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Research Article

Unexplained altitude changes in a migrating thrush: Long-flight altitude data from radio-telemetry

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ABSTRACT

Describing and then explaining individual behavior during migration can help us to understand why (on both proximate and ultimate levels) birds migrate; the altitude(s) at which migratory birds fly, for example, can have far-reaching consequences. However, to date, no fine-scale, full-flight altitude data have been available for small (<100 g) migratory birds. We tracked 7 Swainson's Thrushes (*Catharus ustulatus*) carrying altimeters from takeoff until landing or near-landing during 9 migratory flights. The average recorded flight altitude for the 9 flights was 673.0 ± 523.2 m (mean ± SD); average maximum flight altitude for the 9 flights was 1,199.5 ± 862.7 m (range: 319.2–2,744.5 m). Initial ascent rates (0.42 ± 0.15 m s^{-1}, $n = 8$) matched predictions; final descent rates were 0.55 ± 0.30 m s^{-1} ($n = 5$). Contrary to expectations, the thrushes made numerous (9.33 ± 4.42), significant (>100 m) altitude adjustments during their flights (1.44 hr^{-1}), not including initial ascent and final descent. The repeated changes in flight altitude that we observed should cause these birds to use more energy than they would if they flew at or near a single altitude for several hours at a time. We speculate that these altitude modifications may result from variation in atmospheric conditions or from the birds descending toward anthropogenic light sources during the flights.

Keywords: flight altitude, migration, radio-telemetry, bird strikes, light pollution, flight energetics

Cambios inexplicables de altitud en un zorzal migrante: datos de altitud de vuelos largos a partir de radio telemetría

RESUMEN

Describir y luego explicar el comportamiento individual durante la migración puede ayudarnos a entender por qué (tanto a nivel próximo como último) las aves migran; las alturas a las que vuelan las aves migratorias, por ejemplo, pueden tener múltiples consecuencias. Sin embargo, a la fecha no existen datos detallados de altitud de vuelos completos para aves migratorias pequeñas (<100 g). Seguimos 7 individuos de *Catharus ustulatus* que portaban altímetros desde el despegue hasta el aterrizaje y cerca del aterrizaje durante 9 vuelos migratorios. La altura promedio de vuelo registrada para los nueve vuelos fue 673.0 ± 523.2 m (media ± d.e.); la altura máxima promedio de vuelo para los nueve vuelos fue 1199.5 ± 862.7 m (rango 319.2-2744.5 m). Las tasas iniciales de ascenso (0.42 ± 0.15 ms^{-1}, n=8) concordaron con las predicciones; las tasas de descenso final fueron 0.55 ± 0.30 ms^{-1} (n=5). Contrariamente a los que esperábamos, los zorzales realizaron numerosos (9.33 ± 4.42) y significativos (>100 m) ajustes de altitud durante sus vuelos (1.44 hr^{-1}), sin incluir el ascenso inicial y el descenso final. Los cambios repetidos en la altura de vuelo que observamos podrían causar que estas aves usen más energía de la que usarían si volaran a o cerca de una única altitud por varias horas por vez. Especulamos que esas modificaciones de altitud pueden deberse a variaciones en las condiciones atmosféricas o a que las aves bajan hacia fuentes de luz antropogénica durante los vuelos.

Palabras clave: Altura de vuelo, choque de aves, energética del vuelo, migración, polución lumínica, radio telemetría

INTRODUCTION

Our understanding of avian migration is incomplete because we know so little about how individual birds use the aerosphere (Kunz et al. 2008). Without this knowledge, we cannot truly understand the evolution of migratory behavior (Bowlin et al. 2010). Small (<100 g) migrants represent the largest gap in our understanding as they cannot carry GPS transmitters, which can provide researchers with detailed information about in-flight

behavior such as altitude (Bridge et al. 2011). Information about flight altitude and associated atmospheric conditions can be used to inform many different aspects of avian migration biology; recently, for example, authors have used altitudinal information collected from GPS transmitters to predict when migrants will use 'emergency' staging sites (Shamoun-Baranes et al. 2010) and to better understand the physiological capabilities of migratory birds (Bishop et al. 2015). Flight altitude may also affect a bird's probability of dying: If an individual flies too low, it may strike a building, radio tower, or other man-made structure (Longcore et al. 2013). Every year in Canada, ~51 million birds die from so-called 'tower-kill' (Calvert et al. 2013). Certain birds also may be attracted by lights and fly around the source of the light until exhausted or dead, especially in poor weather (Squires and Hanson 1918).

