Title: Individual tracking reveals long-distance flightpath control in a nocturnally-migrating moth

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Abstract: Each year, trillions of insects make long-range seasonal migrations. These movements are relatively well understood at a population level, but how individual insects achieve them remains elusive. Behavioral responses to conditions en route are little studied, primarily due to the challenges of tracking individual insects. Using a light aircraft and individual radio-tracking, we show that nocturnally-migrating death's-head hawkmoths maintain control of their flight trajectories over long distances. The moths did not just fly with favorable tailwinds, but during a given night adjusted for head and crosswinds to precisely hold course. This behavior indicates

that the moths employ a sophisticated internal compass to maintain seasonally beneficial migratory trajectories independent of wind conditions, shedding light on how insects traverse long distances to take advantage of seasonal resources.

One-Sentence Summary: Migrating hawkmoths continually adjust their flight headings in response to winds to maintain favorable migratory trajectories.

Main Text: Insect migration takes place on an enormous scale, with trillions of individuals performing bidirectional seasonal movements that have important impacts on ecosystem function and provision of essential services (*1–5*). However, the navigational mechanisms and behavioral strategies used by night-flying migrants, especially larger nocturnal lepidopterans (macro-moths), during these long-range journeys have been unknown for more than 100 years.

The view in the first half of the 20th Century, promoted by C.B. Williams, was that migrant moths controlled their movement direction irrespective of the wind and maintained straight flightpaths over long distances (*6, 7*). Empirical evidence of persistent, self-directed tracks was lacking, however, and by the second half of the 20th Century C.G. Johnson and L.R. Taylor downplayed the importance of orientation behavior and emphasized the role of wind in determining migratory trajectories (*8, 9*). The modern view has swung back again, as radar observations of free-flying migrants (*10–12*), and experimental manipulation of tethered individuals (*13, 14*), have both clearly demonstrated that nocturnally-migrating moths can select adaptive headings, and modify them with respect to ambient wind conditions. However, due to the methodological constraints of tracking such small animals over long distances at night (*15*), individual moths have never been tracked throughout their migration, and so the capability of these migrants to maintain straight flightpaths, over long distances and in seasonally-beneficial directions, is unknown.

We used animal-borne radio-telemetry to record complete tracks of individually-tagged moths over a full night during autumn migration, within the context of the fine-scale wind-fields experienced as they migrated southwards through the Alps of Central Europe. Our study species, the death's-head hawkmoth (*Acherontia atropos*, Sphingidae; Fig. 1A), is Europe's largest lepidopteran with a rich folklore stemming from its sinister skull-like thoracic markings, unusual

habit of raiding beehives to steal honey, and startling acoustic capabilities (*16, 17*). *Acherontia atropos* is a long-distance Afro-Palearctic migrant, arriving to breed in Europe north of the Alps each spring. The subsequent generation returns south the following autumn to winter-breeding regions in the Mediterranean Basin and likely also sub-Saharan Africa (*16, 17*), covering a distance of up to 4000 km. The moths are extremely large for flying insects, weighing up to 3.5 g (mean ± SE, 2.65 ± 0.15 g, $n = 14$) and capable of carrying tiny VHF radio transmitters. We used a light aircraft (Cessna 172) to track hawkmoths fitted with transmitters (Fig. 1A) and recorded precise (± 150 m) GPS locations from the aircraft (*18*) at regular intervals, throughout their migration (5–15 mins when possible).

