

WINGBEAT FREQUENCY OF TWO *CATHARUS* THRUSHES DURING NOCTURNAL MIGRATION

ROBERT H. DIEHL¹ AND RONALD P. LARKIN

Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820, USA

ABSTRACT.—Radio transmitters emitting continuous signals were mounted on Swainson's Thrushes (*Catharus ustulatus*) and Veerys (*C. fuscescens*) during two spring migration seasons. Wingbeats modulated the continuous signals, and signal-processing techniques permitted examination of wingbeat frequency (WBF) during nocturnal migration. Distinct takeoff and cruising-flight phases were evident in both species. As birds climbed during the takeoff phase (which usually lasted about 15 min), WBF typically declined exponentially by at least 4 Hz. Median cruising WBF from seven flights varied from 9.2 to 10.9 Hz, values similar to those calculated from published equations predicting WBF based on flight mechanics. Cruising WBF typically varied slowly and irregularly throughout all flights by about 1 Hz. During takeoff and cruising flights, all birds flapped continuously, showing no evidence of the flap-coasting pattern common in passerine migrants previously studied with other techniques such as radar. All five birds exhibited departure times, course directions, and flight distances typical for migrating thrushes. Received 23 May 1997, accepted 11 November 1997.

EXCEPT FOR BRIEF PERIODS, such as when birds cross the face of the moon, researchers rely mainly on indirect means to study nocturnal flight. Empirical study of wingbeat frequency (WBF) in birds intensified when researchers considered using tracking radar to identify species by their wingbeat characteristics. Although WBF in insects varies interspecifically (Moore et al. 1986), intraspecific variation in WBF in birds has been too great for species identification (Emlen 1974, Vaughn 1974). A more enduring body of theoretical and empirical work considers WBF in the context of understanding powered flight (Pennycuik 1968, 1989; Tucker 1973; Rayner 1979). Better data on WBF may increase our understanding of bird flight performance by providing a more complete theoretical picture of mechanical power output of flight muscle (Pennycuik and Rezende 1984), helping explain flight strategies in flapping versus soaring flight (Hedenström 1993), and improving estimates of WBF during cruising flight (Hedenström and Alerstam 1992).

Most radar tracks of WBF are short, typically less than a few seconds (Williams et al. 1972, Vaughn 1974, Larkin unpubl. data), and they seldom include birds taking off and landing (but see Hedenström and Alerstam 1994). In addition to radar, methods of measuring WBF

include using broken-light beam (Moore et al. 1986), microphone (Payne 1981), and high-speed video both outside wind tunnels (Butler and Woakes 1980, Norberg 1991, Tobalske 1996) and inside (Butler et al. 1977, Rayner and Thomas 1991). Of these, only wind-tunnel methods allow monitoring WBF for durations comparable to nocturnal migration (Pennycuik et al. 1996). However, data from wind-tunnel studies may not be directly comparable to data from free-flying migrants (Rayner and Thomas 1991, Pennycuik et al. 1996).

The pioneering work of W. W. Cochran provided an opportunity to measure WBF when radio transmitters emitting continuous signals yielded serendipitous data on respiration and wingbeats of Mallards (*Anas platyrhynchos*; Lord et al. 1962). Taking advantage of this property of radio transmitters emitting continuous signals, we studied Swainson's Thrushes (*Catharus ustulatus*) and Veerys (*C. fuscescens*) to obtain long records of WBF during nocturnal migration.

METHODS

Over two seasons in May, two Swainson's Thrushes and three Veerys were captured in mist nets in a forest fragment near Champaign-Urbana, Illinois. We measured wing chord and mass for each bird and attached modified 302-MHz radio transmitters weighing about 1.5 g (4 to 5% of body mass) dorsally near the center of gravity (Raim 1978). Most birds

¹ E-mail: rdiehl@uiuc.edu

were captured in the morning, held for about 45 min during transmitter attachment, and released long before the onset of nocturnal migration. Transmitters emitted continuous signals. They had shortened life compared with pulsed transmitters but operated for the few days required to obtain WBF data and radiated sufficient power to maintain radio line-of-site contact (Cochran 1980) at distances often exceeding 10 km. The continuous signal varied in frequency and amplitude when the bird moved about; during flight, the modulations reflected wingbeats. We later estimated WBF from records of signal modulations.

