Avocetta – vol. 50
doi: 10.30456/avo.30339

Migratory performance and potential high-altitude flight in Black-winged Stilt inferred from GPS tracking and atmospheric modelling

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Abstract

Understanding how migratory birds adjust their flight behaviour to cope with environmental challenges is essential to identify the limits of their aerial performance. Black-winged Stilts Himantopus himantopus are considered medium-distance migrants, yet detailed information on their migratory performance remains limited.

Using GPS tracking data from two individuals, we describe migratory routes, timing, travel rates, stopover behaviour, and seasonal differences between post-breeding and pre-breeding movements. Both birds completed long-distance migrations between the Balearic Islands and West Africa using predominantly rapid and direct movements, consistent with "jumping" migration strategies.

In several migratory segments, observed ground speeds exceeded the predicted maximum range speed (Vmr = 50 km/h). When combined with vertical wind profiles derived from ERA5 reanalysis data, these episodes were consistently associated with stronger tailwind components at mid- to high-level atmospheric layers. Although flight altitude was not directly measured, the observed displacement patterns are compatible with the potential use of atmospheric layers between approximately 2000 and 7200 m.

Because altitude was inferred indirectly from wind-field modelling and aerodynamic expectations, these estimates should be interpreted cautiously. Nonetheless, the results suggest vertical flexibility in flight behaviour and highlight the potential role of atmospheric structure in shaping migratory performance in H. himantopus. Further studies incorporating direct altitude measurements are needed to confirm the prevalence and ecological significance of hight-altitude flight in this species.

Keywords: Flight speed; GPS tracking; Migration; Wading birds; Wind assistance

INTRODUCTION

Many bird species leave their natal and breeding areas after the breeding season and migrate to other regions that support them during the non-breeding season. In general, those movements are from higher to lower latitudes, meaning that migratory birds in the Northern Hemisphere predominantly travel southwards (Newton 2024). One of the key factors enabling birds to complete such long-distance migrations is the ability to meet the high energetic costs involved. To do so, a wide range of physiological and behavioural strategies have evolved to reduce energy expenditure and ensure adequate food intake and fat deposition prior to and during migration (Newton 2024).

The use of optimization approaches to migratory behaviour, first formalised by Pennycuick (1969), has been instrumental in explaining how birds select flight speeds, altitudes, and stopover use to maximise performance (Alerstam & Lindström 1990). Time minimization is among the most empirically supported strategies (Dänhardt & Lindström 2001), but other trade-offs include minimizing energy costs (Liechti 1995, Hedenström & Alerstam 1997) or exposure to predation (Alerstam & Lindstrom, 1990; Alerstam, 1993; Schmaljohann & Dierschke, 2005). In all cases, the timing, direction, and magnitude of wind can substantially alter the energetic profitability of flight (Alerstam 1979, Alerstam 2011, Horton et al. 2016). Wind assistance can increase ground speed by 30%, and birds that respond adaptively to wind conditions may reduce energy costs by nearly half (Bruderer & Liechti 1998, Liechti 2006).

Some studies have shown that many species, particularly long-distance migrants, adjust their flight altitude to optimise wind support (Liechti 2006, Schmaljohann et al. 2009). Some shorebirds, for example, ascend to altitudes exceeding 4,000 m when crossing ecological barriers such as the Sahara, where vertical wind gradients are steep and energy-saving opportunities are greatest (Schmaljohann et al. 2009). However, direct evidence for high-altitude migration in wading birds remains scarce, especially for medium-distance migrants such as the Black-winged Stilt *Himantopus himantopus* Linnaeus, 1758.

This species exhibits diverse migratory behaviours depending on population and geography (Pierce 1996). In Western Europe, northern populations are typically migratory, whereas southern populations tend to be resident or partially migratory (Cramp et al. 1993). The Balearic Islands (Spain), located along a major migratory flyway of the Western Palearctic, support a small wintering population and serve as a breeding site during spring and summer. Although previous studies have described general migratory pathways and wintering sites (Tinarelli 1987, Pigniczki et

al. 2019), the species' flight performance, strategies, and use of the aerial environment remain poorly understood.

In this study, we tracked the full annual migration of two *H. himantopus* individuals ringed at the Es Trenc-Salobrar de Campos Natural Park (Mallorca, Balearic Islands), to describe their migratory routes, timing, travel performance, and seasonal differences between post-breeding and pre-breeding movements. By combining GPS tracking data with vertical wind profiles obtained from ERA5 reanalysis, we further explored how observed flight speeds related to atmospheric layers. This integrative approach provides an initial framework to investigate the interaction between migratory performance and wind support in a medium-distance migrant for which detailed information on flight remains scarce.

MATERIALS AND METHODS

Study Area

Fieldwork was conducted in the Es Trenc–Salobrar de Campos Natural Park in southern Mallorca, a coastal wetland complex located between 39.3660°N, 3.0026°E and 39.3438°N, 2.9986°E. The area consists of brackish marshes and salt pans and hosts a breeding population of *H. himantopus*.