We recorded nocturnal migratory flights of 14 moths, eight at high spatio-temporal frequency, as they migrated towards the Mediterranean (Fig. 1B, C; table S1). Moths initiated migration at a similar time after sunset (62 ± 4.9 mins, range 42–81 mins, $n = 8$) and were then followed for a minimum of 1 h and up to 3.65 h (2.5 ± 0.30 h, $n = 8$; table S1). The moths were followed for a mean distance of 62.7 ± 6.7 km ($n = 8$) and up to 89.6 km (Fig. 1C; tables S1, S2), the longest distance over which any insect has been continuously tracked in the field. The overall migration direction was towards the SSW (Rayleigh test: mean ± SD = 208.70° ± 0.42°, $r = 0.917$, $P \leq 0.001$, $n = 14$; Fig. 1D). This track direction is very similar to the preferred headings of a range of migratory insects (moths, butterflies and hoverflies) observed with radar in Western Europe (*2, 10, 19, 20*), including hawkmoths (*10*), all of which likely follow a similar western route to the Mediterranean or Northwest Africa.

We obtained detailed tracks for seven of these moths, each with three or more locations in a single night (table S2). Moths travelled with a mean ground speed of 9.4 ± 0.4 m/s (33.8 km/h; n segments = 99; Fig. 1E), and a maximum recorded ground speed of 19.4 m/s (69.7 km/h). The

mean ground speed recorded (Fig. 1E) is consistent with what we expect the upper limit of self-powered flight in *A. atropos* to be (*21*), suggesting that moths modulated their self-powered airspeed and/or received relatively modest wind assistance. While there was variation in individual migration direction, all moths maintained straight tracks (straightness index: mean = 0.95, range = 0.80–0.99, $n = 7$; Fig. 1C, table S2) along their entire flightpaths lasting many tens of kilometers, despite being subjected to winds of varying strength and direction throughout their course (Fig. 2). Two of the seven moths evidently crossed the Alps during a single night, as they were relocated south of the Alps during searches early the following morning. Their locations were consistent with their individual trajectories recorded the preceding night, suggesting that they had maintained straight tracks even while transiting the Alps [covering distances of 173.9 and 161.8 km from the release point (Fig. 1C, table S1)].

To answer the question how are moths able to maintain straight tracks relative to the ground, while exposed to varying winds, we calculated the distribution of the angle of deviation, β (the difference between the track and the downwind direction) to determine the extent to which the self-powered heading influenced the trajectory (*22*). The analysis revealed that moths employed three distinct behavioral strategies, which resulted in the flightpaths of the moths grouping into three directional clusters (Fig. 1C,D). These clusters appeared to be partly determined by the ambient wind conditions experienced along the flightpath (Fig. 2) and partly by the topography of the landscape (Fig. 1C).

The first strategy was utilized under opposing wind directions and resulted in moths taking the most direct route to the wintering grounds by maintaining a constant southward track (Fig. 2A,B). Under this strategy, the moths continuously adjusted their headings so that distributions of β had 95% CI that overlapped 180°, and with mean β close to that value (Fig. 3A, table S2),

resulting in more-or-less upwind flight (Fig. 4A–D). Examination of ground speeds and wind-speeds along the track (Figs. S1,S2) (*21*) indicated that moths employing this orientation strategy must have flown close to the ground (50 m or lower), i.e., within their 'flight boundary layer' [the lower-most layer of the atmosphere within which the insect's self-powered flight speed exceeds the wind speed, allowing control their trajectory (*4,22*)].

The second and third strategies were both utilized under favorable wind directions (i.e., occasions when southward flight would expose moths to some degree of tailwind assistance). We predicted that moths using tailwind assistance would fly in the layer where winds were fastest, as previously observed in studies of noctuid moths (*10*, *19*). However, examination of ground speeds and airspeeds on these occasions indicated that hawkmoths employing these strategies flew about 300 m above the ground, significantly lower than the wind speed maxima available (Figs. S1,S2), but high enough to receive some wind assistance (Fig. 4E–G). Under these conditions, moths appear to balance speed with direction, as seen in other migrant moths (*10*). The second orientation strategy involved flying relatively close to the south-westward downwind direction (Fig. 2C,D), but individuals modified their heading to achieve a straight trajectory lying somewhat further south of the strongest wind (as supported by values of *β* around -30° to -50°, and for which the 95% CI do not overlap with 0°; Fig. 3B, table S2). The final orientation strategy, employed by a single individual (moth 5), involved flying directly downwind (as indicated by the 95% CI of *β* overlapping 0°; Fig. 3C, table S2), achieving a track towards the WSW (Fig. 2D) with a higher ground speed than any other moth (Fig. 4H).

