Article

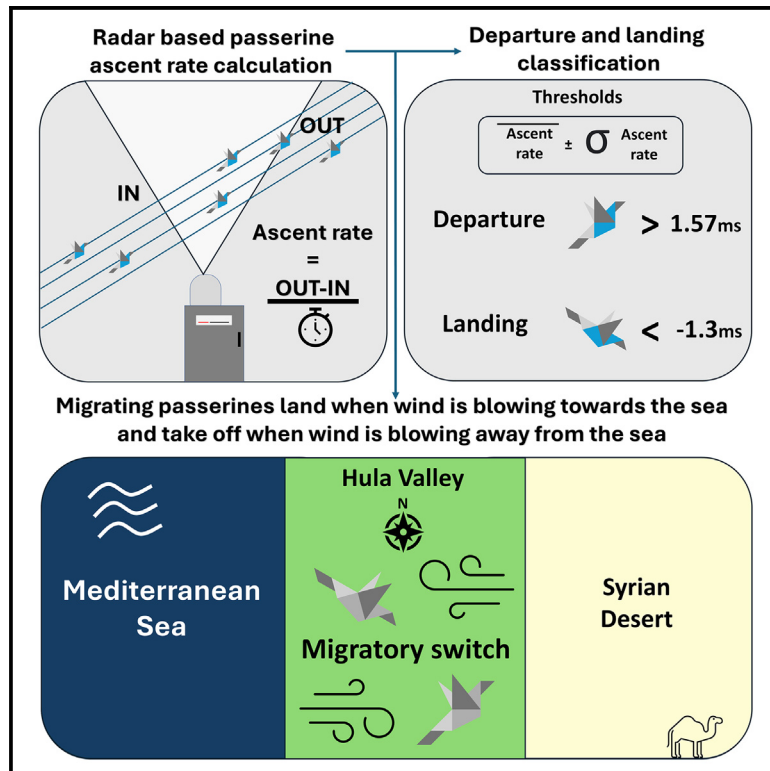# Radar-measured passerine vertical speeds reveal a migratory switch near a major barrier

Graphical abstract

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In brief

Ecology; Zoology; Ornithology

Highlights

- Vertical-looking radar is used to accurately calculate passerine vertical speed

- Radar-calculated vertical speeds are used to characterize migration behavior

- Migrating passerines in the Hula Valley land to avoid drifting toward the sea

- Migrating birds avoid detrimental conditions by timing departure and landing

CellPress

Article

Radar-measured passerine vertical speeds reveal a migratory switch near a major barrier

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SUMMARY

Successful accomplishment of long-distance migration necessitates optimal decision-making processes. Throughout their migration, birds need to constantly choose to fly or to stop. Passerine migrants integrate internal (e.g., lipid deposition) and external (e.g., prevailing winds) factors resulting in specific departure or landing times. We calculated individual departure and landing timing using vertical-looking radar in the Hula Valley, compiled nightly departure and landing ratios (departure and landing amounts relative to total migration flux), and explored how these are affected by meteorological conditions. Crosswind direction emerged as a key factor affecting departure and landing decisions during autumn migration in the area. Birds avoided drifting toward the Mediterranean Sea by landing and preferred taking off when winds blew away from the sea. Our findings represent an undescribed migration initiation and termination switch with implications for flight and stopover scheduling. The method extends the scope of aeroecological research for addressing individual-level migration behavior.

INTRODUCTION

Long-distance aerial migration is an important biological phenomenon during which animals quickly fly through vast expanses in a seasonally repetitive manner. Migrants must undertake short bursts of intense flight activity, requiring dedicated physiological processes (e.g., lipid deposition, organ and tissue atrophy and regeneration,[1] and high tolerance to oxidation stress[2]) and behavioral changes such as hyperphagia and nocturnal "zugunruhe."[3] Flight and stopover scheduling are critical aspects of bird migration[4–6] that have important implications for migrant physiology, migration phenology, and carryover effects, including reproductive output in the breeding seasons following migration.[7,8]

While on route, migrants constantly make decisions regarding departure for flight and landing for stopover until they reach their destination. These decisions are based on intrinsic factors (e.g., lipid deposition) and extrinsic conditions (e.g., prevailing wind).[9–11] A migratory bird will initiate its departure flight when it is physiologically prepared, balancing potential benefits from staying in its stopover habitat with progress toward the destination and future benefit from next stopover sites. Once airborne, migrants face ambient weather, which changes across altitudes and along the route, directly affecting the cost of travel, which is related to metabolic expenses of flight and migration time.[12,13] Thus, at any given moment, birds choose between flying and landing (with the exception of flight that must continue when flying over hostile terrain like open sea for migrating landbird). These decisions greatly affect travel duration and energetics, as well as the probability of completing the journey. It is therefore assumed that they evolved to maximize bird fitness.[9]

Departure decisions, made on the ground, have been the subject of extensive study.[14] Landing decisions, which occur at high altitude, have only been rarely studied,[15] possibly because they are much more challenging to detect. Here, we employ radar to document bird ascent rates, analyze both departure and landing decisions, and explore the factors affecting them. The BirdScan MR1 vertical-looking radar (VLR) detects individual passerine-sized biological objects and can accurately resolve flight parameters (altitude, speed, and direction)[16] and target properties (size, shape, and wing flapping frequencies) up to a kilometer above ground.[17,18] MR1 radar systems are spread throughout Europe[19] and the Middle-East,[20] documenting aerial activity of birds, bats, and insects over long periods for monitoring, research, and conservation. We used the MR1's fine altitudinal resolution of 1.5 m to calculate vertical speed (Figure 1) and create a set of vertical movement-related parameters and classified all nocturnally migrating passerine targets as "ascending," "descending," or "cruising." Our strict classification criteria ensured that descending migrants were most likely intending to land and ascending migrants were likely departing. Our preliminary exploration of ascent and descent patterns throughout the night in different seasons supports our classification, forming a basis for further analysis (Figures 2 and S1).