Capture and Tracking

Two adult individuals were captured on the nest using a bird-triggered cage. Each bird was ringed with a metal ring (ESA scheme) and a coloured PVC ring and fitted with a 4.5 g GPS data logger (model GPSLR-M4.5, Microsensory). Devices were embedded in epoxy resin for waterproofing, resulting in a final weight of 5.2 g. GPS positions were recorded hourly when battery voltage exceeded 4 V, and every 4 hours when below this threshold. Data were downloaded via radio link when birds were within a 5 km range.

Biometric measurements collected included body mass (g), wing length (mm), third primary (P3, mm), and tarsus length (mm) (Table 1).

Distances between consecutive GPS fixes were calculated as great-circle (haversine) distances on a sphere (Earth radius R = 6,371 km) using the geosphere package (v.1.5-20; Hijmans (2023)) in R.

Flight segments were defined as sequences of positions in which the bird's ground speed exceeded 1 m/s, a threshold commonly used to distinguish flight from local or stationary behaviour (Bruderer & Liechti 1998, Bouten et al. 2013). Migratory flights were those covering more than 100 km between consecutive fixes (Klaassen et al. 2014).

Stopovers were defined as periods during which the bird remained stationary or moved at speeds ≤ 1 m/s for at least two consecutive GPS fixes, occurring after a migratory flight. A stopover ended either when a new migratory flight began or at the end of the tracking period (Bayly et al. 2018). However, due to gaps in

the GPS data, it was not always possible to determine the precise start and end times of these events. As a result, stopover duration could not be reliably estimated in all cases.

Total migration distance was calculated as the cumulative sum of all migratory segments, and migration speed was defined as the total distance divided by the number of days between the first and last fix of each migration phase, thus representing overall progress including potential stopovers.

To assess flight performance, we compared the observed ground speed (V_{obs}) with the maximum range speed (V_{mr}), which minimizes energy expenditure per unit distance (Pennycuick 1998). For *H. himantopus*, V_{mr} was estimated at ~45–55 km/h based on body mass and wing morphology (Pennycuick 2008). We used a fixed reference value of 50 km/h, consistent with previous migration studies (Bruderer & Boldt 2001), to detect cases where V_{obs} exceeded V_{mr}.

Segments with $V_{obs} > V_{mr}$ were interpreted as cases of wind assistance or enhanced performance at higher altitude (Hedenström & Alerstam 1998). Pressure levels were inferred indirectly by comparing V_{obs} with V_{mr} and calculating the tailwind component (TWC) using wind data from the ERA5 reanalysis dataset provided by the European Centre for Medium-Range Weather Forecasts (ECMWF). Wind data were extracted at multiple pressure levels for the grid point closest to each GPS location and timestamp. No spatial or temporal interpolation was applied, as the ERA5 reanalysis provides a relatively high spatial (0.25°) and temporal (1-hour) resolution, and GPS fixes were already widely spaced. This resolution ensures that each extraction represents a robust local estimate of synoptic wind conditions, while finer-scale effects remain beyond the model's scope. TWC was calculated as:

$$TWC = Vwind \cdot cos(\theta)$$

Where V_{wind} is the wind speed at the relevant altitude, and θ is the angular difference between the wind direction (origin) and the bird's flight direction (destination), computed as:

$$\theta = (windDir - flightDir + 360) \mod 360$$

Flight altitudes were calculated from the pressure level using the International Standard Atmosphere model (SA; International Organization for Standardization 1975: ISO 2533:1975). While real atmospheric conditions may vary, this model provides a consistent reference widely used in avian flight studies.

The bird's flight direction at each point is estimated based on successive GPS coordinates recorded during its displacement. Specifically, the heading is calculated between the current point and the subsequent one, using the differences in latitude and longitude to determine the angle relative to geographic north. This calculation relies on a spherical navigation formula that yields the azimuth (or bearing) in degrees, where 0° corresponds

to north, 90° to east, 180° to south, and 270° to west. The resulting value provides an estimate of the bird's horizontal orientation during that segment of its migratory trajectory. As the GPS devices recorded locations at 1- to 4-hour intervals, the estimated flight direction (azimuth) was based on straight-line displacement between successive fixes. This assumes linear flight within each segment, which may oversimplify actual paths, especially over complex terrain or during prolonged intervals. However, similar assumptions have been adopted in previous studies using hourly GPS data to infer flight direction and wind support (Shamoun-Baranes et al. 2010, Kemp et al. 2013). Given the scale of the displacements (often exceeding 100 km per segment) and the relatively stable atmospheric flow at cruising altitudes, this approximation is considered acceptable for estimating average flight headings over migratory segments. Nonetheless, the angular resolution is subject to increasing uncertainty with longer fix intervals, and potential deviations from the actual heading must be acknowledged as a source of error in tailwind estimation.

As GPS tags do not provide altitude information, we inferred likely flight altitude based on the match between observed ground speeds, theoretical maximum range speed, and tailwind component estimated from vertical wind profiles at different pressure levels. This approach assumes that unusually high ground speeds can be explained by wind assistance occurring at specific altitudes and has been applied in previous studies investigating high-altitude flight behaviours (Liechti 2006, Schmaljohann et al. 2009).

The hour of each GPS fix was recorded to qualitatively assess whether flight segments occurred predominantly during the day or night.