In general, there was a negative relationship between airspeed and wind assistance, with airspeed increasing in headwinds and decreasing in tailwinds (Fig. 4). Furthermore, median ground speed was relatively similar across the orientation strategies (Fig. 4H). Thus, moths

modulated their ground speed by varying their self-powered flight vector under different wind conditions to achieve a preferred ground speed, similar to that documented in many insects (*23*), which may be beneficial in the trade-off between energy consumption and travel speed (*22*).

The maintenance of consistently straight tracks and regulation of ground speed throughout the night under variable wind conditions strongly suggests that *A. atropos* has an internal compass mechanism. Flight simulator studies have demonstrated that migrating Bogong moths (*Agrotis infusa*) use a combination of visual landmarks and the Earth's magnetic field to navigate towards a goal (*13*). This has yet to be demonstrated in free-flying migratory insects, but we predict that migrating hawkmoths, which have excellent nocturnal vision (*24*), use a similar suite of sensory modalities to navigate over very large spatial scales during migration (although nothing is yet known of the capability of hawkmoths to detect magnetic fields). At the landscape scale, we propose that the moths used topographical cues to visually navigate, as magnetic cues are unlikely to be accurate enough to maintain such straight trajectories. Overlaying the straight tracks on a topographical map (Fig. 1C) shows that the three orientation strategies, and their directional clusters, are each clearly aligned with a topographical feature that would also result in avoiding the highest elevations of the Alps (high-altitude passes running due south and south-west through the Alps, and a wide valley running WSW that would enable circumventing the Alps altogether).

Here we provide evidence that large night-flying insects actively select an orientation strategy in response to environmental conditions, at least for some part of their migratory journey. To maintain such straight trajectories over long periods of time, as seen here, the moths must regularly update their position relative to whichever navigational cues they rely on. However, complete compensation has not been previously documented in a long-range migratory

insect and is generally an unusual and very rare strategy in long-range migrants (*25*). Our results show that complex migratory strategies are not limited to vertebrates.

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Competing interests: The authors declare no competing interests.

Data and materials availability: Data and custom code for the extraction of wind variables are available in the supplementary materials (Data S1, S2) and via MoveBank (doi created upon acceptance).