Both small portable tracking radars (Schmaljohann et al. 2008) and Doppler weather radar (Gauthreaux et al. 2003) allow researchers to study the flight altitudes of small migrants by analyzing 'bioscatter': radar signals reflected by animals (birds, bats, and insects) moving in the atmosphere. However, in most cases radar data are limited in duration to several minutes per bird, and nothing is known about the individuals tracked except their size. Thus, most radar studies have focused on large-scale timing and altitude of migration in response to changes in weather patterns (Richardson 1978, 1990, Kerlinger and Moore 1989, Bruderer et al. 1995, Dokter et al. 2010, Bridge et al. 2011, La Sorte et al. 2015). A few studies have tracked individuals up to several tens of minutes or even hours, but have not investigated altitude or changes in altitude per se (e.g., Gudmundsson 1994). From the former, we know that passerine migrants fly relatively low in the atmosphere (<1,000 m) most nights (Gauthreaux 1991), and that the flight altitudes of large groups of migrants can be affected by air temperature, location of boundary layers, turbulence, precipitation, and other atmospheric variables (Richardson 1978, 1990, Kerlinger and Moore 1989, Bruderer et al. 1995).

Cochran and Kjos (1985) used adjustable antennas to measure the altitudes of individual thrushes outfitted with pulsed radio-transmitters and estimated each thrush's altitude 2–5 times during its flight. The authors observed within-flight altitudinal variation and argued that the majority of the changes that they observed were due to birds selecting flight altitudes based on wind speed and direction. For example, they posited that thrushes tended to ascend to the highest altitude at the beginning of the flight to sample the winds, and then flew at that altitude if no better winds were found or descended to an altitude with less unfavorable winds. They argued that altitude adjustments following initial ascent thus appeared to be restricted to large descents and small ascents (Cochran and Kjos 1985).

Here, we present continuous altitudinal data from 7 Swainson's Thrushes (*Catharus ustulatus*), 2 of them on 2 nights, for 9 full or nearly full flights. Swainson's Thrushes are common passage migrants in the Midwestern United States where we worked; they do not breed in the area. In the past, most migration researchers have assumed that nocturnal passerine migrants typically ascend to a chosen altitude and then fly at or near that altitude until descent (e.g., Irschick and Garland 2001, Cochran et al. 2008, Pennycuick 2008). In Pennycuick's (2008) classic migration program, for example, the modeled migrants ascend, cruise at a predetermined altitude until they run out of fuel, and then land. Bishop et al. (2015), however, recently found that Bar-headed Geese (*Anser indicus*) flying over the Himalayas flew close to the ground, partly to take advantage of updrafts resulting from changes in topography, and partly because the energetic cost of flight increased with increasing altitude during horizontal flight. This 'undulating' flight strategy was a result of the geese attempting to fly at a lower average altitude than if they had ascended to their highest flight altitude (dictated by the elevation of the mountain passes), cruised, and then descended (Bishop et al. 2015).

The only study on the energetic costs of flight during ascent and descent (Tucker 1968) suggests that, at migratory flight speeds, it costs more energy for birds to ascend than they save by descending. Without mountain passes to clear in the Midwestern United States, and in the absence of any wind assistance, we expected our thrushes to 'choose' an altitude and fly at or near that altitude after initial ascent (Irschick and Garland 2001), much like a commercial aircraft. The Reynolds' number, an aerodynamic parameter that allows researchers to compare the effects of drag with the effects of viscosity in a fluid, is smaller for birds than for commercial aircraft due to their relative sizes. However, the effects of drag are dominant in both situations; birds experience drag whether ascending, flying horizontally, descending, or even hovering (Pennycuick 2008). Furthermore, Swainson's Thrushes do not save energy by gliding during descent; instead, they actively flap their wings (Cochran et al. 2008). It should therefore cost more in terms of energy for Swainson's Thrushes to ascend than they would save by descending, much as the amount of potential energy stored in an object due to its height cannot be completely converted into kinetic energy when it falls. The most efficient flight behavior in terms of energy spent per unit time would thus minimize the number of ascents and descents during a single migratory flight. If the wind selection hypothesis of Cochran and Kjos (1985) is correct, we might also expect to observe some of the thrushes flying higher during the initial ascent phase than during the 'cruise' phase of the flight in order to sample wind conditions.