We followed the birds with a vehicle-mounted directional Yagi antenna during nocturnal migration while recording bearings relative to the vehicle or, when possible, with a compass. From bearings of birds' positions, migratory routes were estimated by the method of Cochran (1972). We recorded continuous receiver signal (beat-frequency oscillator output) on analog reel-to-reel tape (RRT) in 1981 and on digital audio tape (DAT) in 1994. Because wow and flutter on RRT introduced unwanted variation in analog recordings, we provided a reference for subsequent correction of receiver signal by playing a 1,000-Hz timing signal into a second channel while recording on RRT.

Receiver signal was filtered (for DAT: B and K band-pass filter type 1621 at 3% band-pass) and then played through a Schmitt trigger to obtain receiver-signal period. The mean of every 10 receiver-signal periods was computed, corrected for variation in tape speed (for RRT), and saved to a hard disk. Changes in receiver-signal period due to RRT speed variation were corrected during playback, and receiver-signal frequency was reconstructed digitally by:

$$f = \frac{1}{\tau_c} = \frac{1}{\tau \cdot 0.001/\tau_t'} \quad (1)$$

where f is receiver-signal frequency (Hz), τ_c is corrected receiver-signal period (s), τ is uncorrected receiver-signal period (s), and τ_t' is timing-signal period (s). Cumulative periods provided an elapsed time base, and from the inverse period we reconstructed receiver-signal frequency (Fig. 1). Data from RRT were filtered via software where frequency samples >3 standard deviations from the median frequency were omitted. The filtering of DAT and RRT data was done to remove environmental interference (see below) and ignition noise. These data were then divided into 0.5-s epochs, which are long enough to estimate WBF, yet short enough to permit a compute-intensive method of estimating WBF for each epoch. To remove sudden changes in receiver signal caused by tuning, we normalized the data by fitting linear regressions to each epoch and subtracting residuals, leaving a sinusoid-like waveform with a mean of zero.

Using a Pascal program, we estimated WBF, am-

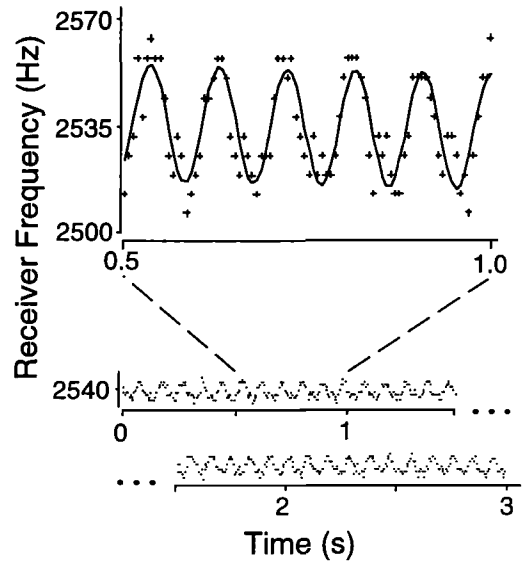


FIG. 1. Bottom: Three seconds of digitized receiver signal of a Swainson's Thrush 5 min after takeoff. Top: One-half second is enlarged and the fitted sine wave superimposed over the data. During this epoch, WBF = $10.8 \pm$ SE of 0.14 Hz, amplitude ($\hat{\alpha}$) = 19.2 ± 2.50 Hz, phase (ϕ) = $-48.5 \pm 14.8^\circ$. Such continuous flapping was typical of all the flights.

plitude, and phase of wingbeat modulation from a sine wave fitted by least squares to each epoch of digitized receiver signal:

$$i = 1, \dots, N, 0 \leq t_i \leq 0.5, \\ f_i = \hat{\alpha} \cdot \sin(2\pi \cdot \text{WBF} \cdot t_i + \phi), \quad (2)$$

where N is number of digitized signal samples within an epoch (N is ≥ 30 and usually $\gg 50$, comprising around five wingbeats; Fig. 1), f_i is the digitized receiver frequency (Hz), $\hat{\alpha}$ is the estimated amplitude of the fitted sine wave (Hz), t_i is sample time (s) within each epoch, and ϕ is the estimated phase of the sine wave. The sine-fitting algorithm was constrained to $7 < \text{WBF} < 17$ Hz, because preliminary exploratory data analysis showed WBF for these thrushes to be well within this bandwidth. WBF estimates from the Pascal program were validated by the facts that: (1) fitted sine waves were visually comparable to the digitized receiver signal (Fig. 1); (2) Pascal program results were nearly identical to SAS PROC NLIN (SAS Institute 1990) program results (a completely different but much slower method of calculation); and (3) Fourier transforms of digitized receiver signal agreed with Pascal and NLIN results (Fourier transforms were not used for the calculations themselves because they lack the precision of sine-wave fits in estimating a single frequency). To determine the accuracy of WBF estimates, NLIN was

used on every 20th epoch to generate the standard error of the sine-wave fit.

