Brazil. Papeis Avulsos de Zoologia (Sao Paulo) 33:1–25.

WILLSON, M. F., AND J. J. ARMESTO. 1996. The natural history of Chiloé: On Darwin's trail. Revista Chilena de Historia Natural 69: in press.

WILLSON, M. F., T. L. DE SANTO, C. SABAG, AND J. J. ARMESTO. 1994. Avian communities of fragmented south-temperate rainforests in Chile. Conservation Biology 8:508–520.

Time Of Departure by Summer Tanagers (*Piranga rubra*) from a Stopover Site Following Spring Trans-Gulf Migration

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Nocturnal passerine migration typically commences within an hour of sunset (Drury and Nisbet 1964, Casement 1966, Cochran et al. 1967, Parslow 1968, Gauthreaux 1971, Hebrard 1971, Åkesson et al. 1996), and the bulk of migrants depart before the end of nautical twilight (which ends when the sun is 12° below the horizon or almost an hour after sunset). This "window" of nightly departure is probably tied to the availability of directional information from a wide array of environmental cues (Emlen 1980, Moore 1987, Piersma et al. 1990) as well as to the onset of atmospheric conditions favorable for migratory flight (Kerlinger and Moore 1989).

Although several orientation studies have quantified the cage activity of migrants during this "window" of time (see Moore 1987), species-specific departure of free-ranging passerines has been reported in only a few species (Cochran et al. 1967, Åkesson et al. 1996). Discounting birds artificially stimulated to initiate flight, 7 of 12 radio-tagged *Catharus* thrushes that departed under clear skies during spring migration through Illinois did so within an hour of sunset, while greater variation occurred when birds ($n = 6$) departed on overcast evenings (Cochran et al. 1967). Åkesson et al. (1996) found that half of the 10 radio-tagged Song Thrushes (*Turdus philomelos*) that stopped over on the island of Öland, Sweden, initiated migration before the end of nautical twilight or within about 90 min of sunset, whereas the others departed much later in the night and possibly the next morning. We report the time of departures of Summer Tanagers (*Piranga rubra*) from a stopover site along the northern coast of the Gulf of Mexico following trans-Gulf migration and consider several factors (e.g. fat loads) that might explain observed variation.

Methods.—Observations were made on Horn Island (30°14'N, 88°40'W), a barrier island located 20 km off the Mississippi Gulf coast, during the spring migrations of 1992–94. Summer Tanagers were caught shortly after arrival on the island using mist nets, and 24 birds were fitted with radio transmitters (Custom Telemetry and Consulting, Inc., Watkinsville, Georgia) to study movement in relation to habitat during stopover. Transmitters were attached to the base of the rectrices using cyanoacrylate glue and a small cable tie. Each transmitter weighed 1.3–1.4 g and had a range of 1 km and a lifespan of seven days.

After release at their place of capture, birds were tracked using a hand-held, 2-element Yagi antenna. Tracking continued until the bird left the island (i.e. continued migration) or the transmitter failed. Although continuous daily tracking stopped at approximately 1800 CST, the signal was monitored hourly after dark. Some birds roosted close enough to our living quarters that the signal could be detected at night using the Yagi antenna. If a bird's signal could not be detected using the hand-held antenna, the receiver was connected to a Yagi antenna attached halfway up a 66-m radio tower, which was centrally located on the 22-km-long island. Signals were not monitored after 2300. If a signal was not received at sunrise the following day, and there was no indication of impending transmitter failure the previous night, we assumed the bird had migrated. Birds whose signals were lost prior to 2300 were considered to have migrated between the time the signal was last received and the time when the signal was no longer received. Although it is possible that a bird moved out of receiving range during the night, this explanation is unlikely. The five radio-tagged tanagers that stayed on the island beyond the day of capture did not change locations during the night. Moreover, birds did not make any long-distance movements during the day, and there was no reason to expect they would do so at night unless they were initiating migration.

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TABLE 1. Time of departure and departure conditions for Summer Tanagers on Horn Island, 1992 to 1994.