METHODS

The transmitters that we used, designed by J. Cochran, weighed 1.0–1.2 g (~3% of the thrushes' body weight) and had 95 mm antennae. They included a factory-calibrated sensor that encoded both pressure and temperature data in the signal. We programmed the transmitters to transmit data every 15 s (2012–2013) or 30 s (2011) from 20:00 to 07:00 local time, while also transmitting a continuous frequency signal that contained wingbeat frequency data in between the temperature and pressure bursts during flight. During the daytime, the transmitters only transmitted temperature and pressure data every 30 min and otherwise beeped once every 30 s for location purposes.

We checked the transmitter measurements in the laboratory by comparing ambient pressure, obtained from a local weather station, with the pressure data from the transmitter. Temperature data from the transmitter were checked against a digital thermometer. We also took a transmitter up in a small aircraft and simultaneously recorded the altitude data from both the plane's altimeter and the transmitter. The data from the transmitter closely matched measurements from the plane's altimeter ($r^2 = 0.99$; Figure 1); the slight discrepancy between the two was most likely due to our method of estimating altitude from temperature and pressure data (see below) and/or the rapid rate at which the aircraft changed altitude compared with the frequency at which we recorded data from its altimeter (1 min intervals).

We captured Swainson's Thrushes using mist nets in a small forest fragment south of Urbana, Illinois (40°N, 88°W), USA, in May, 2011–2013. We opened the mist nets as needed (see Table 1 for capture and flight dates). Once we captured the thrushes, we took a variety of standardized measurements and then attached the transmitter. The transmitter was sewed and superglued to a bit of cloth, which we then attached to the bird with nontoxic eyelash glue following Raim (1978). The transmitters were ~5 mm thick, so in order to avoid contact between the wings and the transmitter in flight, our target attachment site was posterior to the area directly in between the wings. Once the glue had dried, we released each bird near the location where it was caught.

We monitored thrushes until they took off on a migratory flight and then followed them with a radio-tracking vehicle outfitted with a 7-element Yagi antenna. An AOR receiver (AOR USA, Torrance, California, USA) received the signal, which was then recorded directly onto a Sony digital recorder (Sony Corporation of America, New York, New York, USA) as a .wav file. We recorded locations, times, and bird bearings onto a separate digital recorder and also in writing during the flights. We used previously described methods (Cochran and Kjos 1985) to follow the thrushes with the vehicle, but emphasized obtaining continuous altitudinal data over obtaining the exact positions of the birds during the tracking and therefore obtained few crossover points per flight. We were able to follow 7 thrushes during 9 flights for at least 4.5 hr or until the birds landed. We also obtained data from 3 Swainson's Thrushes that we lost shortly after the beginning of their flights, due to either tracking or equipment failure, and 1 individual that made a short (2 hr), low-altitude flight. We did not include the latter individual in our average measurements because it did not