Only high-speed segments ($V_{obs} > V_{mr}$) were used to estimate tailwind components and potential flight altitudes, as these provided the most reliable evidence of wind-assisted movement.

To minimize the risk of GPS-related artefacts, all exceptionally high-speed segments were manually checked by inspecting the preceding and subsequent fixes to confirm temporal continuity, trajectory coherence, and consistency with the overall migratory movement. Only segments embedded within coherent migratory displacement sequences were retained for interpretation and altitude inference.

All data processing and spatial analyses were performed using R version 4.4.1 (R Core Team, 2024).

RESULTS

Two individuals of *H. himantopus* provided data covering full migratory journeys between Mallorca and West Africa (Table 1).

Table 1. Summary of data from marked specimens.

ID	Ring	Date	Coord.	Age	Sex	Weight (g)	Wing length (mm)	P_3 (mm)	Tarsus length (mm)
495	MX-008064	19/06/2021	39.35411, 3.00898	6	F	99.7	229	156	1120
496	MX-008068	20/06/2021	39.353965, 3.00999429	6	M	162	244	160	1222

Migration route and strategy

The two tracked individuals used distinct wintering areas (Fig. 1A). Female 495 migrated to the lower Senegal River estuary, whereas male 496 settled in the Inner Niger Delta (Mali). These sites, characterised by extensive post-monsoon floodplains, are well-established wintering and staging areas for Palearctic shorebirds (Hahn et al. 2009). During spring migration (Fig. 1B), both birds returned to Mallorca following more direct routes across the western Mediterranean. A summary of the main migratory parameters for both individuals is provided in Table 2.

Post-breeding Migration

Female 495 initiated post-breeding migration between 6 and 12 August 2021. Although the exact departure time is uncertain due to the 129-hour interval between the last (6 August, 19:25 h) and next (12 August, 04:41 h) GPS fixes, the bird covered 656 km during this period, suggesting a sustained migratory movement that likely included a stopover. Based on typical active flight speeds of 40–50 km/h for the species, a departure around 11 August is inferred for subsequent calculations.

From northern Algeria (Lac Dayet el Ferd), individual 495 travelled 3158 km over five days, arriving at her wintering site on 15 August. On 14 August, beginning at 10:32 h, a series of six consecutive segments (50.9–71.9 km/h, mean = 63.7 km/h) indicated sustained diurnal migration. This was followed by an extended nocturnal flight between 14:32 h on 14 August and 13:33 h on 15 August, during which the bird covered 1294.5 km at an average of 56.2 km/h. These values suggest high-altitude, tailwind-assisted movement—a well-documented strategy for minimising energetic cost and thermal stress (Liechti 2006, Sjöberg et al. 2023).

The uninterrupted, high-speed segments support the use of a “jumping” strategy, whereby individuals perform long flights with few or no intermediate stopovers (Alerstam et al. 2003, Catry et al. 2024). Moreover, the trajectory and speeds are consistent with a fly-and-forget model of decision-making, where route adjustment during flight is minimal

(Schmaljohann et al. 2012).

Male 496 began migration approximately one month later, on 9 September 2021. Between 19:36 h and 03:37 h (10 September), he covered >400 km, with speeds exceeding 50 km/h—indicative of nocturnal, active flight. By 13 September, he had reached the Inner Niger Delta, where he remained for at least five days.

On 14 September, renewed high-speed movement (68.5, 75.0, and 80.0 km/h between 05:14 and 07:29 h) marked a probable transition within the wintering range. These velocities are consistent with short high-altitude migratory segments (Sjöberg et al. 2023). The individual then remained stationary until 18 September. The next fix, recorded on 10 October—248 km further south—may represent a single relocation event or gradual movement, although the 23-day data gap precludes definitive interpretation.

Thus, individual 496's post-breeding migration comprised: (1) a long initial nocturnal flight, (2) a brief staging or early settlement phase, (3) high-speed intra-range adjustments, and (4) a potential relocation event. This pattern suggests a flexible strategy combining elements of both "jumping" and "skipping" migration (Alerstam et al. 2003, Liechti 2006), modulated by local conditions and habitat availability (Kemp et al. 2013).

Figure 1. (A) Autumn migration and (B) spring return migration routes of two *Himantopus himantopus* individuals tracked with GPS from the Balearic Islands. Each colour represents a different individual and season: (A) 495 in red, 496 in blue; (B) 495 in green, 496 in purple. Dots indicate GPS locations recorded during migratory flights.