Of 12 thrush flights, four were short, lasting less than 15 min (precise landing time was difficult to determine). The eight long flights were either greater than 100 min, or showed takeoff behavior similar to that preceding other long flights (i.e. veer4b; Table 1). Seven long flights were selected to examine cruising-flight WBF during migration. We used LOWESS smoothing (locally weighted regression; Cleveland 1979) to highlight trends in WBF over time. LOWESS incorporates a smoothing parameter that is the proportion of the total sample of points used in each regression within the LOWESS function. Higher values of the parameter increase the amount of smoothing. Smoothing consistently across different sample sizes was achieved by varying the smoothing parameter as the ratio of 550 over the number of observations in the data set. Although 550 was somewhat arbitrary, this number served LOWESS well in reflecting overall trends in WBF.

Declining WBFs attributable to a takeoff phase ($n = 7$) were separated from the long WBF records for further analysis. The point of transition from takeoff phase to cruising flight was designated from LOWESS fits to WBF data to be the time when LOWESS values first ceased to decline after takeoff, except in two flights where data were missing during the point of transition. In these two cases, the beginning of the data gap defined the end of the takeoff phase (Table 1). Because WBF during takeoff appeared to decline exponentially, takeoff phases were compared by fitting negative exponentials to the data:

$$\text{WBF}_t = \text{WBF}_0 \cdot t^{-k}, \quad (3)$$

where t is time (s) of each WBF estimate (in Hz), WBF_0 is WBF at $t = 0$, and k is the estimated rate of WBF decline. This exponential description was validated by comparing mean squared error (MSE) of exponential and LOWESS fits to data from the takeoff phase. Similar MSEs suggest that the exponential accurately describes the takeoff. Unlike an exponential, LOWESS assumes no parametric form in fitting the data, but it permits later WBF values to influence WBF values at takeoff; therefore, the LOWESS estimates at $t \approx 0$ will be biased low.

Of several published equations predicting WBF (Greenewalt 1975; Pennycuik 1978, 1990, 1996; Rayner 1988, 1995), the most recent two were selected for comparison with observed WBFs. Both equations represent a compromise between simplicity in application and precision in explaining variation, and their similarity in form demonstrates some convergence of theory. Because Pennycuik's (1996; and we assume Rayner's [1995]) equation predicts a bird's WBF for "steady cruising flight," median cruising WBF was determined from data remaining after removing both the takeoff phase from the beginning of a WBF record and an equal duration from the end of

the record to remove a possible landing phase (see Results). Three morphological measures are required for WBF prediction: (1) body plus transmitter mass, (2) wing span, and (3) wing area. We measured wing span and wing area of non-radiotagged *Catharus* thrushes as outlined in Pennycuik (1989:8-13; see also <http://detritus.inhs.uiuc.edu/~rdiehl/wingdata.html>) and used log correlations between each variable and wing chord to estimate wing span and area for radiotagged birds.

RESULTS

Modulations of the continuous signals reflected the activity of birds as they moved about the habitat prior to and after migration. The signals fluctuated irregularly during daytime. A period of steady, intense signal that varied from 4 to 41 min, presumably corresponding to a quiescent period, occurred immediately before takeoff (Hebrard 1971).

The extensive road system and open habitat typical of the central United States simplified maintaining radio contact while following migrating birds on courses through five states (Fig. 2). Nonetheless, four WBF records ended because birds were lost. For example, a Swainson's Thrush (swth1; Table 1) was lost in northwestern Indiana as it appeared to head out over Lake Michigan. Other migrants evaded us when they encountered strong tail winds or assumed courses difficult to follow over the ground.