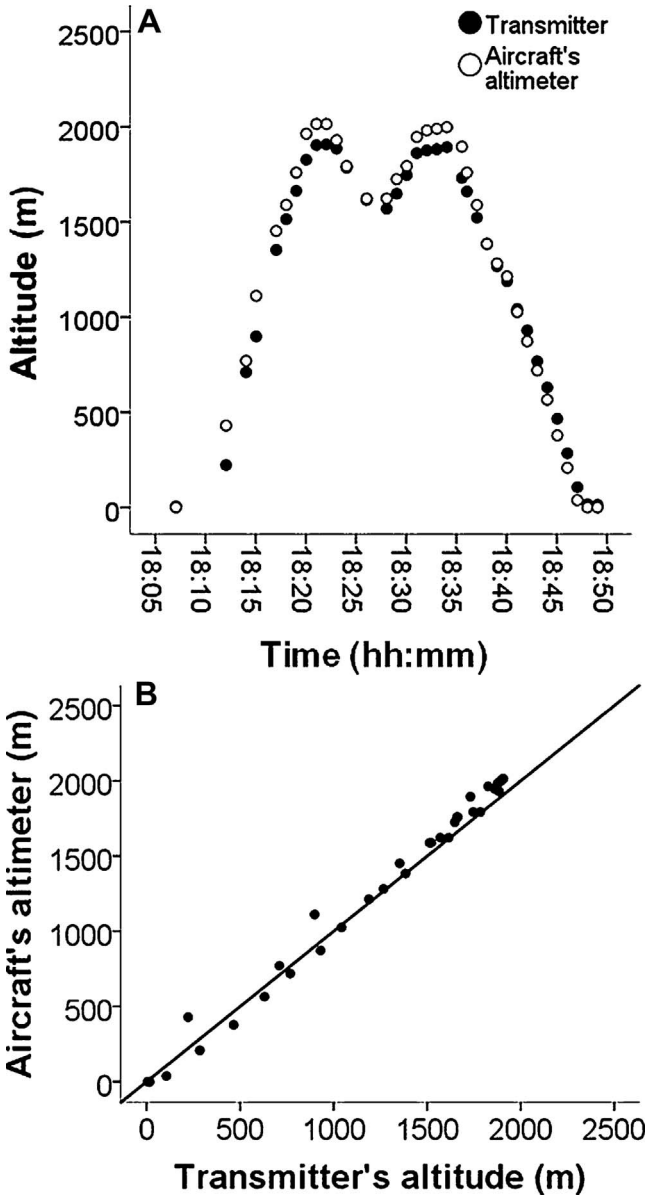

FIGURE 1. Data from an altitude transmitter taken aloft in a small aircraft, with data recorded simultaneously from the aircraft's altimeter. Part (**A**) shows the time course of altitude changes, and part (**B**) shows the correlation between the two altitude measurements, with a 1:1 line for reference.

TABLE 1. Capture and flight dates for Swainson's Thrushes carrying altitude transmitters.

Bird number	Year	Capture date	First flight date	Second flight date
Figure 4				
1	2011	May 14	May 19	—
2	2011	May 27	May 29	—
3	2012	May 9	May 15	—
4	2012	May 18	May 22	—
5	2012	May 24, June 2*	June 4	June 5
6	2013	May 24	May 24	May 28
7	2013	May 19	May 19	—
Figure 5				
1	2011	May 21	May 29	—
2	2013	May 14	May 14	—
3	2013	May 7	May 17	—
4	2013	May 29	May 30	—

*Bird 5 from 2012 was captured a second time in order to replace its transmitter's battery.

ascend to at least 100 m; thus, it could not vary its altitude like the other individuals.

We obtained temperature and pressure measurements from the sound files, at first by visual interpretation of the binary (32-bit) signal (2010; Figure 2), and later with a custom-built analysis program created by T. Borries (2011–2012). Each bit was encoded into the signal as either audio on (1) or audio off (0). The analysis program allowed the user to manually line up a data burst with a template. The program then determined which bits were 'on' and which ones were 'off' and, when instructed, recorded the data. The user could see which bits the program considered to be on vs. off, so the user was able to avoid capturing incorrect data.

We did not include any altitude measurements for which we had questionable pressure readings (e.g., the signal was not strong, or it appeared that some bits were missing due to the antenna turning during recording); when we had accurate pressure readings but questionable temperature readings, the temperature reading nearest in time to the pressure reading was substituted for the missing reading, up to a maximum of 10 min. When the signal was poor, we often collected only a good temperature reading or a good pressure reading for a given data burst; combining these points allowed us to obtain additional altitudinal data. We analyzed data from the 9 long flights in order to determine the magnitude of the error that this method introduced into the questionable-temperature altitude estimates. On average, the difference between one temperature reading and the next (including data gaps and initial ascent, where temperature typically changed rapidly) was 0.068 ± 0.033°C, which correlated with an average difference in altitude of 4.65 ± 3.14 m. We therefore do not feel that this process greatly altered our results.

We used the pressure data (mb) from the transmitters to estimate altitude. We used rawinsonde soundings taken from the monitoring station closest to each bird's takeoff and landing location (see http://weather.uwyo.edu/upperair/sounding.html for details) to calculate the change in m mb^{-1} for that day. The average distance from the birds' takeoff locations to the rawinsonde sounding locations was 105.8 ± 3.9 km; the average distance from the landing locations to the rawinsonde sounding locations was 154.8 ± 84.4 km. The soundings were taken at 18:00 and 06:00 local time, so the surface pressure usually changed before the bird took off (typically around 21:00–22:00 local time). We therefore used our pressure data from the birds in the woods ~1–2 hr prior to takeoff as our surface pressure, and calculated approximate altitude accordingly. Once we had obtained approximate altitude, we counted the number of ascents or descents >100 m for each flight.