We present a study of passerine migration through the Hula Valley, a major migration hotspot on the globally important Eurasian-Afrotropical migration flyway, exploring how migration departure and landing vary through time and meteorological conditions over a 5-year period. Our novel use of individually tracked radar targets to directly study takeoff and landing is important for a fundamental understanding of decision-making
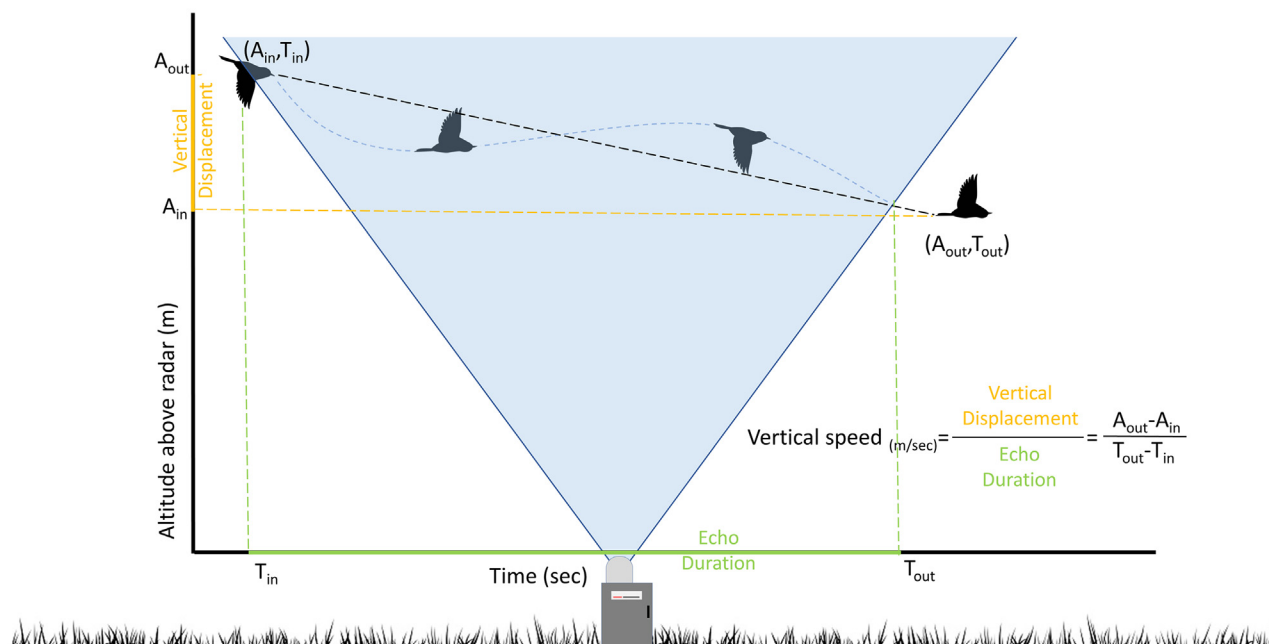
Figure 1. Vertical speed calculation from BirdScan MR1 radar data, based on flight altitude and timestamp of entry (A_{in}) and exit (A_{out}) points, forming target vertical displacement ($A_{out} - A_{in}$) and tracking duration ($T_{in} - T_{out}$)

Vertical speeds (vertical displacements/tracking duration) are used for classifying targets as "departing," "cruising," or "landing" using extreme values (mean ± SD). These behavioral groups (departing, landing, and cruising) are explored throughout the manuscript in terms of phenology and response to environmental conditions.

processes made by birds on the move, as well as for mitigating anthropogenic threats to aerial habitats and migration systems.

RESULTS

We used VLR data to study departure and landing decisions of passerines in the Hula Valley, an important site for migrants preparing to cross the Sahara or recovering from its crossing. We used these data to calculate vertical velocities of individual passerines when passing through the radar cone, which allowed us to identify general patterns of songbird stopover/departure decisions by classifying each bird based on its vertical speed as "departing," "cruising," or "landing" using statistically defined and literature-supported thresholds. We study the products of identifying individual departure and landing decisions (Figure 1) in five years of VLR data from the Hula Valley, describing migration phenology and the meteorological factors affecting it.

VLRs detect every vertebrate passing through their detection range, meaning our data necessarily contain an unknown proportion of local movements by foraging or commuting residents and also local movements by migrants on stopover. These do not set out on migration when detected by the VLRs. Strong migration-related patterns, including an expected vertical velocity distribution throughout the night (Figure 2) and expected yearly phonologies that differ between migration and non-migration months (Figures S4 and S5), which clearly stand out in our database, lead us to believe that migration is the dominant ecological process during migration seasons in the Hula Valley. We further rely on very low nocturnal passerine activity rates dur-

ing non-migration season (Figures S4 and S5) as a baseline of resident activity rate in the region and regard all activity above the baseline as migration related (either migration flight or local stopover movements). Thus, we interpreted our results as describing migration-related processes.

Departing and landing passerines in the Hula Valley

Using songbird vertical speed measurements and applying thresholds for identifying landing and departure events based on mean +SD values of the speeds, we identified landing if vertical speed of descent was at least 1.57 m/s and departure if vertical speed of ascent was at least 1.30 m/s. Using these thresholds, we estimated average amounts of landing and departing migrating passerines in the Hula Valley, as summarized in Table 1.

Evening nautical twilight was the busiest departure period during the night, with 23.26% of passerines departing in this period in spring and 16.68% in autumn (landing rates in the same period were 12.89% and 10.29%, respectively). Morning civil twilight was the busiest landing period, with 18.43% of passerines landing in this period in spring and 21.95% in autumn (departure rates in the same period were 7.74% and 7.00%, respectively. See Table S3 for full breakdown).