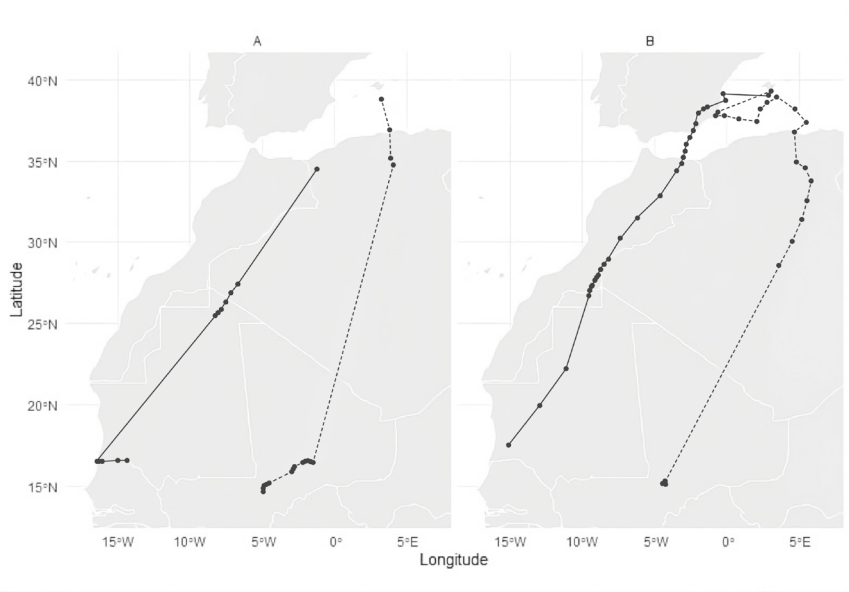


Table 2. Summary of post-breeding and pre-breeding migration parameters of two *Himantopus himantopus* individuals tracked with GPS. For each migration, total distance, number of days with active flight, and mean migration speed are shown. For individual 496, arrival at the breeding site could only be estimated within an interval due to intermittent signal loss; the total duration (22 days) is therefore approximate. Migration speed for this individual should thus be interpreted as a minimum estimate.

Post-breeding migration	495	496
Departure from breeding area	11/08/2021	09/09/2021
Total duration (days)	5	5
Maximum speed (km/h)	71.86	75.03
Migration distance (km)	3158	2623.77
Migration speed (km/day)	631.6	524.8
Stopovers	Minimal	1 stop
Notable patterns	Jumping migration, high-speed nocturnal flight	Delayed migration, shorter route
Wintering period		
Arrival at wintering area	15/08/2021	13/09/2021
Departure from wintering area	09/04/2022	16/03/2022
Duration of wintering period (days)	246	179
Pre-breeding migration		
Arrival at breeding area	19/04/2022	28/03/2022-07/04/2022
Total duration (days)	10	22
Maximum speed (km/h)	133.84	187.67
Migration distance (km)	3359.28	3870.54
Migration speed (km/day)	335.9	175.9
Stopovers	Brief Iberian	Probable stops, long pause (Murcia)
Notable patterns	Rapid long-distance burst, short repositioning	Long detour, eastward deviation near Mallorca

Wintering Behaviour

Both individuals remained within discrete wintering ranges for the majority of the non-breeding season. Movements were mostly restricted to <30 km, with occasional excursions >150 km by the female. The duration of wintering was 246 days for individual 495 and 179 days for 496.

Pre-breeding Migration

Female 495 departed on 9 April 2022. Over the following 48 hours, the female travelled over 2800 km, maintaining an average speed >60 km/h, with peak segment speeds surpassing 130 km/h—indicative of wind-assisted, high-altitude nocturnal migration (Liechti 2006, Kemp et al. 2013). On 11 April, she paused near the Alfonso XIII reservoir (Murcia, Spain), remaining mostly stationary for six hours. After 19:37 h, she executed three short relocations (speeds: 53.5, 55.2, 23.5 km/h), possibly reflecting fine-scale habitat assessment or settling behaviour (Alerstam et al. 2003, Schmaljohann et al. 2009).

By 19 April, she reached her breeding area at Salobrar de Campos, completing the final 275.9 km in 26 hours (mean = 10.6 km/h), likely involving stop-and-go flight. Her migration was rapid and direct, consistent with a "jumping" strategy (Catry et al. 2024), supported by GPS-documented segments consistently exceeding 70–100 km/h, including a peak of 133.8 km/h on 11 April (Shamoun-Baranes et al. 2010, Schmaljohann et al. 2012).

Male 496 likely began his spring migration between 12 and 16 March 2022. The earliest fix outside his wintering area was on 16 March, already 1694 km north, confirming early departure. This protandrous timing (i.e., males migrating earlier to secure territories) aligns with previous findings (Coppack & Pulido 2009).

Despite the early start, the journey took at least 22–26 days—more than twice as long as that of the female. This range reflects uncertainty in the exact arrival date due to intermittent GPS signal loss near the end of migration. The extended duration may therefore partly result from this data gap, although suboptimal wind conditions and more circuitous route could also have contributed. Between 16 and 17 March, 496 moved across the Sahel and Maghreb in a series of high-speed segments (up to 180 km/h), likely wind assisted. Some extreme velocities may result from GPS artefacts and should be interpreted with caution (Liechti 2006).

After entering Iberia, the bird deviated westwards, reaching southeastern Spain and pausing near Murcia from 18 to 28 March. The final leg, including a 152 km flight, concluded with arrival in Mallorca by 7 April. Compared to his autumn route, the spring migration was longer by over 1250 km. Although spring migration is usually shorter and faster in many bird species due to time constraints associated with breeding (Pennycuick 2001), similar patterns have been observed in some long-distance migrants (e.g. *Pluvialis squatarola* in Catry et al. (2024)), and

may be explained by adverse wind conditions, energy constraints after wintering or the need to pause on route while waiting for favourable conditions at high-latitudes breeding sites.