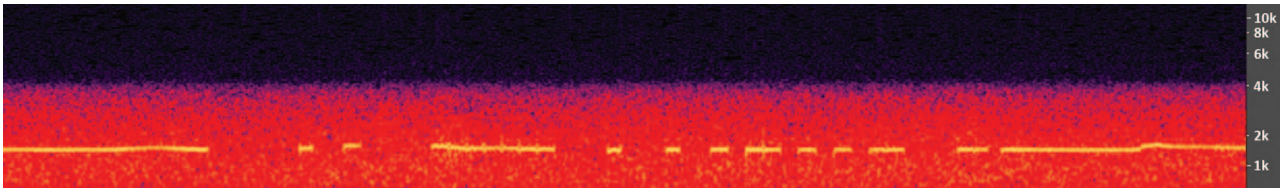

FIGURE 2. A data burst from a .wav file of an altitude transmitter, shown as a spectrogram with time on the *x*-axis and frequency on the *y*-axis. The signal includes a short pause, a start–stop bit, 16 bits of temperature data, a second start–stop bit, a short pause, a third start–stop bit, 16 bits of pressure data, and a final start–stop bit before the continuous frequency signal resumes. The audio signal is on for bits that equal 1, and off for bits that equal 0.

TABLE 2. Changes in barometric pressure during the flights of Swainson's Thrushes depicted in Figures 3 and 4, calculated from North American Regional Reanalysis data (http://www.emc.ncep.noaa.gov/mmb/rreanl/), and the corresponding changes in altitude and the elevation of the land from the beginning to the end of the flights. The final column shows the change in altitude estimates from the beginning to the end of each flight due solely to changes in barometric pressure during the flights (i.e. the variation not due to changes in topography from takeoff to landing).

Bird number	Change in surface pressure (mb)	Corresponding altitude change (m)	Elevation change (m)	Remaining altitude change (m)
1	−2.97	−26	−42	−68
2	−17.74	−160	108	−52
3	−13.13	−124	0	−124
4	−12.04	−117	20	−97
5a	1.81	17	−39	−22
5b	−32.28	−291	247	−44
6a	−0.18	−2	25	23
6b	−5.50	−50	17	−33
7	−11.54	−118	63	−55

We calculated changes in surface pressure during the long flights (Table 2) using data from the North American Regional Reanalysis model (NARR-A; http://www.emc.ncep.noaa.gov/mmb/rreanl/). We used NARR data from the latitudes, longitudes, and approximate times (NARR data is produced every 3 hr) of takeoff and landing for each flight. The average change in altitude corresponding with changes in surface-level barometric pressure during the flights was −96.94 ± 95.01 m. The average elevational difference between the takeoff and landing locations (Table 2) was 44.33 ± 89.13 m, meaning that changes in our estimates of altitude due solely to changes in barometric pressure during the flights averaged −55.44 ± 42.50 m. In other words, at the end of the flights, the actual altitudes of the birds were ~55m lower than our estimated altitudes. Because this discrepancy was small, varied among flights, and its analysis involved estimating several variables, we did not correct for it in our other analyses.

We measured initial ascent rates from the first data point that indicated ascent to a time where the bird descended for at least 2–3 min. None of the birds leveled off after ascending without first descending for >2 min. We measured final descent rates from the last peak in altitude to the final altitude measured. We were not able to obtain final descent rates for all 9 of the full or nearly full flights because we were not always close enough to the bird when it landed to record the entire descent. All of the average results that we report are given as mean ± SD.

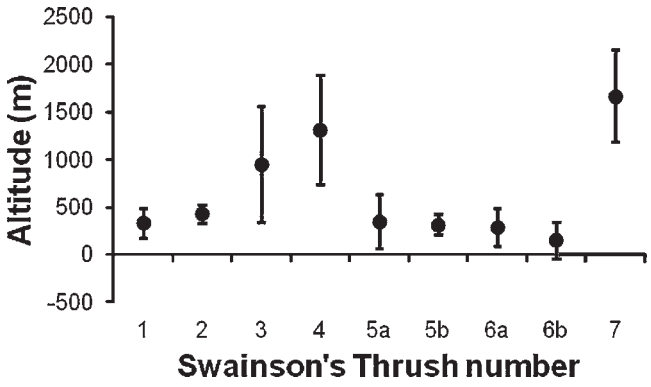

FIGURE 3. Average altitude (mean ± SD) of 7 Swainson's Thrushes (birds 1–7) making 9 migratory flights over the Midwestern United States (letters denote more than one flight by the same individual).

RESULTS

Initial ascent rates (0.42 ± 0.15 m s^{-1}, $n = 8$) closely matched previous estimates (Cochran and Kjos 1985); final descent rates were slightly faster than initial ascent rates, at 0.55 ± 0.30 m s^{-1} ($n = 5$). Average recorded flight altitude for the 9 flights was 673.0 ± 523.2 m (Figure 3); average maximum flight altitude was 1,199.5 ± 862.7 m (range: 319.2–2,744.5 m).