Yearly phenology

Migration traffic rate (MTR), a standardized measure of bioflow, describes the number of birds crossing a 1 km transect of airspace. It is calculated based on the number of detected targets (in our case classified as passerines) and considers each
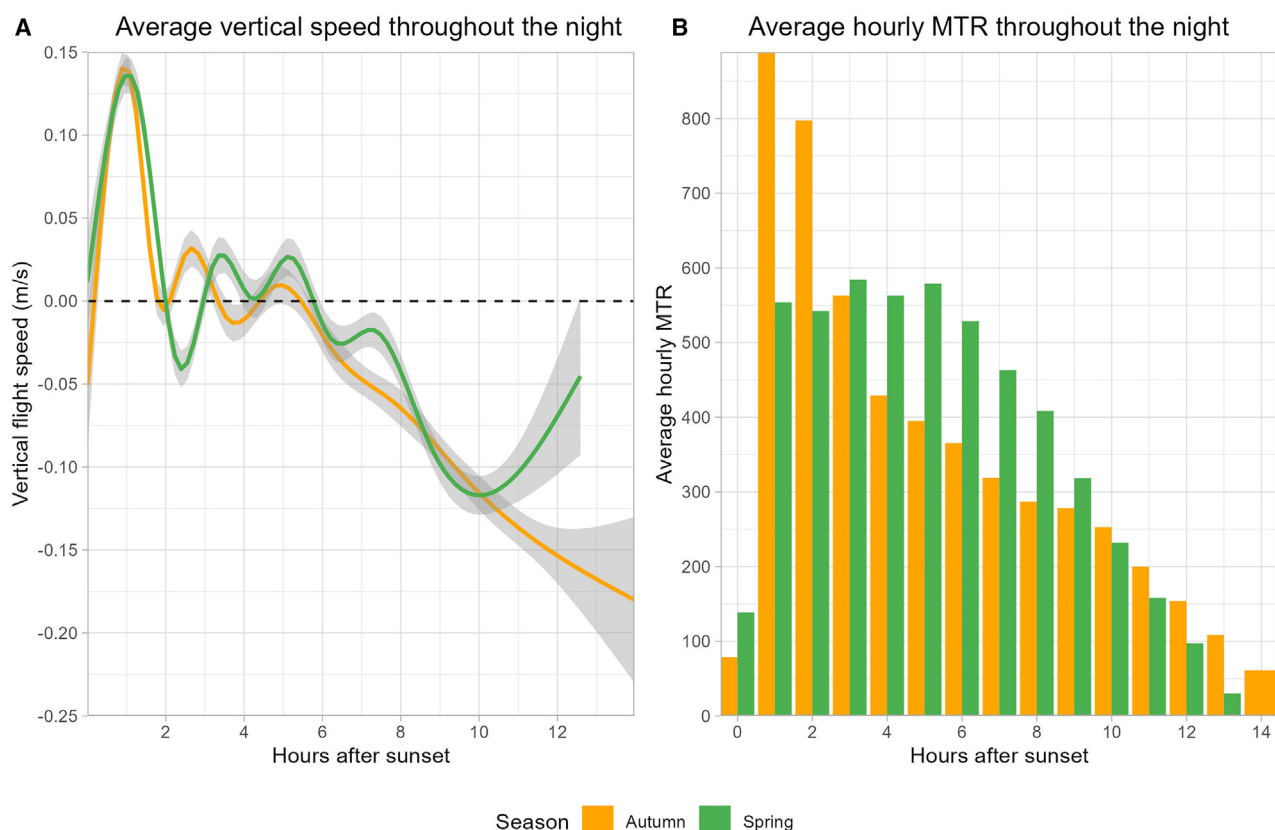
A Average vertical speed throughout the night

B Average hourly MTR throughout the night

Season ▮ Autumn ▮ Spring

Figure 2. Passerine vertical speeds throughout the night during migration seasons in the Hula Valley
(A) Average vertical speeds throughout the night show the expected passerine migration pattern of steep ascents after sunset, indicating mass departures, and steep descents before sunrise, indicating mass landing. During the middle part of the night, mean vertical speed is around zero, indicating cruising flight.
(B) Hourly migration traffic rates (MTRs) throughout the night during migration seasons, revealing high nocturnal passerine activity.

echo's radar cross section and altitude in order to account for size- and range-related detection biases. Yearly nocturnal passerine phenology in the Hula Valley exhibits low activity in summer and winter and high migration fluxes, including departure and landing activity during spring and autumn (Figure S4A).

We found that the dynamics of the landing phenology is similar to that of the general passerine migration phenology, as indicated by a strong, significant correlation between nightly landing and total MTR (Table S3, r > 0.72) resulting in a drastic increase in the number of passerines landing in the valley during migration seasons when the overall migration of passerines was more intense (Figures S4A and S4B). Landing ratios (landing MTR/total MTR), which standardized landing and departing numbers in relation to the overall flow, reveal that the relative amounts of landing passerines in migration seasons (11.8% ± 6%), when

millions of passerines pass through without landing, are significantly lower (Wilcoxon $p < 0.0001$) and steadier than those during non-migration seasons (13.7% ± 7%, Figure S4C), as expected since non-migration periods are characterized by much lower traffic rates.