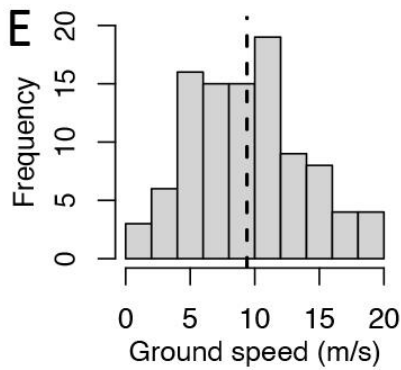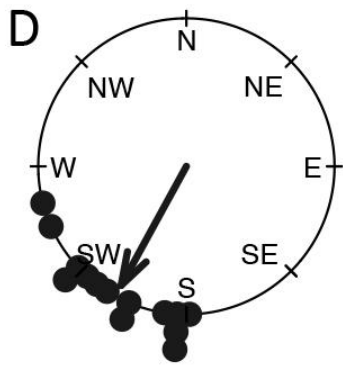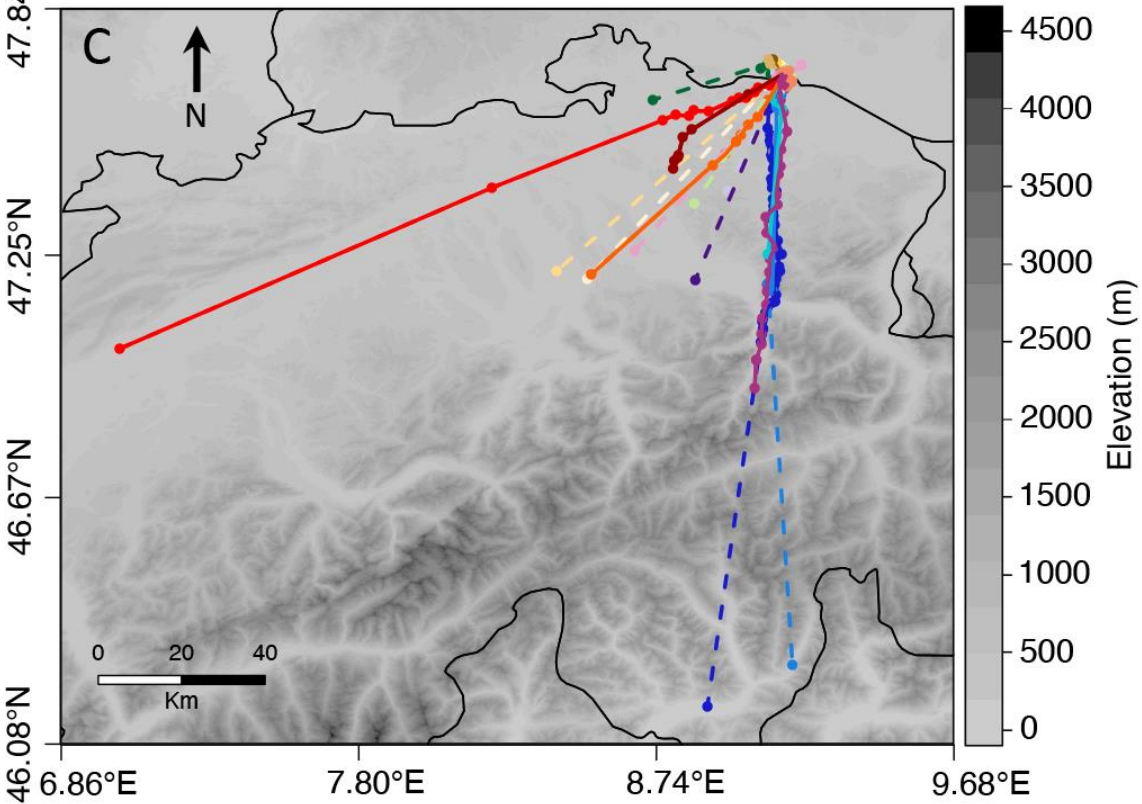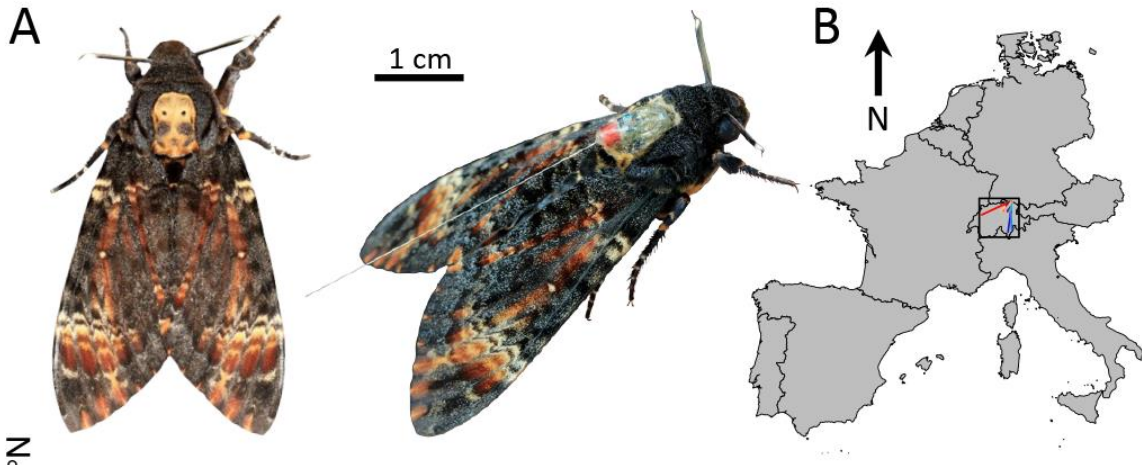**Supplementary Materials**