Assessment of High-speed Movements

Flight segments with velocities >100 km/h were recorded for both individuals. For 495, a notable nocturnal bout on 14–15 August 2021 included five hourly segments averaging 63.7 km/h, culminating in 1294.5 km covered in 23 hours (56.2 km/h average). During spring 2022, speeds exceeded 100 km/h across several segments, peaking at 133.8 km/h. Individual 496 similarly recorded speeds up to 103.9 km/h on 16–17 March 2022. These values, supported by the coherence of the trajectories and consistent with meteorological conditions, are interpreted as evidence of wind-assisted migratory flight rather than artefacts (Nilsson et al. 2013).

During migration, both individuals performed flight segments in which the observed ground speed (V_{obs}) exceeded the theoretical maximum range speed (V_{mr} = 50 km/h).

In the case of the female (495), two segments were identified: Seg. 1 during post-breeding migration and Seg. 2 during pre-breeding migration (Table 3). In Seg. 1, V_{obs} ranged from 63.5 to 71.9 km/h, with the most favourable tailwind component (TWC) detected at 450–500 hPa (altitudes between 5,575 and 6,344 m). This segment occurred entirely over continental areas, primarily across the North African landmass. In Seg. 2, observed speeds ranged from 51.5 to 133.8 km/h, and in all cases, the maximum TWC corresponded to 400 hPa (altitude ~7,186 m), with increasing wind support along the trajectory (from 8.1 to 20.7 km/h). Seg. 2 took place predominantly over land (87.5% of fixes), before the bird initiated the Mediterranean crossing during the final phase of the northward return flight.

For the male (496), one segment during post-breeding migration (Seg. 3) and two during pre-breeding migration (Seg. 4a and 4b) were identified (Table 3). Seg. 3 was conducted at dawn over continental areas, with V_{obs} ranged from 60.4 to 80.1 km/h, with optimal TWC values between 13.2 and 16.3 km/h at 600 hPa (~4,207 m), except for the final point (800 hPa, ~1,949 m; TWC = 2.3 km/h). Seg. 4a also occurred entirely over continental regions and showed the highest V_{obs} (up to 187.7 km/h) coincided with strong tailwind conditions at 400 hPa (~7,186 m), with TWC values reaching 44.2 km/h. In contrast, Seg. 4b, corresponding to the final phase of the spring return migration, occurred predominantly over marine areas, with 66.7% of fixes located over the Mediterranean Sea. In this segment, speeds ranged from 46.8 to 103.9 km/h, and optimal TWC was observed at variable pressure levels (400–950 hPa).

Two segments included GPS fixes with observed ground speeds (V_{obs}) exceeding 120 km/h, which is considerably higher than the expected maximum range speed

Table 3. Summary of flight segments with observed ground speeds (V_{obs}) exceeding 50 km/h. For each segment, the number of GPS fixes and the mean, maximum, and minimum, observed ground speed (V_{obs}), and tailwind component (TWC) are shown. Segments 1–2 correspond to female 495, and segments 3–5 to male 496. Mean values represent the average of all fixes within each flight segment. Values for additional segments with ground speeds below the 50 km/h threshold are provided in Supplementary Tables S1 and S2.