Nightly vertical speed pattern

Passerine migration in this region occurs primarily at night with most birds taking off after sunset and landing at the end of the night, before sunrise (Figure 2, see Table S3 for detailed breakdown of evening and morning twilight periods). During migration seasons, positive vertical speeds (indicating departures) were observed in the first third of the night, negative vertical speeds (indicating landings) during the last third, and vertical speeds of roughly zero during the middle part of the night, suggesting that most birds are in steady cruise flight during this time (Figure 2). During non-migration seasons (winter: December–February, summer: June and July), nightly patterns are different and likely represent local and stochastic processes, as nocturnal passerine movement is much lower during non-migration nights, as indicated by the low monthly sample sizes in these seasons (Figure S1). The analysis validates our method (Figure 2) by clearly showing the expected nightly pattern during migration

Table 1. Radar-based estimated amounts of landing and departing passerines in the Hula Valley during migration seasons

Season	Landing passerines		Departing passerines	
	1 km transect	Hula Valley	1 km transect	Hula Valley
Spring	50,945 ± 22,405	407,560	53,096 ± 21,035	424,768
Autumn	68,007 ± 3,519	544,000	77,922 ± 10,268	623,376

seasons, as described in previous studies,[21–26] and its absence in summer and winter when nocturnal passerine movement is largely absent (Figure S4). During migration periods, the mean (SD in parentheses) for the first part of the night = 0.018 (0.25) m/s, the mean of part 2 of the night = −0.03 (0.21) m/s, and the mean for part 3 of the night = −0.11 (0.2) m/s. Accordingly, differences between the second part of the night (when migrating passerines are mostly engaged in cruising flight) and the first or third parts of the night (when, during migration, passerines are taking off and landing, respectively) were highly significant during migration seasons: t(1–2) = 4.7, p(1–2) < 0.00001, t(2–3) = 7.4, and p(2–3) < 0.00001. These were not significant during non-migration seasons (mean of part 1 of the night = −0.22 (0.61) m/s, mean of part 2 of the night = −0.15 (0.89) m/s, and mean of part 3 of the night = −0.22 (0.5) m/s; t(1–2) = −1.2, p(1–2) = 0.19, t(2–3) = 1.5, p(2–3) = 0.13).

Meteorological factors affecting descent and ascent ratios

During autumn, the W-E (West-East) component of the wind vector was the most important covariate affecting both descent and ascent ratios, but in a contrasting manner (Figure 3). The relative number of descending passerines nearly doubled when winds blew westwards toward the Mediterranean Sea, accounting for more than 23% of the variance explained by the model. The relative number of ascents increased to more than twice the minimum when winds were blowing toward the east, away from the Mediterranean Sea, accounting for nearly 32% of the variance explained by the model. Interestingly, the lowest departure and landing rates were found when crosswind was calm. These results provide important insights regarding the birds' decision-making process, describing a migratory switch in departure and landing behavior depending on crosswind direction. Interestingly, the difference between the W-E component of the wind vector of a given day and the preceding day on the ground was the third most influential factor in the departure ratio model (relative importance: 8.94), with higher departure ratios when the wind was blowing more toward the west the previous night, causing more birds to land in the area. The same parameter had no tangible effect on landing ratio (relative importance: 1.93), as expected since descending individuals were arriving from distant locations and were not exposed to local conditions on the previous night. Variability between years, the second most important parameter in both models, was substantially higher for landing ratios (relative importance: 22.15, up to ∼40% difference between consecutive years), with both departure and landing ratios showing similar inter-year variation that was nonetheless more strongly influencing the landings. The relative importance of all other weather covariates, as well as moon covariates, is given in Table 2. The autumn landing ratio model had a cross-validation correlation (indicator of model accuracy based on consistency of output over multiple iterations[27]) of 0.70, and that of the departure ratio was 0.62.

In spring, ordinal date was the most important covariate explaining landing ratios (relative importance: 31.44, up to ∼80% maximal difference), suggesting that the number of passerines landing in the Hula Valley is substantially higher in the second half of the season. This, together with rather stable departure ra-

tios, implies that passerines accumulate in the valley, possibly corroborating its known function as a major regional stopover area as well as being an important breeding area for individuals not migrating further north.[28–30] The S-N (South-North) component of the wind (tailwind speed) was the most important covariate in the departure ratio model (relative importance: 17.32, up to ∼35% maximal difference), indicating an increased tendency to depart in favorable tailwind conditions as wind blows toward the north. The same parameter had a weaker (relative importance: 6.12), opposite effect on the landing ratio, suggesting a tendency of migrants to stop over under headwind conditions. Difference in temperature between a given migration night and the previous night proved influential for departure ratio (12.84% of total variance explained, up to ∼30% maximal difference), with higher departure ratios when a warm day is preceded by a much colder day. The spring landing ratio model had a cross-validation correlation of 0.72, and that of the landing ratio was 0.40.

DISCUSSION

Migrating passerines undertake astonishing feats under extreme physiological stress. In order to optimize their progress,[9,11] migrants constantly balance overall costs and benefits of departing for flight with those of landing for stopover. These decisions form crucial junctions where a wrong turn may lead to death, delay in arrival at the final destination, or completing the journey in a degraded physiological condition.[7,8] The latter two likely entail detrimental carryover effects on reproduction success, especially in spring, due to hampered breeding conditions and environmental circumstances at the time of arrival (unavailable territory and resources and asynchrony with food web components).[31–33] Thus, suboptimal decisions induce strong selective pressure against making the wrong choice.

The BirdScan MR1, radar capable of characterizing individual animal activity in the air, is an excellent platform for studying aerial animal decision-making.[16] In our case, departure and landing properties of passerines during migration seasons were comprehensively studied. Our stringent approach for defining targets as departing or landing efficiently filtered sporadic altitudinal changes, as demonstrated by the hourly pattern of passerine vertical speeds throughout the night (Figure 2A), which were statistically different between migration and non-migration seasons (Figures 2 and S1). When studying migration using animal-borne devices, an animal's propensity to migrate is usually studied in individuals that have been identified to the species level and for which age, sex, and morphology are determined. Furthermore, in some cases, the animal's physiological state (e.g., level of subcutaneous lipid stores) is also considered. Yet, these are currently unobtainable through VLR tracking. Radar methodologies are oriented toward macro-scale observation or analysis, and we accordingly rely on phenological and ascent rate-related patterns. We base our conclusions on analysis of more than half a million individual observations as the basis of our approach as being descriptive of migration in the study area.