Date	Estimated fat (g)	Estimated flight range (km)	Time of departure (CST)	Wind (km/h)	Cloud cover
28 Mar 92	5.5	625	>2300	SW 16	Clear
2 Apr 92	2.4	291	2000–2100	SW 16	Partly cloudy
4 Apr 92	2.8	337	>2300	SW 16	Partly cloudy
21 Apr 92	3.7	437	>2300	N 16	Clear
25 Apr 92	3.2	381	>2300	N 24	Clear
1 May 92	3.3	392	2000–2100	S 16	Clear
3 Apr 93	1.3	208	>2300	SW 16	Clear
4 Apr 93	1.6	217	>2300	NE 8	Cloudy
4 Apr 93	1.3	208	>2300	NE 8	Cloudy
8 Apr 93	0.7	88	>2300	NE 32	Cloudy
9 Apr 93	7.2	791	>2200	NW 24	Partly cloudy
15 Apr 93	2.1	256	>2300	SW 24	Clear
25 Apr 93	4.7	542	>2300	SE 16	Cloudy
27 Apr 93	3.2	381	2000–2100	SE 16	Partly cloudy
3 Apr 94[a]	6.7	742	2000–2100	S 16	Cloudy
17 Apr 94	7.0	771	>2200	N 8	Partly cloudy
17 Apr 94	4.6	531	>2200	N 8	Partly cloudy

[a] Bird stayed beyond day of capture, migrating the night of its second day on island.

Wind direction was determined by looking at a wind vane mounted on the radio tower, and wind speed was estimated to the nearest 5 km/h. Cloud cover was categorized as "clear" (0–25% clouds), "partly cloudy" (25–75%), and "cloudy" (75–100%). The mass of each bird's fat stores was estimated by subtracting the average fat-free mass of Summer Tanagers (i.e. 24.7 g; Odum 1993) from body mass at time of initial capture. Using this estimate of fat load, we calculated the flight range for each bird under conditions of no wind (Pennycuick 1989). Capture-recapture data suggest that Summer Tanagers either maintain or gain a little (0.1 g) mass during the day preceding departure (Moore and Aborn unpubl. data).

Results.—We obtained data on time of departure for 18 of the 24 radio-tagged Summer Tanagers. Of the remaining six birds, four either lost or carried failed transmitters, one was taken by a predator, and one roosted outside the range of the tower antenna and was gone the next morning. Departure time could not be estimated from four of the five birds that stayed beyond the day of capture because the transmitter failed or was lost before the end of the day.

Individuals were tracked continuously throughout the day, and no bird was observed leaving during daylight hours (Table 1). Two Summer Tanagers departed near the time of sunset within civil twilight. Sunset occurred between 1817 (late March) and 1937 (early May) during the period of our observations. Civil twilight ends when the sun is 6° below the horizon and lasts about 25 min at this latitude. Winds were southerly (i.e. following for northward migration) in each case, and cloud cover was clear or partly cloudy. Two other birds departed with southerly winds and under partly cloudy to cloudy skies at least one-half h after the end of nautical twilight. We infer that

14 birds departed as late as 2200 or 2300 based on their presence at night up to that hour and absence the following morning (Table 1). Both wind direction and cloud cover varied among those nights; on some nights winds were out of the NE and the sky was cloudy, and on other nights southerly winds prevailed and skies were clear.

Estimated fat loads varied widely (Table 1). These fat loads translated into flight-distance estimates of 88 to 791 km under still-air conditions (Table 1). The two birds that departed shortly after sunset could have flown approximately 400 km on the 3 + g of fat they carried, which is similar to the average estimated flight distance (420 ± SD of 223 km) for birds present on the island after 2200 or 2300. Some of the birds that did not depart until well after civil twilight carried fat loads that would have been completely catabolized had they flown all night (even under still-air conditions), whereas others carried enough fat to have flown all night and arrived with a margin of fat sufficient to fly another night without refueling.

Discussion.—Summer Tanagers stopping on Horn Island following trans-Gulf flight re-initiated migration at least 2 to 3 h after sunset, and possibly much later in the night, which is not consistent with the expected pattern of departure shortly after sunset. How might we explain the observed variability?

First, the addition of a radio transmitter might have affected time of departure, although we found no effect of the transmitter on the daytime behavior of Summer Tanagers (pers. obs.). If the additional wing loading from the transmitter affected the decision to depart, we would expect to see a relation between fat load and departure time, but we did not (see below).

Second, when crossing large bodies of water such as the Gulf of Mexico, songbirds typically wait for

following winds before departing (Gauthreaux and Able 1970, Nisbet 1970). Summer Tanagers stopping on Horn Island have yet to complete their trans-Gulf flight. Thus, they may be unaware of the relatively short distance (ca. 20 km) to the mainland, and they may be especially sensitive to atmospheric conditions, which are most favorable for migration along the northern coast of the Gulf of Mexico after 2200 (Kerlinger and Moore 1989).