During the 9 flights, none of the thrushes maintained a constant flight altitude (Figure 4). The birds made an average of 9.33 ± 4.42 large (>100 m) deviations from their previous flight altitude (1.44 hr^{-1}), not including initial ascent and final descent. Two birds (3 and 7) continued increasing their altitude throughout much of their flight, 2 birds flew up to 600+ m and then descended to <400 m after 1–2 hr (birds 5a and 6a), and 3 remained below 700 m throughout their entire flights, but ascended and descended repeatedly (birds 1, 2, and 5b). One (bird 6b) flew at an altitude below 100 m for >1 hr and only then ascended to ~400–600 m, and one (bird 4) reached its maximum altitude (~2,100 m) several hours into the flight, after which it gradually descended to ~800 m only to ascend to ~1,150 m before landing.

All 3 of the thrushes that we lost (Figure 5) varied their altitude >100 m in the relatively short time that they were tracked, consistent with our observations of the birds that we followed from takeoff until landing. We believe that the

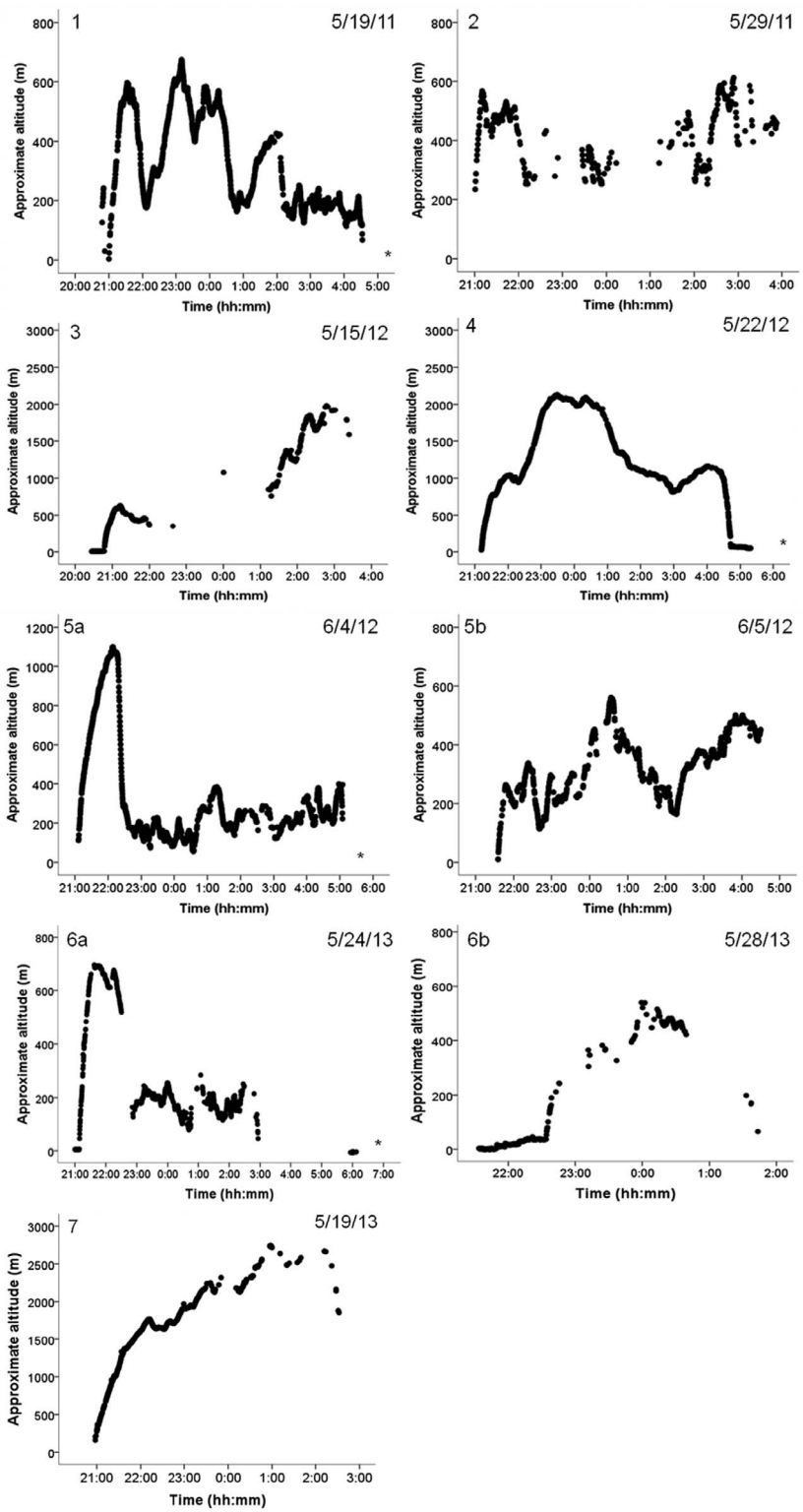

FIGURE 4. Altitude data for 7 Swainson's Thrushes (birds 1–7) making 9 migratory flights over the Midwestern United States (letters denote more than one flight by the same individual). Flights for which we are certain that birds landed immediately or shortly after we lost the signal are marked with an asterisk; times given are local (CST).

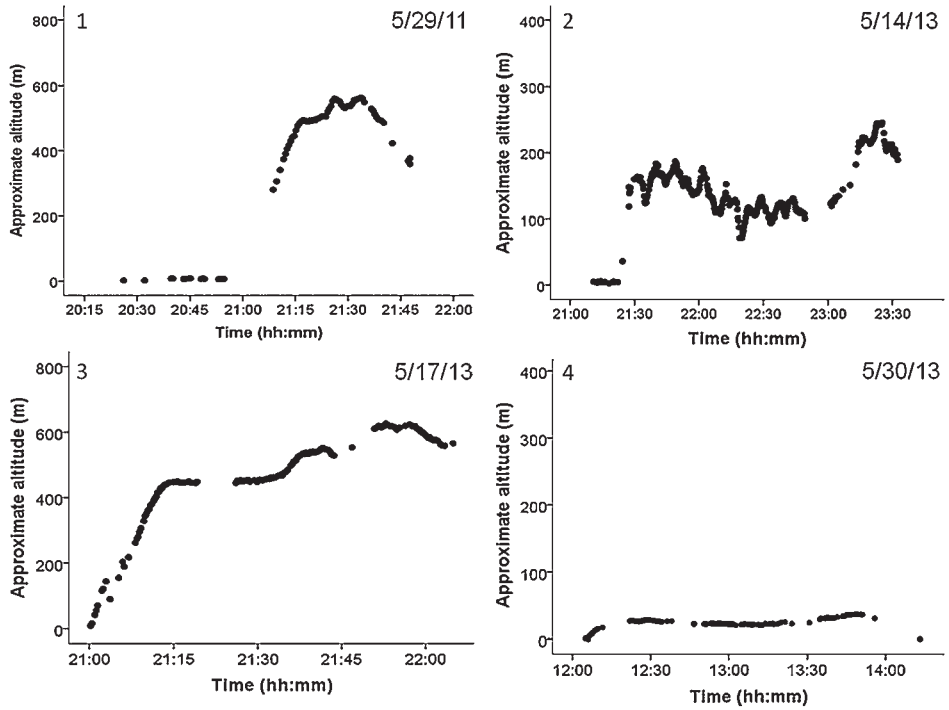

FIGURE 5. Data from 3 additional Swainson's Thrushes lost after 0.75–2.00 hours (birds 1–3) and 1 (bird 4) that made a very short, low-altitude flight. Bird numbers are for different birds from birds shown in Figures 3 and 4.