Here we present the first method to study these decisions (both takeoff and landing), which form the temporal structure of individual migration journeys and scale up to shape entire migration
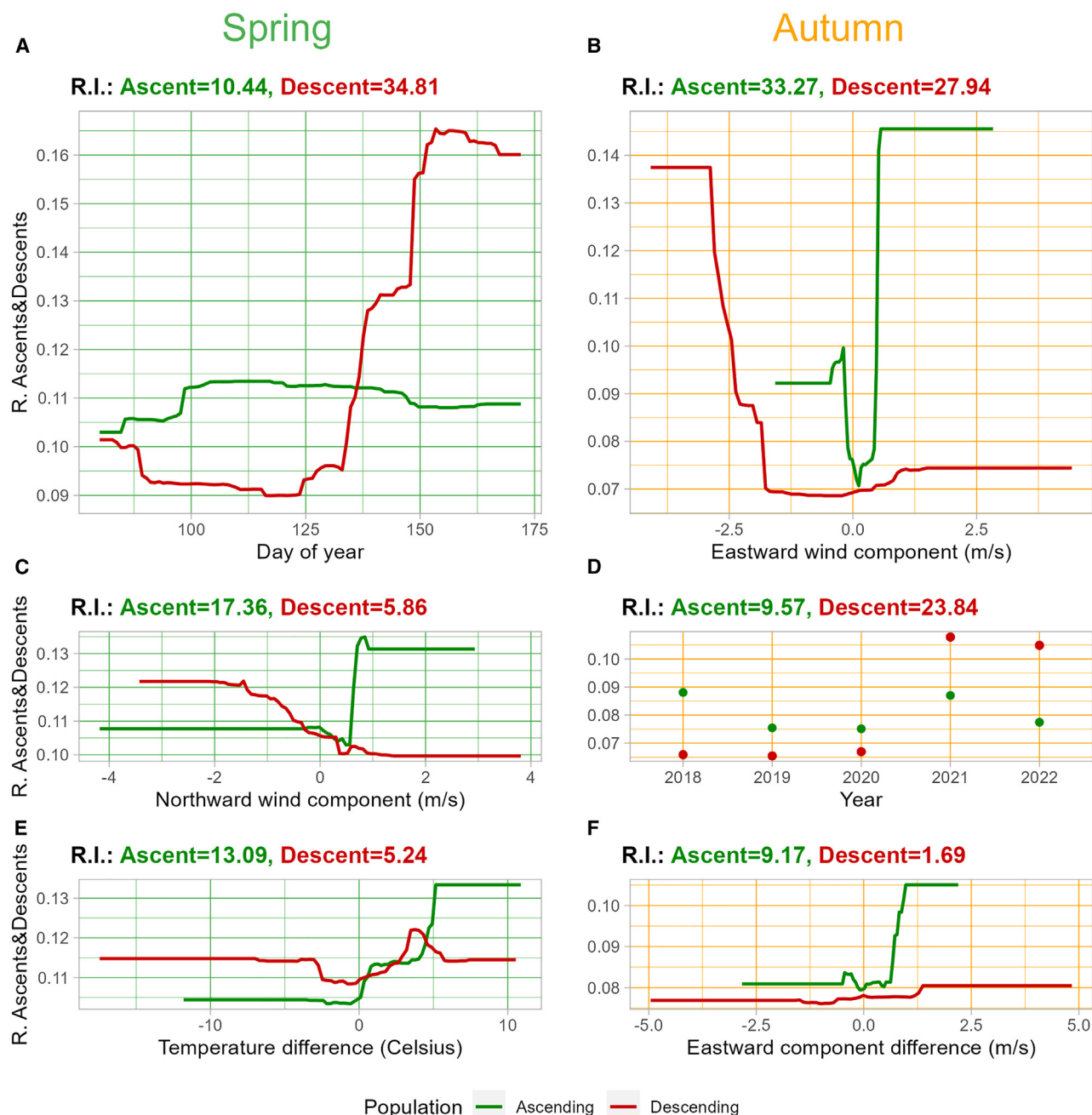
Spring

A

R.I.: Ascent=10.44, Descent=34.81

Autumn

B

R.I.: Ascent=33.27, Descent=27.94

C

R.I.: Ascent=17.36, Descent=5.86

D

R.I.: Ascent=9.57, Descent=23.84

E

R.I.: Ascent=13.09, Descent=5.24

F

R.I.: Ascent=9.17, Descent=1.69

Population — Ascending — Descending

Figure 3. Boosted regression tree model results of effects of the most influential environmental covariates during migration seasons on departure and landing ratios

Relative importance (R.I.) is provided for each parameter in the departure ratio and the landing ratio models. Full model details are provided in Table 2.

systems, based on real-time observations of passerines by radar. The output of our method, i.e., long term, individual-level datasets detailing departure and landing decisions across hundreds of thousands of individuals, enables application of data-science approaches to the study of takeoff and landing decisions, stopover ecology, and relationships between the aforementioned and various environmental factors. Exemplified here in the study of

nocturnal passerine movements during migration in one location, radar-based takeoff and landing analysis can be implemented on other types of birds, bats, and insects documented in any station of the quickly expanding network of BirdScan MR1 radar.[19] Such large-scale application, which would be straightforward based on principles and technique presented here, will add a new level of detail to migration research, namely that of individual-level takeoff

Table 2. Model output tables for departure and landing ratios for spring and autumn