Third, birds differed in their fat stores, and time of departure may be tied to fat load. Energetic condition is known to influence the expression of migratory activity (e.g. Gwinner and Czeschlik 1978, Biebach 1985, Yong and Moore 1993), but the relationship is not a simple one (e.g. Able 1977). Birds with fat stores insufficient for an entire night's migration might depart later in the evening to ensure arrival at their next stopover with some margin of fat remaining (Moore and Kerlinger 1991). Assuming our estimates of fat load are correct, many of the birds we monitored carried insufficient fat for a night's migration if we assume a ground speed of 40 km/h and a flight time of 7 h for birds departing at 2300, or a flight time of 9.5 h for birds departing as early as 2000. Those birds either land well before daybreak or depart later in the night. Five of the birds departing after 2300 carried more than enough fat to have left earlier and flown all night (i.e. 10.5 h), whereas three of the four birds that departed between 2000 and 2100 carried just enough fat to fuel an all-night flight (i.e. 9 h assuming departure at 2030). It is worth noting that flight range estimates calculated according to Pennycuick's (1989) model are conservative and may underestimate actual flight ranges (e.g. Davidson 1984).

If migratory activity depends on a "setpoint" or threshold fat load (Biebach 1985), we would expect the relationship between migratory activity and energetic status to be influenced by ecological context (Alerstam 1990, Sandberg and Moore 1996). Once an ecological barrier is crossed, the selective pressure for a "margin of safety" may be relaxed and the setpoint for nocturnal activity may be relatively low and variable (see Moore and Kerlinger 1991), which appears to be true for Summer Tanagers departing from Horn Island. In any case, until we know the bird's exact time of departure and the time it spends aloft, it will be difficult to assess flight strategies in relation to energetic condition.

Fourth, the expression of migratory activity is influenced by habitat quality and the probability of rebuilding fat stores (Biebach 1985; Gwinner et al. 1985, 1988; Terrill 1988). If Summer Tanagers perceive Horn Island to be a less-than-suitable place to stopover, they may be better off continuing their migration and departing with little regard for time of departure in relation to energetic condition. Although most Summer Tanagers depart on the night of the day they arrive on the island (unpubl. data; see Kuenzi et al. 1991), birds that stay can expect to gain mass

at a rate of 0.10 g per day (unpubl. data), which suggests that the site is not necessarily poor. Of course, habitat quality is relative and depends on the likelihood the migrant will encounter a better site (Alerstam and Lindström 1990).

Fifth, the relationship between migratory activity on a night-to-night basis and fat load may break down as individuals approach the end of their migration (Yong and Moore 1993). The breeding range of Summer Tanagers extends across the Southeast, including southern Mississippi and Alabama, and variation in fat load may be related to factors other than migratory distance (e.g. expected conditions on breeding grounds).

Finally, observed variation in time of departure should not be construed as evidence that Summer Tanagers do not integrate directional information during the transition between daylight and darkness (twilight) prior to departure. Birds could integrate information and select a direction around sunset (or earlier, for that matter), transfer that information to landmarks or stars, and depart later that same night.

LITERATURE CITED

ABLE, K. P. 1977. The orientation of passerine nocturnal migrants following offshore drift. Auk 94: 320–330.

ÅKESSON, S., T. ALERSTAM, AND A. HEDENSTRÖM. 1996. Flight initiation of nocturnal passerine migrants in relation to celestial orientation conditions at twilight. Journal of Avian Biology 27:95–102.

ALERSTAM, T. 1976. Nocturnal migration of thrushes (*Turdus* spp.) in southern Sweden. Oikos 27:457–475.

ALERSTAM, T. 1990. Bird migration. Cambridge University Press, Cambridge.

ALERSTAM, T., AND Å. LINDSTRÖM. 1990. Optimal bird migration: The relative importance of time, energy, and safety. Pages 331–351 in Bird migration (E. Gwinner, Ed.). Springer-Verlag, Berlin.

BIEBACH, H. 1985. Sahara stopover in migratory flycatchers: Fat and food affect the time program. Experientia 41:695–697.

CASEMENT, M. B. 1966. Migration across the Mediterranean observed by radar. Ibis 108:461–491.

COCHRAN, W. W., G. G. MONTGOMERY, AND R. R. GRABER. 1967. Migratory flights of *Hylocichla*

thrushes in spring: A radiotelemetry study. Living Bird 6:213-225.