Even when the tracking vehicle was close to the migrant, radio contact frequently was interrupted by environmental interference (i.e. garage door openers or alarm systems; see Cudak et al. 1991) or obstructed by trees and buildings. Signal strength was diminished if the receiving antenna was oriented either fore or aft of the bird and its transmitting antenna (in a head or tail null; Cochran and Kjos 1985). Poor signal-to-noise ratios and difficulties in use of RRT explained occasional gaps in WBF records (Fig. 3), although use of DAT in place of RRT greatly improved the continuity of these records. Overall, use of continuous-signal transmitters proved effective for gathering WBF data on migrating thrushes. Oftentimes signals were received from more than 10 km away when we were in line-of-sight contact. Wingbeat modulations were more sinusoidal than the spiked or picket-fence waveforms often seen in tracking radar records of bird wing-

TABLE 1. Wingbeat frequency (WBF) measurements for eight flights of Swainson's Thrushes and Veerys.

Flight number ^a	Mass (g) ^b	Wing chord (mm) ^b	Civil sunset (CST)	Date	Time (CST)	Rate of change (\pm SE) ^c	Duration (min) ^d	Initial WBF (Hz \pm SE)	Predicted			Flight duration (min) ^f	Est. flight distance (km)
									Median WBF (Hz)	Penny-cuick	Rayner		
swth1	39.0	101	1910	5/25/81	1957	0.038 \pm 0.001	19 ^g	13.9 \pm 0.6	10.0	11.4	11.8	>149	>210
swth2a	36.9	97	1908	5/24/94	0017 ^h	0.026 \pm 0.002	14	12.9 \pm 1.9	10.7	12.3	12.6	218 ⁱ	152
swth2b	—	—	1917	5/26/94	2003	0.041 \pm 0.002	12	14.9 \pm 0.7	10.9	—	—	>306	>250
veer3	39.7	98	1906	5/21/81	1946	—	—	—	10.8	12.3	12.6	475	450
veer4a ^j	35.4	102	1854	5/08/94	2031	0.058 \pm 0.002	15	14.7 \pm 1.1	9.2	10.8	11.2	100	125
veer4b	—	—	1858	5/10/94	1954	0.049 \pm 0.002	20 ^g	14.5 \pm 1.0	—	—	—	>24	>30
veer5a	38.4	102	1903	5/17/94	1958	0.059 \pm 0.001	44	16.0 \pm 0.7	9.6	11.2	11.5	160	149
veer5b	—	—	1911	5/18/94	2001	0.060 \pm 0.002	14	13.7 \pm 0.7	10.0	—	—	>263	>460

^a Each number is a different bird, and each letter is a different flight (swth = Swainson's Thrush; veer = Veery).
^b Measured prior to each bird's flight.
^c Rate of change in WBF (parameter *k* from equation 3).
^d Missing values indicate records that were inadequate to estimate flight duration.
^e Calculated from Penny-cuick (1996; equation 9) and Rayner (1995; equation 8); missing values result from no data on body mass, a variable needed in each equation.
^f Exact moment of termination of flight was unknown for all flights.
^g The end of the decline in WBF occurred at a gap in the data.
^h An earlier brief flight on that evening began at 1955.
ⁱ Equipment failure prevented WBF estimation during last 80 min of flight.
^j This bird made a brief flight beginning at 2143 on 5/09/94; civil sunset was at 1857.

