic waders departing from the coast of Ghana in spring. Ibis 116:165–171.

KEETON, W. T. 1980. Avian orientation and navigation: new developments in an old mystery. Pp. 137–157, *in* R. Nöhring, ed. Acta XVII Congr. Int. Ornithol. Deutsche Ornithologen-Gesellschaft, Berlin.

LACK, D. 1963. Migration across the southern North Sea studied by radar. Part 5. Movements in August, winter and spring, and conclusion. Ibis 105:461–492.

LANK, D. B. 1979. Dispersal and predation rates of wing-tagged Semipalmated Sandpipers *Calidris pusilla* and an evaluation of the technique. Wader Study Group Bull. 27:41–46.

———. 1983. Migratory behavior of Semiplamated Sandpipers at inland and coastal staging areas. Ph.D. dissertation, Cornell University, Ithaca, New York.

MOORE, F. R. 1980. Solar cues in the migratory orientation of the Savannah Sparrow, *Passerculus sandwichensis.* Anim. Behav. 28:684–704.

———. 1985. Individual variability in the migratory orientation of the Savannah Sparrow *Passerculus sandwichensis.* Z. Tierpsychol. 67:144–153.

———. 1987. Sunset and the orientation behavior of migrating birds. Biol. Rev. 62:65–86.

MORRISON, R. I. G. 1984. Migration systems of some New World shorebirds. Pp. 125–202, *in* J. Burger and B. L. Olla, eds. Shorebirds: migration and foraging behavior. Plenum Publishing, New York.

NISBET, I. C. T. 1955. Atmospheric turbulence and bird flight. Brit. Birds 48: 557–559.

PIENKOWSKI, M. W., P. N. FERNS, N. C. DAVIDSON, AND D. H. WORNALL. 1984. Balancing the budget: measuring the energy intake and requirements of shorebirds in the field. Pp. 29–56, *in* P. R. Evans, J. D. Goss-Custard, and W. G. Hale, eds. Coastal waders and wildfowl in winter. Cambridge University Press, Cambridge.

RICHARDSON, W. J. 1978. Timing and amount of bird migration in relation to weather: a review. Oikos 30:224–272.

———. 1979. Southeastward shorebird migration over Nova Scotia and New Brunswick in autumn: a radar study. Can. J. Zool. 57:107–124.

STODDARD, P. K., J. E. MARSDEN, AND T. C. WILLIAMS. 1983. Computer simulation of autumnal bird migration over the western North Atlantic. Anim. Behav. 31:173–180.

VAN TYNE, J., AND M. H. TRAUTMAN. 1945. Migration records from Yucatan. Wilson Bull. 57:203–204.

TORRE-BUENO, J. R. 1978. Evaporative cooling and water balance during flight in birds. J. Exp. Biol. 75:231–236.

YAPP, W. B. 1956. Two physiological considerations in bird migration. Wilson Bull. 68: 312–319.

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