DAVIDSON, N. C. 1984. How valid are flight range estimates for waders? Ringing and Migration 5:49-64.

DRURY, W. H., AND I. C. T. NISBET. 1964. Radar studies of orientation of songbird migrants in southeastern New England. Bird-Banding 35:69-119.

EMLEN, S. T. 1980. Decision making by nocturnal bird migrants: The integration of multiple cues. Pages 553-560 *in* Acta XVII Congressus Internationalis Ornithologici (R. Nöhring, Ed.). Berlin, 1978. Deutsche Ornithologen-Gesellschaft, Berlin.

GAUTHREAUX, S. A., JR. 1971. A radar and direct visual study of passerine spring migration in southern Louisiana. Auk 88:343-365.

GAUTHREAUX, S. A., JR., AND K. P. ABLE. 1970. Wind and the direction of nocturnal songbird migration. Nature 228:476-477.

GWINNER, E., AND D. CZESCHLIK. 1978. On the significance of spring migratory restlessness in caged birds. Oikos 30:364-372.

GWINNER, E., H. BIEBACH, AND I. VON KRIES. 1985. Food availability affects migratory restlessness in caged Garden Warblers (*Sylvia borin*). Naturwissenschaften 172:51.

GWINNER, E., H. SCHWABL, AND I. SCHWABL-BENZINGER. 1988. Effects of food deprivation on migratory restlessness and diurnal activity in the Garden Warbler *Sylvia borin*. Oecologia 77:321-326.

HEBRARD, J. L. 1971. The nightly initiation of passerine migration in spring: A direct visual study. Ibis 113:8-18.

HELBIG, A. J. 1991. Dusk orientation of migratory European Robins, *Erithacus rubecula*: The role of sun-related directional information. Animal Behaviour 41:313-322.

KERLINGER, P. 1987. Flight strategies of migrating hawks. University of Chicago Press, Chicago.

KERLINGER, P., AND F. R. MOORE. 1989. Atmospheric structure and avian migration. Current Ornithology 6:109-142.

KUENZI, A. J., F. R. MOORE, AND T. R. SIMONS. 1991. Stopover of Neotropical landbird migrants on East Ship Island following trans-Gulf migration. Condor 93:869-883.

MOORE, F. R. 1987. Sunset and the orientation behaviour of migrating birds. Biological Reviews

of the Cambridge Philosophical Society 62:65-86.

MOORE, F. R., AND P. KERLINGER. 1991. Nocturnality, long-distance migration, and ecological barriers. Pages 1122-1129 *in* Acta XX Congressus Internationalis Ornithologici (B. D. Bell, Ed.). Christchurch, New Zealand, 1990. New Zealand Ornithological Congress Trust Board, Wellington.

NISBET, I. C. T. 1970. Autumn migration of the Blackpoll Warbler: Evidence for long flight provided by regional survey. Bird-Banding 41:207-240.

ODUM, E. P. 1993. Body masses and composition of migrant birds in the eastern United States. Pages 313-354 *in* CRC handbook of avian body masses (J. B. Dunning, Ed.). CRC Press, Boca Raton, Florida.

PARSLOW, J. L. F. 1968. The migration of passerine night migrants across the English Channel studied by radar. Ibis 111:48-79.

PENNYCUICK, C. J. 1989. Bird flight performance: A practical calculation manual. Oxford University Press, Oxford.

PHILLIPS, J. B., AND F. R. MOORE. 1992. Calibration of the sun compass by sunset polarized light patterns in a migratory bird. Behavioral Ecology and Sociobiology 31:189-193.

PIERSMA, T., L. ZWARTS, AND J. H. BRUGGEMANN. 1990. Behavioural aspects of the departure of waders before long-distance flights: Flocking, vocalizations, flight paths and diurnal timing. Ardea 78:157-184.

SANDBERG, R., AND F. R. MOORE. 1996. Migratory orientation of Red-eyed Vireos, *Vireo olivaceus*, in relation to energetic condition and ecological context. Behavioral Ecology and Sociobiology 39: in press.

TERRILL, S. B. 1988. The relative importance of ecological factors in bird migration. Pages 2180-2190 *in* Acta XIX Congressus Internationalis Ornithologici (H. Ouellet, Ed.). Ottawa, Ontario, 1986. National Museum of Natural Science, Ottawa.

YONG, W., AND F. R. MOORE. 1993. Relation between migratory activity and energetic condition among thrushes (Turdinae) following passage across the Gulf of Mexico. Condor 95:934-943.