fourth bird in Figure 5 may have been making a short flight to escape the area, as it took off after midnight (00:05), later than all of the other thrushes, and flew for <2 hr at <40 m.

DISCUSSION

As predicted by radar studies (Gauthreaux 1991), 5 of our 9 flights took place at altitudes entirely below 1,000 m. However, Swainson's Thrushes did not behave like commercial aircraft, ascending to a particular altitude, leveling off, and then making a final descent (Irschick and Garland 2001, Cochran et al. 2008, Pennycuick 2008). Nor did they behave according to predictions that they would sample the winds before descending to a particular flight altitude, or that they would be restricted to small ascents following initial ascent (Cochran and Kjos 1985). Instead, all of the thrushes repeatedly made large (>100 m) ascents and descents throughout their flights (Figure 4).

On the surface, our results appear to be similar to those of Bishop et al. (2015), who found that Bar-headed Geese saved energy when crossing the Himalayas by ascending and descending more often than necessary (an 'undulating' flight strategy). However, this strategy saved energy only because the geese were able to lower their average flight altitude by flying close to the ground, and flight costs increased dramatically with altitude. The geese would not have ascended to high altitudes, except that they had to successfully cross the mountain range. Had there been no mountains to fly over, an undulatory flight strategy would not have been the most energetically efficient strategy; 'cruising' at a low, constant altitude would have been more cost-effective (Bishop et al. 2015). The terrain that our Swainson's Thrushes flew over changed little in elevation (maximum of $\sim$250 m), so an undulatory flight strategy such as that observed by Bishop et al. (2015) could not have benefited our birds.