Materials and Methods

Figs. S1 to S2

Tables S1 to S2

References (*25–40*)

Data S1 to S2

MDAR Reproducibility Checklist

Fig. 1. Individual tracking reveals consistently straight flightpaths in migrating hawkmoths. (**A**) Death's-head hawkmoth (*Acherontia atropos*) showing the characteristic skull-like marking and fitted with a miniaturized VHF radio-transmitter (weighing 240 mg). (**B**) Map of Europe and inset of the tracking region, with the release site ~50 km north of the Swiss Alps. (**C**) Night-time tracks of migrating hawkmoths showing persistently straight trajectories throughout a night's flight; solid lines indicate moths that were tracked continuously throughout a night and dashed lines indicate presumed tracks of moths to their relocation position during searches in the following day(s). Colors represent different individuals and are consistent between figures. (**D**) Mean track directions of the 14 moths that demonstrated migratory behavior. Each point represents the track direction of an individual moth. The arrow indicates the overall mean direction (208.70°) and arrow length indicates the directedness ($r = 0.917$). (**E**) Ground speeds per segment for the seven moths that were continuously tracked on migration ($n = 99$ segments). Dashed line indicates the mean of 9.4 m/s. Photos: Christian Ziegler.

A

1 cm

B

N

C

47.84°N

N

47.25°N

46.67°N

46.08°N

6.86°E   7.80°E   8.74°E   9.68°E

Elevation (m)

4500
4000
3500
3000
2500
2000
1500
1000
500
0

0   20   40
Km

D

N
NW   NE
W   E
SW   SE
S

E

20
15
10
5
0

Frequency

0   5   10   15   20
Ground speed (m/s)

16

Fig. 2. Migrating hawkmoths continuously compensate for wind to maintain straight flightpaths. Tracks of migrating *Acherontia atropos* in relation to wind direction and speed (length of the arrows). The moths exhibit different strategies under different wind conditions, travelling due south through the Alps when primarily encountering headwinds (**A**) and (**B**), but travelling towards the southwest and thus skirting the Alps under tailwind conditions (**C**) and (**D**). Colors represent different individuals and are consistent between figures. Wind layers are derived from the COSMO-1 model and represent conditions at 50 m a.g.l (A, B) and 300 m a.g.l (C, D), the estimated altitude at which the moths were flying in the corresponding cases.