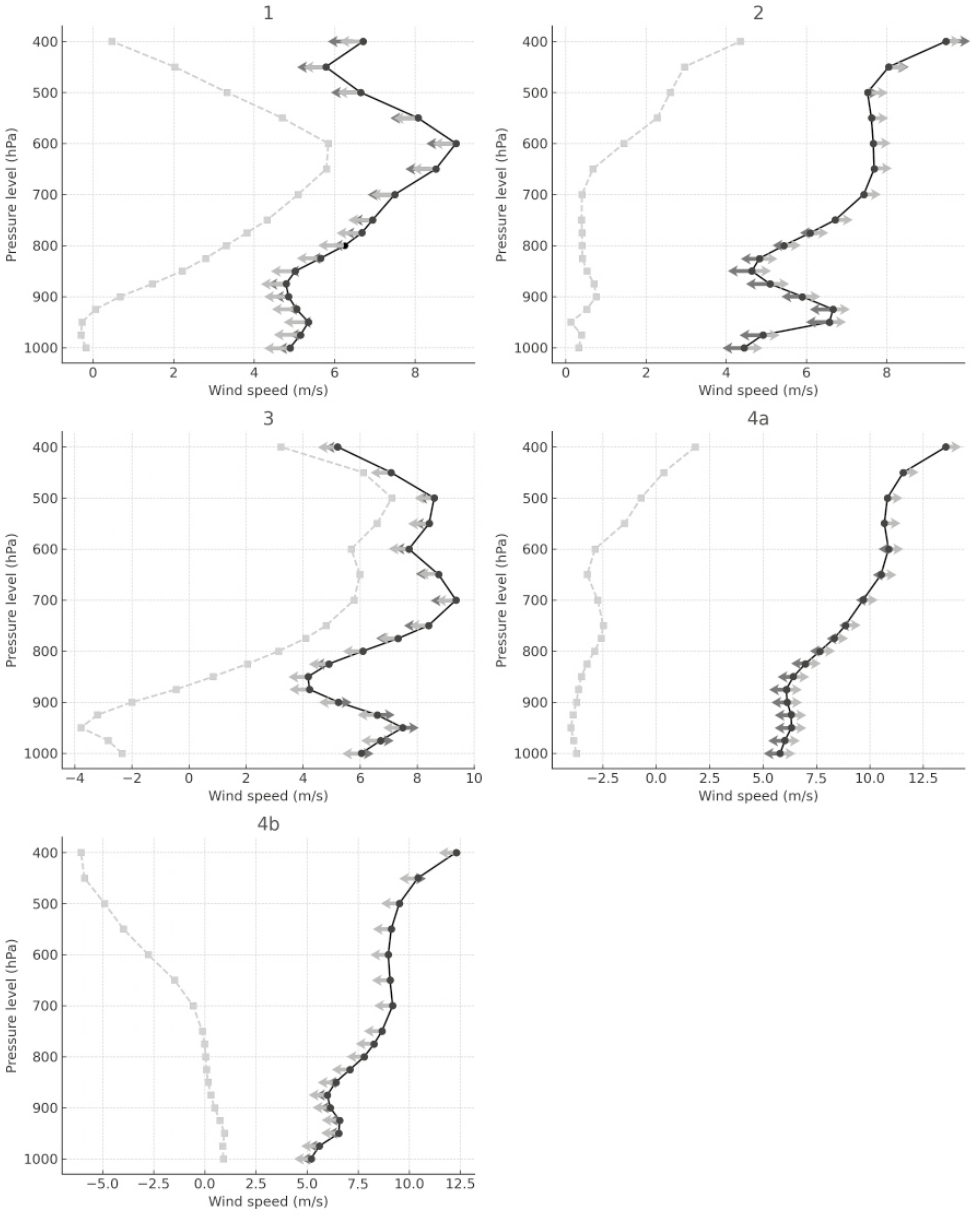
Seg.	Num. points	Mean V_{obs} (km/h)	Max V_{obs} (km/h)	Min V_{obs} (km/h)	Mean TWC (km/h)	Max TWC (km/h)	Min TWC (km/h)
1	4	67.71	71.86	63.45	12.2	13.61	10.33
2	22	90.17	133.84	51.46	14.35	20.67	5.04
3	4	70.99	80.05	60.35	11.84	16.26	2.33
4a	5	143.93	187.67	99.72	34.72	44.19	17.62
4b	8	65.77	103.92	46.8	15.84	26.44	8.77

(V_{mr}) for *H. himantopus*. In segment 1 of the female's pre-breeding migration, one fix showed a V_{obs} of 133.84 km/h. This value was preceded by three consecutive fixes (at 30–31 min intervals) with high but more plausible speeds ranging from 43.86 to 64.69 km/h, suggesting a sustained phase of rapid movement. In segment 4a of the male's post-breeding migration, four fixes registered V_{obs} values above 120 km/h, with the remaining points in the segment also showing elevated speeds (>100 km/h). These results deviate substantially from expected cruising speeds and could reflect either exceptional wind support or positional artefacts, particularly in short-duration segments.

The proportion of segments with observed ground speeds exceeding Vmr ranged between 7.7% and 28.6%, depending on individual and season. For female 495, such segments represented 10% of post-breeding and 18.2% of pre-breeding migratory segments. For male 496, the proportion was higher during post-breeding migration (28.6%) and lower during spring migration (7.7%). These values indicate that segments compatible with mid- to high-altitude wind support were episodic rather than dominant components of the migratory journey.

The vertical wind profiles associated with the five segments (Fig. 2) in which observed ground speeds exceeded the theoretical maximum range speed (V_{mr}) consistently show increased wind speeds and more favourable tailwind components (TWC) at mid to high altitudes, particularly between 400 and 600 hPa. In all cases, tailwinds were positive and generally strongest at these levels, supporting the observed displacement patterns. Notably, wind directions were more closely aligned with the birds' trajectories at these altitudes, while near-surface layers (e.g. >800 hPa) often showed reduced or

Figure 2. Vertical profiles for segments with V_{obs} exceeding V_{mr}. Each panel shows the vertical profile of mean wind speed (black line) for segments 1, 2, 3, 4a and 4b, along with the mean tail wind component (TWC, orange dashed line), mean flight direction (green arrows), and mean wind direction (blue arrows) by pressure level. Presathe International Standard Atmosphere (ISA): 800 hPa ≈ 1,950 m; 600 hPa ≈ 4,200 m; 500 hPa ≈ 5,600 m; 450 hPa ≈ 6,300 m; 400 hPa ≈ 7,200 m.



adverse wind conditions. These profiles, summarised across the entire trajectory of each segment, reaffirm the segment-level calculations and support the interpretation that birds adjusted flight altitude to exploit favourable wind conditions and enhance migratory performance.