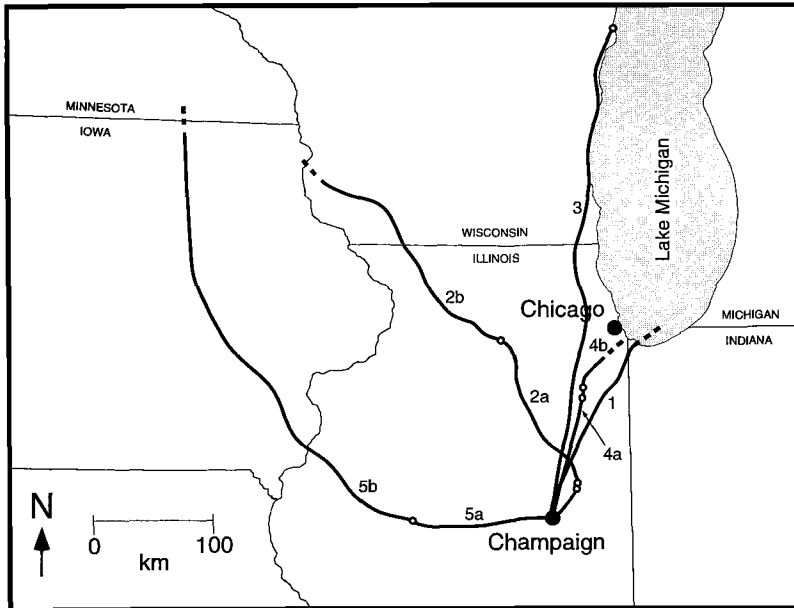


FIG. 2. Approximate migratory tracks of three Veerys and two Swainson's Thrushes through the north-central United States. Small circles along each track's path mark landings. Dashes indicate where radio signals were lost during tracking. Flights lasting longer than about 15 min are labeled and correspond to flight numbers in Table 1.

beats (Flock 1974:433). Although wingbeats were sometimes detected in amplitude modulations of the receiver signal, they were more often detected in its frequency modulation. Most recorded receiver signal was sufficiently free of noise to allow precise WBF estimation by sine-fitting (range of median WBF SEs of eight long flights was 0.09 to 0.45 Hz).

Four of the five migrants exhibited two distinct phases of WBF change, a takeoff phase characterized by rapid exponential decline in WBF, and a subsequent cruising-flight phase where WBF varied gradually (Figs. 3 and 4). Three long flights were tracked to landing (veer3, veer4a, veer5a; Table 1), and each showed a general increase in WBF toward the end of the flight (Figs. 3 and 4). Such WBF increases prior to landing may represent a landing phase (but see Pennycuik et al. 1996). During cruising flight, long-term variations in WBF dominated trends in the data (Fig. 4), whereas epoch-to-epoch variation superimposed over these long-term variations tended to vary over a narrow range (interquartile range from 0.45 to 1.13 Hz). We attribute long-term variations to the birds' behavior (see below), whereas the epoch-to-epoch variations appear to be attrib-

utable to a combination of sampling error, an artifact of the method of data analysis, and probably some short-term variation in WBF.

Receiver signal was visually inspected for wingbeat pattern. Regardless of the phase of flight, the examined receiver signal showed no indication of flap-coasting (Larkin et al. 1979) or pausing (Bloch et al. 1981) wingbeat patterns common to many nocturnal migrant passerines (Vaughn 1974, Williams and Williams 1980, Larkin and Frase 1988). Except when cluttered by noise, only epochs showing continuous wingbeating similar to that in Figure 1 were apparent.

Median time of departure for the first flight of an evening ($n = 9$) was 1958 CST; seven of these departures occurred 40 to 56 min after sunset (Table 1; Moore and Aborn 1996). Immediately after takeoff, WBF declined exponentially (see Fig. 3); this rate of decline was greater for Veerys than for Swainson's Thrushes (Table 1). All of the ratios of MSE (LOWESS fit) to MSE (exponential fit) were between 0.97 and 1.01, substantiating an exponential description of declining WBF during the takeoff phase. Migrants appeared to assume cruising flight about 15 min after takeoff (Table 1, Fig. 3), and