Spring descending ratio model results	Relative importance	Spring ascending ratio model results	Relative importance
Day of year	31.44	S-N wind vector	17.32
Year	12.01	temperature diff	12.84
W-E wind vector	8.01	temperature	11.04
S-N wind vector	6.12	day of year	10.09
Moon fraction	5.40	vertical wind velocity	7.64
Vertical wind velocity	5.73	moon phase	5.45
Temperature diff	5.03	humidity	4.05
W-E wind vector diff	3.27	W-E wind vector	4.00
Temperature	3.64	moon angle	4.63
Cloud cover	3.14	year	8.53
Humidity	3.39	cloud cover	4.13
S-N wind vector diff	2.91	S-N wind vector diff	3.01
Moon phase	2.61	W-E wind vector	2.99
Ground level air pressure	3.48	ground level air pressure	2.32
Moon angle	2.71	moon fraction	1.87
Cross-validation correlation	0.72	cross-validation correlation	0.40
Autumn Descending ratio model results	Relative importance	Autumn Ascending ratio model results	Relative importance
W-E wind vector	23.16	W-E wind vector	31.77
Year	22.15	year	9.19
Day of year	9.58	W-E wind vector diff	8.94
Humidity	8.42	humidity	7.57
Vertical wind velocity	6.79	temperature diff	6.96
Moon phase	4.57	S-N wind vector	6.53
S-N wind vector diff	4.24	temperature	6.26
Cloud cover	3.39	vertical wind velocity	4.05
Temperature	2.98	ground-level air pressure	3.76
S-N wind vector	2.97	moon fraction	3.60
Moon angle	2.86	S-N wind vector diff	3.21
Ground level air pressure	2.77	cloud cover	2.38
Moon fraction	2.28	moon angle	2.30
W-E wind vector diff	1.93	day of year	1.84
Temperature diff	1.82	moon phase	1.56
Cross-validation correlation	0.70	cross-validation correlation	0.62

Boosted regression tree models assign a relative importance (R.I.) index to each explanatory variable. These are comparable across models and reflect the strength of the effect each parameter has on the dependent variable.

or landing decisions, which will increase our understanding and improve prediction capabilities.

We calculated vertical speed from BirdScan MR1 output (Figure 1) and directly described both departure and landing behaviors during migration seasons based on yearly, seasonal, and nightly patterns of ascent speed (Figures 2 and S1), providing numeric and relative estimates of departing and landing migrants in different parts of the night and exposing important factors influencing passerine landing and departure in the Hula Valley (Figure 3). We describe a migration switch depending on cross-wind direction for autumn migrating passerines, as well as effects of prior day conditions. During spring migration, tailwinds

induced departure, and landing increased as the season progressed (Figure 3). Thus, our work provides a direct and multifaceted view of migratory decisions including bird landing, departing, and cruising in the heart of a globally important migration flyway, the Eurasian-Afrotropical migration system. By applying our method of detecting departures and landings over several years of data collection, we revealed important aspects of passerine decision-making during migration near two of the flyway's major barriers, the Mediterranean Sea and the Saharo-Arabian desert belt. The Hula Valley is located on a major flyway, such that local migrants arrive from a very wide geographic range.[28,30,34,35] Local migration intensity is thus affected by a

combination of environmental factors and ecological and phenological circumstances at multiple temporal and spatial scales.[36] The use of departure and landing ratios rather than absolute traffic rates (which are affected by a multitude of factors occurring throughout the entire source area of any given migration night) successfully exposed local migration patterns and key explanatory factors. Ratios standardize the nightly, source area-driven, variability in departure and landing counts to migration fluxes, creating standardized measures which are informative regardless of actual bird densities in a given night,[37] allowing the study of departure and landing decisions as a separate process from that driving the overall traffic rate.

Our results suggest a migratory switch depending on the direction of crosswind, such that, in autumn, passerines tend to land when winds blow westward toward the Mediterranean Sea, and more birds depart from the area when the airflow was from the sea toward inland. The decreased tendency to land or depart at zero crosswind conditions is intriguing, possibly suggesting that passerines prefer to keep flying and do not depart or land under no or very weak crosswind. The higher tendency for landing when winds blow toward the sea may result from a general behavioral preference of migrants in the region to avoid a westward drift over the sea or close to the sea.[38] Such a tight connection with specific meteorological factors indicates a clear tendency to react to potentially detrimental conditions, as documented in other systems.[39] We find it reasonable to expect migrants to employ similar (though perhaps weaker) responses to actively optimize their migration rather than to avoid detrimental conditions, as implied by previous works.[6] These are to be expected when conditions are suboptimal for migration (depending on physiological state, age, etc.[40]) and should not exclusively require the existence of extreme spatial features like barriers.

The primary factor moderating departures in spring points to another facet of migration optimization as passerines departed under tailwind conditions and landed when headwinds were prevalent. These imply energy- and time-related considerations that are not necessarily related to the proximity to ecological barriers. Research in various systems indicates that some migrants are highly selective in terms of suitable wind conditions for departure,[41–43] while others are inconsistent.[44] This variability likely results from different considerations of migrants in light of various experienced ecological circumstances. Model results suggest that passerines in the region are overall less selective during spring migration in terms of flight conditions compared with autumn (see also Schekler et al.[45]), possibly due to strong pressure to breed in specific time windows following spring migration.[46,47] In general, it seems that departing birds experience a narrower range of weather conditions compared to landing birds (Figure 3, weather covariates), which is reasonable since departing passerines may respond to local conditions, while landing migrants, which alight long after their departure, are exposed to more variable conditions, commonly over several hundred kilometers during their nocturnal flight, and may integrate information from multiple scales in time and space.

Migration bottlenecks that funnel aerial fauna from vast geographic expanses are conservation "soft spots."[48–50] If damaged or altered, they may have cascading effects for breeding, over-wintering, and stopping-over populations, as well as for their interactions with local flora, fauna, and human societies[51] over several continents. Quantifying migratory departure and landing behaviors and factors affecting them is crucial for understanding these complex processes and for conservation of bird populations and the stopover habitats that support them. Harnessing direct radar observations of individual birds for these purposes enabled exploring these important processes at the altitudes at which they occur,[52] including, for the first time, a comprehensive and detailed analysis of landing patterns and the factors affecting them. Our methodology is applicable to any group of flying organisms detected by radar, including waders and other bird groups,[17] insects,[19] and bats,[20] and can be used over the wide and constantly expanding network of animal radar systems,[19] offering promising opportunities to further enhance our understanding of vertical movements through the aerial habitat in contexts of migration, energy landscape,[53] sensory ecology,[54] etc.