DISCUSSION

Migratory Strategy and Seasonal Differences

Beyond the altitude-related aspects, the tracked individuals provide valuable insight into the migratory performance of *H. himantopus*. Both birds completed long-distance movements between the Balearic Islands and West Africa within relatively short time frames, exhibiting travel rates and displacement speeds comparable to those reported for medium-sized waders undertaking trans-Saharan or Mediterranean crossings. For example, daily migration speeds during post-breeding migration (525–632 km/day) fall within the range documented for other shorebirds employing "jumping" strategies, characterized by long non-stop flights interspersed with minimal stopovers (Alerstam et al. 2003, Catry et al. 2024)).

The post-breeding migrations of both individuals were rapid and relatively direct, particularly in the female, who completed over 3000 km in five days. This pattern is consistent with time-efficient migration strategies observed in several wader species when favourable wind conditions are available. In contrast, spring migration showed greater inter-individual variability. While the female performed a rapid northward return with limited stopover time, the male exhibited a longer and more circuitous route, including a prolonged pause in southeastern Iberia. Although spring migration is often expected to be faster than autumn migration due to time constraints associated with breeding (Pennycuick 2001), variability among individuals and species has been widely documented, particularly when wind conditions, energetic state, or ecological barriers influence route choice and stopover decisions.

The apparent protandrous pattern observed in the male, departing earlier from the wintering grounds, aligns with previous findings in migratory birds where early male arrival may confer reproductive advantages (Coppack & Pulido 2009). However, despite earlier departure, his migration duration was longer than that of the female, illustrating that departure timing alone does not determine total migration speed.

It is important to note that estimates of migration duration and stopover length are subject to uncertainty due to occasional gaps in GPS data transmission. In some cases, the exact timing of departure, arrival, or short stopovers could not be precisely determined, and migration speed for certain phases should therefore be interpreted as approximate or minimum estimates. Consequently, compar-

isons between seasons and individuals must be considered exploratory.

Overall, the migration patterns observed in these two individuals suggest flexibility in route choice and stopover behaviour, consistent with mixed "jumping" and "skipping" strategies described in other wader species (Alerstam et al. 2003, Liechti 2006). These broader ecological patterns provide context for interpreting the role of atmospheric conditions during migration, suggesting that wind support and potentially vertical adjustments within the air column, may represent one component of a multifaceted migration strategy aimed at optimizing time, energy, and environmental conditions.

Wind Support and Flight Performance

Wind support is a central determinant of migratory performance in many bird species, influencing travel speed, energy expenditure, and route decisions. In some species, this optimization involves adjustments in flight altitude typically associated with benefits such as reduced air resistance, lower metabolic cost per unit distance, and access to stronger tailwinds. These advantages are well-documented in species like Bar-headed Geese, Common Cranes, and some shorebirds (Piersma et al. 1997, Gill et al. 2009, Senner et al. 2018). However, such behaviour has rarely been considered in Black-winged Stilts, possibly due to the lack of high-resolution, long-duration tracking data for this species.

In both individuals tracked, several migratory segments showed observed ground speeds (V_{obs}) that substantially exceeded the predicted maximum range speed (V_{mr} = 50 km/h), suggesting the possibility of high-altitude wind assisted flight. To explore this, we analysed vertical wind profiles from ERA5 and selected, for each GPS fix, the pressure level with the strongest tailwind component (TWC). The optimal levels inferred from this analysis ranged from 800 to 400 hPa (~2000-7200 m), depending on segment and atmospheric conditions.

For the female (495), segment 1 occurred over the western Sahara during mid-morning to early afternoon, the estimated optimal flight altitudes were around 5,600–6,300 m (500–450 hPa), although TWC values were relatively modest (10–14 km/h). The elevated V_{obs} in this segment (up to 72 km/h) may be explained in part by reduced air density at these altitudes, which decreases aerodynamic drag and facilitates higher true airspeeds. Furthermore, daytime flight over the desert may have favoured ascent to higher strata to avoid thermal stress, a strategy documented in other desert-crossing migrants. In contrast, Seg. 2 unfolded mostly during the early morning and late evening hours and showed a remarkably consistent selection of the 400 hPa level (~7200 m), with increasing TWC along the trajectory (up to 21 km/h). Only a single GPS fix showed an extreme V_{obs} of 134 km/h. Given the spatial consistency and alignment between V_{obs} and wind profiles, this segment may reflect

a genuine instance of high-altitude wind exploitation.

The male (496) showed three segments with $V_{obs} > V_{mr}$. Segment 3 occurred at dawn, with optimal TWC around 600 hPa (~4200 m), and V_{obs} up to 80 km/h, with moderate wind support (13–16 km/h). The last point of the segment, however, corresponds to a lower altitude (800 hPa, ~2000 m) with minimal TWC, potentially marking a descent or change in strategy. Segment 4a was the most extreme: four out of five GPS fixes in this segment exceeded 120 km/h, with a maximum of 188 km/h. While these values likely include some degree of GPS positional error —especially given the high speeds over short intervals — they occurred in temporal continuity, and the wind data from ERA5 were internally consistent and strongly supportive of exceptional tailwinds (> 40 km/h) at 400 hPa (~7200 m). The directional alignment between flight and wind further supports the interpretation of wind-assisted flight at high altitude. This segment occurred during midday hours over central Algeria, supporting the hypothesis that daytime desert flights may promote ascent both for aerodynamic and thermoregulatory reasons (Sjöberg et al. 2023). Segment 4b was more variable, including both favourable winds at altitude and periods consistent with low-altitude flight (<800 m), particularly during the pre-dawn hours when cooler surface temperatures might reduce the thermoregulatory advantage of higher strata.