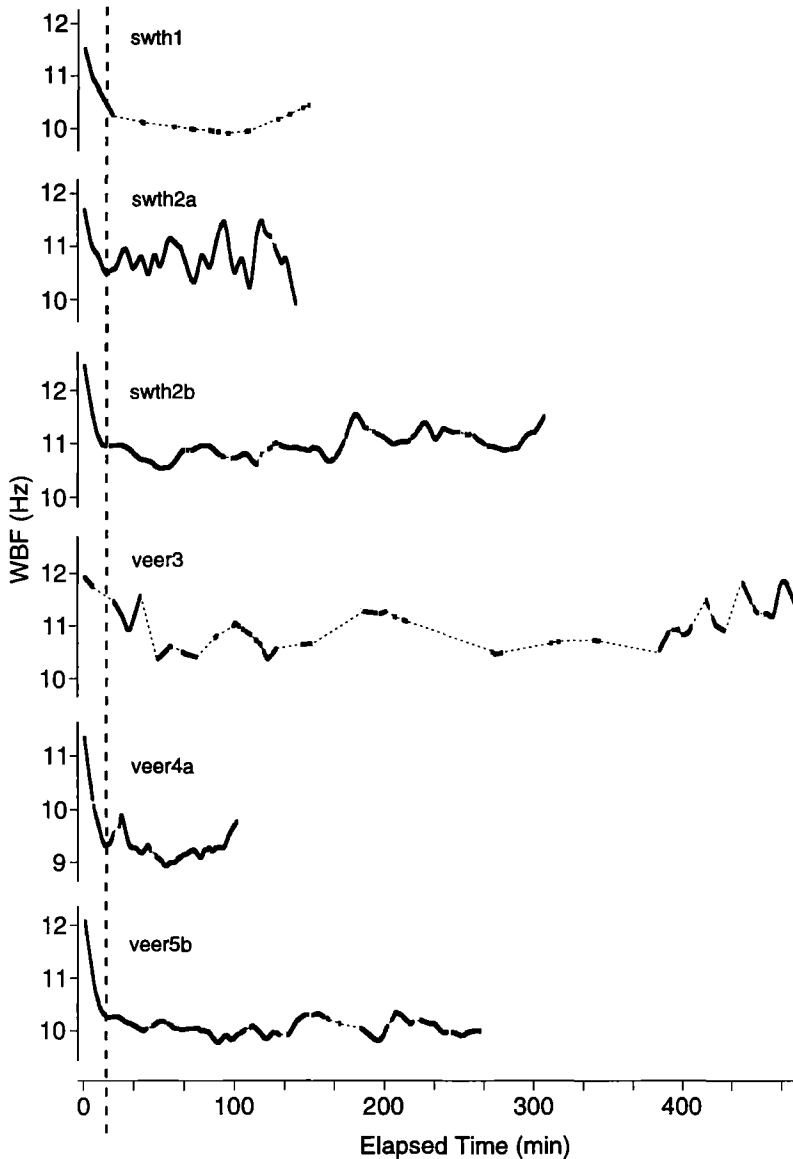


FIG. 3. WBF during six long flights of Swainson's Thrushes and Veerys, estimated by LOWESS. Individual data points are not shown, but their patterns resemble that in Figure 4. Dotted lines connect gaps in these WBF records caused by tape-stopping and low signal-to-noise ratios. The vertical dotted line 15 min after takeoff approximates the transition point from takeoff to cruising-flight WBF.

although for veer5a we report a takeoff phase lasting 44 min, this bird also exhibited a brief leveling of the LOWESS curve after 15 min (Fig. 4). Although long, the flight of veer1 offered insufficient takeoff data for this evaluation. Four shorter flights were not subject to those analyses. For example, veer4 flew 5.5 km and landed in a small forest patch; about 30 min later the

bird took off in a WNW wind, circled once, and landed in the same forest patch about 6 min later.

Seven of 12 flights were long enough to examine cruising-flight WBF trends. LOWESS smoothing showed that cruising WBF varied irregularly over time by as much as 1.6 Hz (e.g. swth2a; Fig. 3) and was seldom truly steady.

Median cruising-flight WBF estimates differed from those predicted by Pennycuick's (1996) and Rayner's (1995) general WBF equations by an average of +1.6 Hz and +1.9 Hz, respectively (Table 1). Slow variations in WBF evident during cruising flight (Fig. 3) did not resolve into patterns of changing WBFs on shorter time scales. Seven 100-s samples of WBF showed no significant autocorrelations (out to lag 32 s) that were not readily accounted for by nonlinear artifacts.

Noisy signals, as opposed to signals dominated by variation in actual WBF, showed overall poor sine-wave fits and simultaneously large goodness-of-fit estimates for all parameters during noisy epochs. This observation was borne out by positive correlations among the standard errors of WBF, $\hat{\alpha}$, and $\hat{\phi}$ for the sine-wave fits ($r = 0.31$ to 0.94 , all $P_s < 0.001$).

DISCUSSION

Most monitored birds took off shortly after sunset, as previously reported for thrushes tracked with pulsed transmitters through central Illinois (Cochran et al. 1967, Cochran and Kjos 1985) and for nocturnal passerine migrants in general (Alerstam 1990:307). During the quiet period prior to takeoff (Hebrard 1971), when thrushes presumably could observe orientation cues such as those provided by the setting sun (Vleugel 1979, Moore 1980, 1987), the signal became almost entirely steady in frequency and amplitude for minutes at a time except for warbles of less than 2 s that we interpret as the bird changing position while perched or flying to a nearby perch. At the moment of takeoff, periodic modulation began suddenly, the received signal grew in strength quickly as the bird cleared the treetops, the azimuth of the signal began to turn toward the departure bearing, and the periodic modulation remained continuous from the moment of takeoff until landing, whenever the receiver could pick up a clear signal. The frequency of the periodic modulations during cruising flight (post-takeoff, pre-landing) was close to WBF predicted from morphologically based equations (Rayner 1995, Pennycuick 1996).