Due to increasing development of human infrastructure into the aerial habitat, studies focusing on the ecological consequences of this rapid expansion are urgently needed.[55–57] Our approach helps identify the birds' selection of different migration behaviors while *en route* in finer detail. On a local scale, the ability to foresee fluxes of landing or departing migrants in known stopover areas could be used to manage human-wildlife interface activities, including light pollution management, and wind-farm operation. A similar approach may be taken by prioritizing human utilization of aerial habitats when migrants deem it unfavorable, e.g., when landing intensifies and departure diminishes. On a larger scale, identifying departure and landing preferences can aid to better assess migration fluxes moving between continents, and also pinpoint specific times when migration is intense to optimize conservation efforts, as it was shown that considerable percentages of passerine migration take place in a small number of nights. As such, this work adds an important facet to our understanding of bird migration aeroecology, promoting responsible, conscious human development into the airspace.

Limitations of the study

The study setup and computational pipeline have two major limitations. First, the radar used in the study detects passerines only up to ~1,000 m above ground, while some of their migration is known to occur also above that range. However, given that departure and landing are ground-related processes, we argue that this is not a major caveat. Second, given lack of knowledge regarding passerine ascent and descent speeds, we resorted to using mathematics-based thresholds for behavioral definitions of landing and departing, using self-properties of the data. While this is not optimal, the resulting classification generated known ecological patterns, suggesting that the definitions are sufficient.

Data and code availability

- User-friendly, edited radar output and derived datasets used throughout the study are publicly available as of the date of publication via the Figshare repository at https://doi.org/10.6084/m9.figshare.26062630 and https://doi.org/10.6084/m9.figshare.26062624.
- All original code has been deposited at https://doi.org/10.6084/m9.figshare.26062642 and is publicly available as of the date of publication and is also available in Data S1.
- Any additional data or digital resources required for handling and analyzing materials related to the study are available upon request from the lead contact.

AUTHOR CONTRIBUTIONS

Y.W. conceived the research and conducted the analysis. N.S. supervised the analysis and secured the funding. Y.W. and N.S. wrote the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- METHOD DETAILS
  - Data collection and processing
  - Vertical speed calculation
  - Departure and landing ratios: Relative amounts of landing and departing individuals
  - Meteorological data acquisition
- QUANTIFICATION AND STATISTICAL ANALYSIS
  - Correlation tests
  - Statistical comparisons
  - Analysis of meteorological effects

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.isci.2025.111892.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Table S4: Individual passerine data sample for Werber and Sapir 2024	https://doi.org/10.6084/m9.figshare.26062630	
Sample data for BRT model pipeline	https://doi.org/10.6084/m9.figshare.26062624	
Software and algorithms		
Code for Werber and Sapir analisys	https://doi.org/10.6084/m9.figshare.26062642	

METHOD DETAILS

Data collection and processing

The Hula Valley, located in north-eastern Israel and part of the Great Rift Valley, is a heterogeneous area composed of agricultural lands, extensive wetlands, and other natural habitats. It is situated less than a night's flight from the wide Saharo-Arabian Desert Belt, a major ecological barrier to Palearctic-Afrotropical migrants.[29,58] The Hula Valley is a major stopover site for many passerine migrants preparing for the ~2,000 km cross-desert journey during autumn migration (August-November) or recuperating from it in spring (March-May), making it an ideal focal point to study landing and departure behaviors.[28–30] The Hula Valley radar station is located near the western tributary of the Jordan River (35°430 E, 33°030 N) and has been operating since August 2018.

The BirdScan MR1 (BSM; Swiss BirdRadar Solution AG, swiss-birdradar.com) is an X-band radar (wavelength 3.2 cm, 9.4 GHz, 25 kW) widely used for wildlife monitoring and research aloft. It is a vertical looking radar with a wide aperture (~60°), and a 20 dB horn antenna that enables continuous acquisition of individual animals for up to 1 min and for flight distances over hundreds of meters, depending on flight altitude (Figure 1). The BSM features a classifier that distinguishes several types of targets (birds, insects, non-biological scatterers) based on their Radar Cross Section (a proxy of target size), shape, and wing flapping characteristics.[17] Continuous, homogeneous tracking of individual targets in busy skies is achieved by applying a Kalman filter which predicts movement based on accumulating target information[59] and minimizes concatenation of multiple individuals to single detections to presumably negligible fraction. When individuals are flying close together (closer than ~10 m when the radar operates in short pulse mode), they are likely to be classified as a single flock[17] (Passerine flock occurrence rate was calculated to be less than 2% of the data) and were excluded from the analysis. Individual passerines are recognized with high probability based on their unique flight features, and even the smallest migratory bird species in the area (Chiffchaff, *Phylloscopus collybita*) is detectable up to ~1000 m above the radar (Figure S2). This value was set as the maximal altitude of the radar coverage to maintain similar detection probabilities for differently sized passerines.

Our data included high quality nocturnal detections classified as passerines by the radar during autumn 2018-spring 2023. Data were collected in 70 ns emission pulses, producing fine resolution detection suitable for individual passerines. Detections made below 100 m above ground were discarded as they are liable to contamination from ground clutter. We acknowledge that numerous passerines fly above and below our selected detection range but consider our data to be the best representative sample obtainable using available methodology. The BSM's classifier outputs a probability value for each target classification (ranging between 0 and 1), and we discarded passerine signals with a probability value lower than 0.2 (5.1% of passerine classified detections) to eliminate low quality data from the analysis.[18] Data from rainy periods, unusable for analysis, were discarded by manual screening and cross-checking with rain measurements from a nearby meteorological station operated by the Israel Meteorological Service (IMS). Passerine detections classified as bats by the designated BATScan classifier, trained on data from the Hula Valley, were excluded to minimize bat contamination.[20] Our migration database consisted of a total of 580,329 individual passerine detections, collected over 586 nights: 310 autumn (August-November) and 276 spring (March-May) nights.