Swainson's Thrushes should use more energy while ascending than they save by descending (Tucker 1968), so they should not repeatedly ascend and descend during flight if they are attempting to minimize energy used per unit time. Note, however, that this energetic relationship only holds in the absence of wind; for migrating birds, wind speed and direction are important variables (e.g., Bowlin and Wikelski 2008). We do know that the variation in altitude that we observed cannot solely have been due to the birds passively encountering up- and downdrafts: Preliminary data on the wingbeat frequency of one of our thrushes indicate that it actively changed its flight altitude by varying its actual and effective wingbeat frequency (see definitions in Cochran et al. [2008]). It flapped continuously and increased wingbeat frequency before it ascended, and it paused and decreased wingbeat frequency before it descended (B. Murphy personal observation). This is consistent with wind tunnel observations of actual and effective wingbeat frequency in relation to vertical airspeeds in passerines (Bruderer et al. 2001).

Unfortunately, until we analyze data on wingbeat frequency and pauses from all of the flights, we cannot pinpoint the exact locations where the thrushes began to ascend and descend. As a result, the ultimate explanation for the behavior that we observed remains unclear. One likely possibility is that the thrushes were responding to fine-scale variation in atmospheric conditions, even though atmospheric conditions near the Earth's surface vary considerably less at night than they do during the day (Stull 1988, Roth et al. 1989). Because migrants attempt to concurrently minimize time, energy, and risk (Alerstam and Lindström 1990), the thrushes may have been using this fine-scale variation to minimize a variable (or variables) other than energy consumption, such as ground speed. Alternatively, cities and towns can create strong thermals during the day that persist into the beginning of the night (Roth et al. 1989). Songbirds could use lift from these thermals to increase their altitude without increasing their flight costs. If so, they might increase actual and effective wingbeat frequency upon encountering the leftover thermals so as to take maximum advantage of the lift provided, much as soaring birds take advantage of thermals by repeatedly circling inside them (e.g., Pennycuick 1998).

Conversely, we know that small migratory birds are attracted to lights in or on communication towers, skyscrapers, lighthouses, and oil rigs (Squires and Hanson 1918, Wiese et al. 2001). It is possible that they are also attracted to the lights in cities and towns, as well as those on lone communication towers, and descend over these areas, after which they ascend to a higher altitude. However, to our knowledge this has never been observed in, for example, radar studies on the flight altitudes of groups of migrants. A final possibility is that the altitude changes involve orientation or navigation strategies. *Catharus* thrushes make few, if any, changes to their headings during flight (Cochran and Kjos 1985, Cochran et al. 2004), suggesting that the birds are not descending to obtain visual cues to reorient themselves. This observation does not, however, preclude more complicated relationships between flight altitude and orientation or navigation.

Although there was a great deal of variation, Swainson's Thrushes tended to fly relatively low as dawn approached. Migratory flight calling rates for thrushes detected from the ground are higher close to dawn than earlier in the night (Ball 1952, Cochran and Graber 1958, Farnsworth 2005). Our data could explain this observation in two ways. First, ground-based microphones may detect birds flying close to the ground more often than they detect birds flying at higher altitudes. Second, thrushes might produce more flight calls as relative bird density increases near dawn when more individuals are flying at low altitudes.

Flying at low altitude can also increase the probability of colliding with man-made structures. At various times, the flight altitudes of many of our Swainson's Thrushes were well within the area of the aerosphere where tower-strike is a possibility (<200 m; Figure 4). Collisions pose a significant risk to migratory birds (e.g., Calvert et al. 2013); if we wish to minimize tower-strike, we need to further elucidate the factors that cause thrushes and other nocturnal migrants to fly at certain altitudes by testing the hypotheses outlined above.

In conclusion, the first detailed full-flight data on the flight altitude of migratory passerines show that Swainson's Thrushes repeatedly ascend and descend throughout their flights. While we believe that these changes are proximately a result of variation in wingbeat frequency, we do not know their ultimate cause. We believe that the most likely explanations are that the thrushes vary their altitude because of the atmospheric conditions or the man-made structures that they encounter during flight. Regardless, this behavior almost certainly affects both the thrushes' energy budgets and collision risks.

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