Monitored thrushes did not show flap-coast patterns typically seen in tracking-radar records of passerine migrants (Bloch et al. 1981). However, this result was not an artifact of the

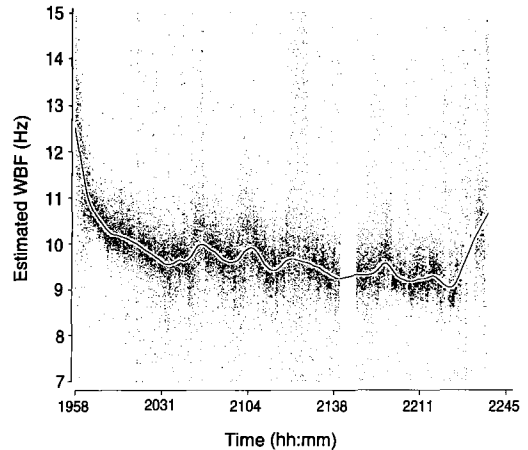


FIG. 4. WBF of veer5a (Table 1) on 17 May 1994. Each point marks one 0.5-s estimate of WBF. The dense cloud of points varies due to both actual variation in WBF (estimated by the LOWESS-fitted curve) and error in WBF estimation (median SE of 0.18 Hz). Point scatter above and below this cloud is mainly an artifact and is prominent when the received signal was weak. The LOWESS curve underestimates WBF immediately after takeoff. The bird departed from Champaign-Urbana, Illinois at 1958 CST and landed 160 min later near Mt. Pulaski, Illinois, about 85 km WSW of Champaign-Urbana (Fig. 2). After takeoff, WBF declined exponentially, and the bird assumed a WNW heading in moderate winds from the NNE.

technique, as indicated by recordings made from a similar transmitter mounted by W.W. Cochran on a Downy Woodpecker (*Picoides pubescens*; Diehl and Larkin unpubl. data) in which bursts of modulated signal directly corresponded to the characteristic undulating flight of woodpeckers (Ritchison 1994). For instance, when we flushed the woodpecker by approaching too closely, we saw directly and heard on the radio receiver the undulating flight to a more distant perch.

Several other lines of evidence, in addition to the thrushes' takeoff behavior and observations of the woodpecker, point to wingbeats as the source of periodic modulations in signal frequency and amplitude described here. Transmitters on thrushes held in our hands prior to release gave steady signals, but when released birds flew into nearby vegetation, periodic modulations coincided with their flying and alighting. In daytime before takeoff and during stopovers, as the birds moved about the habitat,

irregular warbles and short bursts of periodic modulation interspersed with steady signals were characteristic of birds engaged in feeding and other behaviors (Kjos and Cochran 1970).

WBFs observed for the thrushes matched those of similar-sized birds tracked by Vaughn (1974). We are aware of no published data that document whether nocturnally migrating *Catharus* thrushes show a continuous flapping pattern (but see Hedenström and Alerstam 1992), although Pennycuick et al. (1996) reported continuous flapping in Thrush Nightingales (*Luscinia luscinia*) during 16-h flights in a wind tunnel. Twenty-two per cent of unidentified North American migrating birds tracked at night by 3-cm radar (Larkin 1991) and having similar WBFs to the thrushes (9.4 to 11.0 Hz) showed no pauses in flapping (Larkin unpubl. data); however, these results were based on samples of short duration (2 s), and some of the birds undoubtedly were nonpasserines.

We identified distinct WBF phases during takeoff and cruising flight; WBF changes characteristic of landing also may exist. Although the function of these WBF changes remains unclear, the changes are not artifacts generated by the system. Epoch-to-epoch variation in WBF was small and comparable to previously published measures of WBF variation (Griffiths 1969, Emlen 1974), suggesting that both the measurement technique and a bird's control of WBF often were precise. Data collected using both digital and analog recording equipment demonstrated similar slow variation in cruising WBF (Fig. 3), providing strong evidence that the variation is not an artifact.