Vertical speed calculation

We calculated the vertical displacement of each radar-detected passerine echo by subtracting the bird's flight altitude when entering the detection range (A_{in}) from its exit altitude (A_{out}) (Figure 1), creating an accurate measure of vertical displacement independent of the length of the horizontal track. The mean vertical displacement value of all passerine targets is assumed to be zero. Consequently, to eliminate possible bias and standardize the parameter across the entire altitude range, the mean vertical displacement in each 100 m layer, likely representing an inherent bias in the BSM altitude calculation process, was subtracted from the corresponding data subsets (Table S1). The conical detection volume causes detection area to increase with altitude, meaning that high flying passerines are monitored for longer durations over longer distances, which may lead to larger vertical displacements (and potentially

larger bias, see Table S1). This was standardized by dividing vertical displacement with tracking duration (T_{out}-T_{in}), resulting in vertical speed (m/s, Figure 1).

Departure and landing ratios: Relative amounts of landing and departing individuals

A passerine was treated as landing if its vertical speed was lower than.

X = (mean vertical speed - S.D. of vertical speed),

and departing if its vertical speed was higher than.

X = (mean vertical speed +S.D. of vertical speed). This resulted in exclusion of 77.9% of the data (leaving 128,445 birds), such that only steep ascents or descents, presumably indicating departure and landing, respectively, were included in the analyzed dataset.

We used these stringent criteria of landing and departure to exclude potential effects of vertical air flow (which may induce small passive vertical movement) and of bounding flight, in which passerines sinusoidally change their altitude by up to ~10 m during flight.[60] This procedure left us with passerines descending faster than 1.57 m/s labeled as "Landings", and animals ascending faster than 1.30 m/s labeled as "Departures". Studies conducted using tracking radars[61–63] and multi-sensor tags[64] suggest that evening departures are typical of passerine migration (see also[45,65]). Bird vertical speeds in these occasions are usually above 0.5 m/s (see also[13] for detailed data from shorebirds) while during cruising flight that is typical at the middle part of the night, vertical speeds are around 0 m/s and only rarely exceed 0.5 m/s.[66] Unfortunately, empirical data of passerine vertical speeds toward landing during migration are rare. Data from other bird groups such as waders and skuas detected by tracking radar[67] suggest somewhat higher absolute values of negative vertical speed (descents) compared to positive vertical speed (ascents), which is also the case in the present study. Please also see the distribution of filtered and non-filtered vertical displacements (m) and vertical speeds (m/s) in Figure S3.

Migration traffic rate (MTR), a standardized measure of bioflow, describes the number of birds crossing a 1 km transect of airspace. The radar automatically assigns MTR factors to each detection based on size and altitude to standardize detection probabilities across the entire detection range for all target sizes[18] to compensate for detection area/altitude bias caused by the conical shape of the detection range. We calculated nightly departure and landing ratios by dividing the nightly sum MTR of all departing and landing detections by the sum MTR of all detections. Within-night patterns of landing and departure during migration seasons closely correspond to predicted departure and landing of migrating passerines, which depart for cross-country flight after sunset and terminate their flight before sunrise[60] (Figures 2 and S1).

Meteorological data acquisition

Each detected passerine was coupled with meteorological reanalysis data that were the closest to its horizontal and vertical location and time stamp from ECMWF's ERA5 model[68] that produced hourly estimates of meteorological variables at 0.25 ° × 0.25 ° spatial resolution (centered at 35.4° N/33.1° E, covering approximately the area of the Hula Valley), and ~100 m vertical resolution. Estimated variables included W-E and S-N wind vector components, temperature, cloud cover, vorticity, air pressure at ground level and vertical air speed. Detections were also coupled with ground level meteorological measurements that included ground level temperature, relative humidity, and W-E and S-N wind vector components from an IMS weather station located 6 km away from the radar. Sunrise and sunset times, used to determine night length and the "time from sunset" of each detected passerine, were determined using the "sunrise" and "sunset" functions of the "bioRad" R package.[69] Weather parameters were arithmetically averaged to create nightly means for subsequent analysis. Moon cycle parameters were extracted using the "getMoonIllumination" and "getMoonTimes" functions, and twilight times using the "getSunlightTimes" function from the "suncalc" R package.[70]

QUANTIFICATION AND STATISTICAL ANALYSIS

All data preparation, analysis, and graphic generation were done in R version 4.2.1. Underlying code is available as supplementary material (Data S1) and in (https://doi.org/10.6084/m9.figshare.26062642).

Correlation tests

The r "stats" function cor.test was used wherever correlations were described or tested. All statistical details attaining to each correlation procedure are reported in the results alongside the qualitative statement, or in Table S2 for the correlative report of parameters produced in the study (Seasonal e.g., Spring, Autumn or year round, and behavioral e.g., Landing, Departing or Total MTR).

Statistical comparisons

Due to large sample sizes characteristic of radar data and specifically in our study, and based on the central limit theorem, t tests were used to compare groups throughout the study. These were conducted using the t.test function in r "stats". Statistical details are fully disclosed alongside test reports in the results section.

Analysis of meteorological effects

We used Boosted Regression Tree (BRT) models with the "gbm.step" function in the R "dismo" package.[27] Nightly landing-MTR or departing-MTR ratios were set as response variables and weather covariates, ordinal date, year, and moon parameters as predictors.

Pairwise correlations among predictors were examined and were found to be less than 0.7 and generally low. We used Gaussian error distributions and grid searched hyperparameters, choosing 10-fold cross validation, a tree complexity of 12, a learning rate of 0.01, a bag fraction of 0.75 and a minimum of 25 trees per step. Covariates from estimated weather variables at flight altitude (ERA5 reanalysis data at average nightly flight altitude) were used for landing ratio models and data from ground measurements (IMS meteorological measurements) were used for covariates in the departure ratio models, according to the environment where the birds made their decisions (mid-air and on the ground, respectively). Resulting relative importance of parameters are specified in Table 2, and model quality indicator (Cross-validation correlations) is indicated in the results section for Meteorological factors affecting descent and ascent ratios, embedded where appropriate within the text.