Methodological Limitations and Uncertainty in Altitude Inference

A key limitation of this study lies in the indirect nature of the altitude estimates. Flight altitude was not directly measured, as the GPS devices used did not include barometric or altimetric sensors. Instead, altitude was inferred from the combination of observed ground speed, theoretical maximum range speed, and vertical wind profiles derived from ERA5 reanalysis data.

This inference relies on cumulative assumptions related to the wind data, the reconstruction of flight direction, and the conversion from pressure to altitude: ERA5 provides synoptic-scale wind fields at 0.25° spatial and hourly temporal resolution, which may not capture local or mesoscale variability; headings were derived from straight-line displacement between fixes separated by 1–4 h, introducing angular uncertainty in tailwind component estimates; and altitude was derived from pressure levels using the International Standard Atmosphere (ISA), an idealized reference that does not account for real-time thermal or pressure anomalies.

Consequently, the altitude values reported here should be interpreted as plausible atmospheric layers compatible with the observed speeds, rather than as direct measurements of flight height. The results therefore indicate that high-altitude flight is consistent with the available data but cannot confirm the exact altitude at which the birds were flying.

Taken together, the results suggest that *H. himantopus* combine flexible route choice, variable stopover behaviour, and dynamic use of wind conditions during migration. While the exact flight altitudes cannot be confirmed, the repeated association between elevated ground speeds and favourable wind support at mid- to high-level atmospheric layers indicates that vertical positioning within the air column may contribute to migratory efficiency. In this context, potential high-altitude flight should be viewed not as an isolated phenomenon, but as one element within a broader strategy integrating timing, energetics, and atmospheric conditions.

CONCLUSIONS

This study provides new insights into the migratory ecology of Black-winged Stilts *Himantopus himantopus* by integrating GPS tracking data with atmospheric reanalysis. The two tracked individuals completed long-distance migrations between the Balearic Islands and West Africa using predominantly rapid and direct routes, with travel rates and seasonal patterns consistent with flexible "jumping" and "skipping" strategies described in other wader species. Differences between post-breeding and pre-breeding migration, including route directness, stopover behaviour, and total duration, highlight the variability that can occur even within a small sample.

Wind support emerged as key factor associated with migratory performance. Several segments exhibited observed ground speeds exceeding the theoretical maximum range speed (V_{mr}), and these episodes were consistently linked to stronger tailwind components at mid- to high-level atmospheric layers (400–600 hPa). These patterns indicate that atmospheric conditions play an important role in shaping travel speed and displacement efficiency.

Although flight altitude was not directly measured, the combined aerodynamic and meteorological evidence suggests that occasional vertical adjustments within the air column may be compatible with the observed displacement patterns. Segments consistent with mid- to high-altitude wind exploitation represented a limited proportion of the total migratory journey, indicating that such behaviour is likely episodic rather than dominant. Potential high-altitude flight should therefore be viewed as one component within a broader, flexible migration strategy rather than as a specialized or obligate trait.

Given the indirect nature of the altitude inference and the limited sample size, further studies incorporating direct altitude measurements (e.g. barometric or altimetric sensors) across a larger number of individuals are needed to evaluate the prevalence, ecological drivers, and population-level significance of vertical flight adjustments in this species.

Acknowledgments

This study was enabled by a project commissioned by the Es Trenc–Salobrar

de Campos Natural Park, "Monitoring of the avifauna of the wetland and coastal areas of Es Trenc–Salobrar de Campos Natural Park, 2022". We thank the Park's management for coordinating permits and the Park staff for their support. We also acknowledge Salinas de Levante S.A. for providing access and facilitating avian monitoring within their property.

Competing interests

The authors have no competing interests to declare that are relevant to the content of this article.

Ethical Statement

All procedures involving the capture, handling, ringing and tagging of *Himantopus himantopus* fully complied with Directive 2010/63/EU on the protection of animals used for scientific purposes and with the ASAB/ABS guidelines for the ethical treatment of animals. Fieldwork was conducted under the authorizations issued by the Govern de les Illes Balears and the Es Trenc-Salobrar de Campos Natural Park administration, including ringing permits within the ESA scheme and the specific licenses for the deployment of GPS devices. All efforts were made to minimize potential disturbance, and handling time was kept to the minimum necessary to ensure safe device attachment and biometric measurements. No nest desertions, injuries or adverse behavioural responses were observed during or after the procedures.

Data accessibility

The GPS tracking data and processed datasets supporting the results of this study are available upon reasonable request from the corresponding author. Additional derived data and R scripts used for the analyses can be provided as Electronic Supplementary Material if required by the editorial office.

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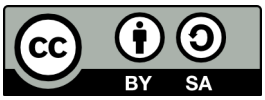

Received: 16 September 2025
First Response: 17 September 2025
Final Acceptance: 27 December 2025
Published online: 15 May 2026
Editor: Davide Dominoni

Version 2