Pennycuick (1996: equation 9) predicts that WBF varies as an inverse function of air density. Because air density decreases with increasing altitude, we may expect a nominal 1-Hz increase in WBF for a 2,000-m increase in altitude (lateral air-density variations from weather systems are negligible in comparison). Although we did not obtain good estimates of altitude during migration (and therefore do not know how altitude varied during cruising flight), we know that altitude increased at takeoff and decreased upon landing. Because the height above ground level of migrating thrushes seldom exceeds 2,000 m (Cochran and Kjos 1985), we conclude that continual changes in air density are not solely responsible for the slow, 1-Hz variations in cruising WBF. More-

over, during takeoffs and perhaps during landings, WBF changed in a direction opposite that expected from an influence of air density alone (Pennycuick 1996: equation 9). Changes in rate of climb more likely are responsible for decreases in WBF during takeoff (Emlen 1974, Williams and Williams 1980), probably swamping the effect of changing air density. WBF estimated during landings generally increased; however, because terrain and structures usually occlude the signal from a descending bird, an effect compounded by our usually being several kilometers from the bird, we had difficulty obtaining clear data during landing segments.

Predicted cruising WBF from Pennycuick (1996: equation 9) and Rayner (1995: equation 8) generally agreed with our empirical estimations (Table 1). Measuring morphological variables (see Pennycuick 1989) directly on radiotagged migrants rather than predicting them from regressions on other thrushes may have improved our estimates of predicted WBF. Pennycuick (1978) predicts that a steadily flapping bird will consume some flight-muscle tissue and that WBF will decline (subject to simplifying assumptions) proportional to the square root of total mass decrease during flight. Although this prediction was borne out in wind-tunnel experiments with a Thrush Nightingale (Pennycuick et al. 1996), we observed no overall decreases in cruising-flight WBF. Presumably, such long-term flight records will permit more exact test of theories concerning bird flight.

Emlen (1974) reported high intraspecific variation in WBF of sparrows dropped from elevated cages and then tracked with radar (see also Vaughn 1974). Veerys and Swainson's Thrushes monitored in our study overlapped substantially in WBF. Indeed, biologically determined, intraindividual cruising-flight WBF variation (1.6 Hz; Fig. 3, Table 1 for swth2a) overlapped by more than one-half the entire range of cruising flight WBFs for all birds tracked (2.9 Hz). Such intraspecific and intraindividual variation in WBF agrees with previous findings that WBF in passerines is not species-specific (Emlen 1974).

The means by which wingbeats modulate a radio signal are unknown. The transmitter, its crystal and antenna, and the bird comprise a complex resonant entity. We suspect that

changes in a bird's shape by the respiratory system, muscles, and flapping wings; inertia-driven small movements of the transmitter and its attachments as they "ride" the flying bird; and flapping of the trailing antenna toward and away from the body and tail all contribute to wingbeat-driven modulation of the signal.

The drag and mass of the transmitters probably influenced the flights of migrating thrushes to some extent, perhaps minor. Caccamise and Hedin (1985) suggested that frontal-area drag of externally mounted transmitters influences power requirements only slightly relative to added mass. Indeed, the transmitter largely rested under the back feathers, so the effect of frontal-area drag on aerodynamics likely was negligible. It is unclear how transmitter mass may have influenced flight behavior and WBF in particular. Pennycuick (1996) and Rayner (1995) predict an increase of about 0.15 Hz in WBF due to the added mass of 1.5 g. In addition, added mass likely increases wingbeat amplitude and the proportion of upstroke to downstroke (Ruppel and Knop 1985, Hughes and Rayner 1991) and decreases rate of climb (Pennycuick et al. 1989, Hedenström 1992, Hedenström and Alerstam 1992), variation in WBF (Ruppel and Knop 1985), and maximum sustained airspeed (Gessaman and Nagy 1988, Hedenström 1992). Added mass may also have increased WBF during the initial climbing portion of the flight (Table 1, Fig. 3). It is possible that the transmitters caused the observed steady flapping pattern, if the added mass reduced the coasting portion of a "normal" thrush flap-coast cycle to zero (Rayner 1985). Nevertheless, the long, oriented, apparently normal flights of these and other thrushes carrying similar transmitters (Cochran 1972, Cochran and Kjos 1985) indicate that the effects of the transmitter on these birds were minor.

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Associate Editor: K. P. Dial