A   2018-09-10

B   2019-09-21

C   2018-09-13

D   2018-10-04
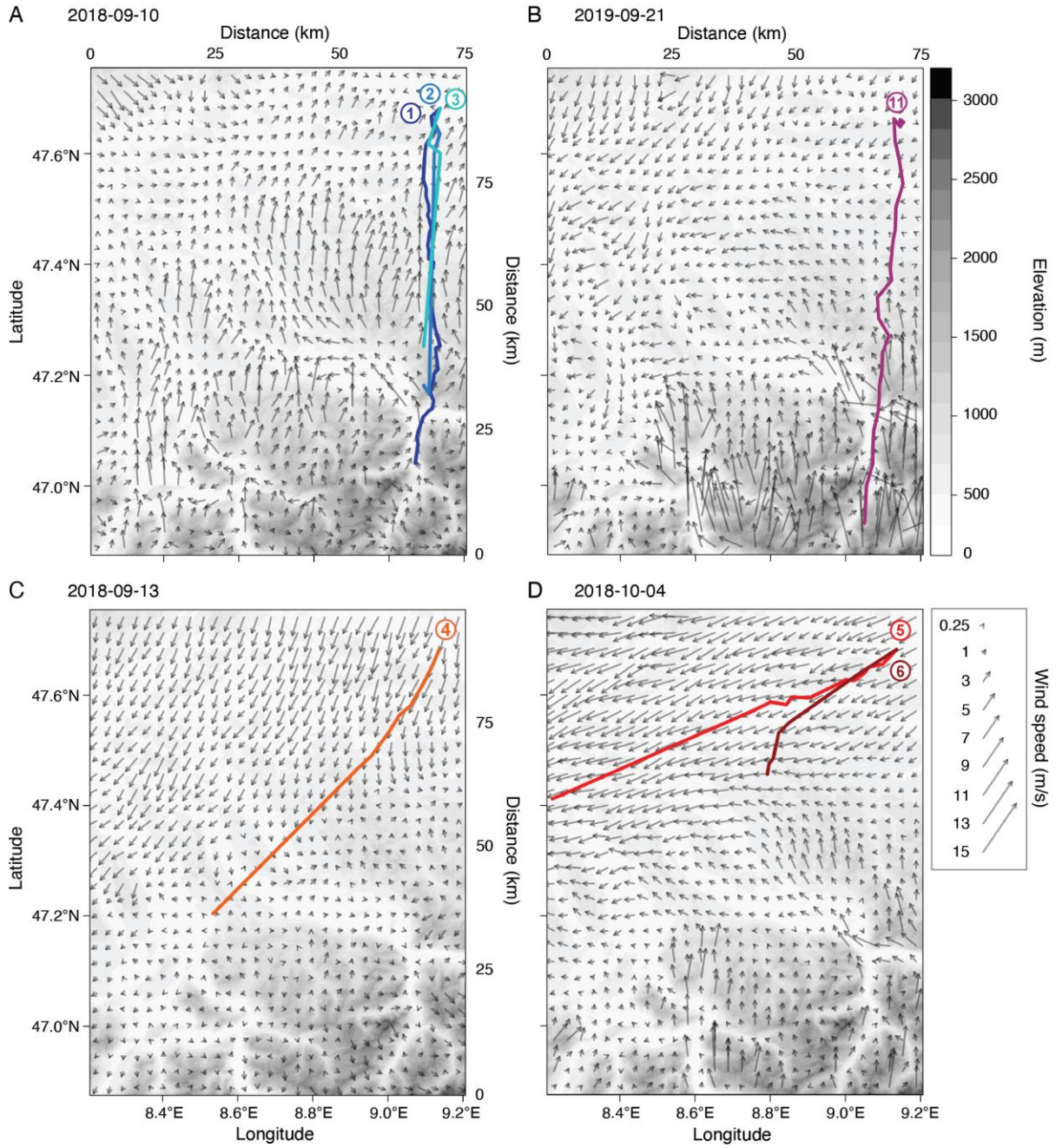
**Fig. 3. Strategies of migrating hawkmoths in relation to winds.** The flight behavior of migrating *Acherontia atropos* in relation to winds encountered along the route was explored by analyzing distributions of the 'angle of deviation' [β, the difference between the trajectory (T) and the wind direction (W)] for each segment of the trajectories of the individual moths shown in Fig. 1. (A) In unfavorable conditions such as headwinds and variable winds, moths had distributions of β with 95% CI that overlapped 180° in all cases (table S1), indicating they compensated for drift and maintained a southwards track by selecting a flight heading (H) directly upwind. Under favorable conditions (i.e., winds blowing towards the southwest), moths showed one of two strategies. (B) Some moths had mean values of β around 45° and 95% CI that did not overlap with 0° (table S1), indicating they partially compensated for drift to migrate closer to south than the downwind flow would transport them. (C) Finally, Moth 5 had a distribution of β that overlapped with 0° (table S1), indicating it headed more-or-less straight downwind. On the circular plots, each point represents the value of β for all trajectory segments of each moth. The arrow indicates the overall mean value of β, and arrow length (r) indicates the degree of clustering around the mean. Illustration: H.J. Williams.
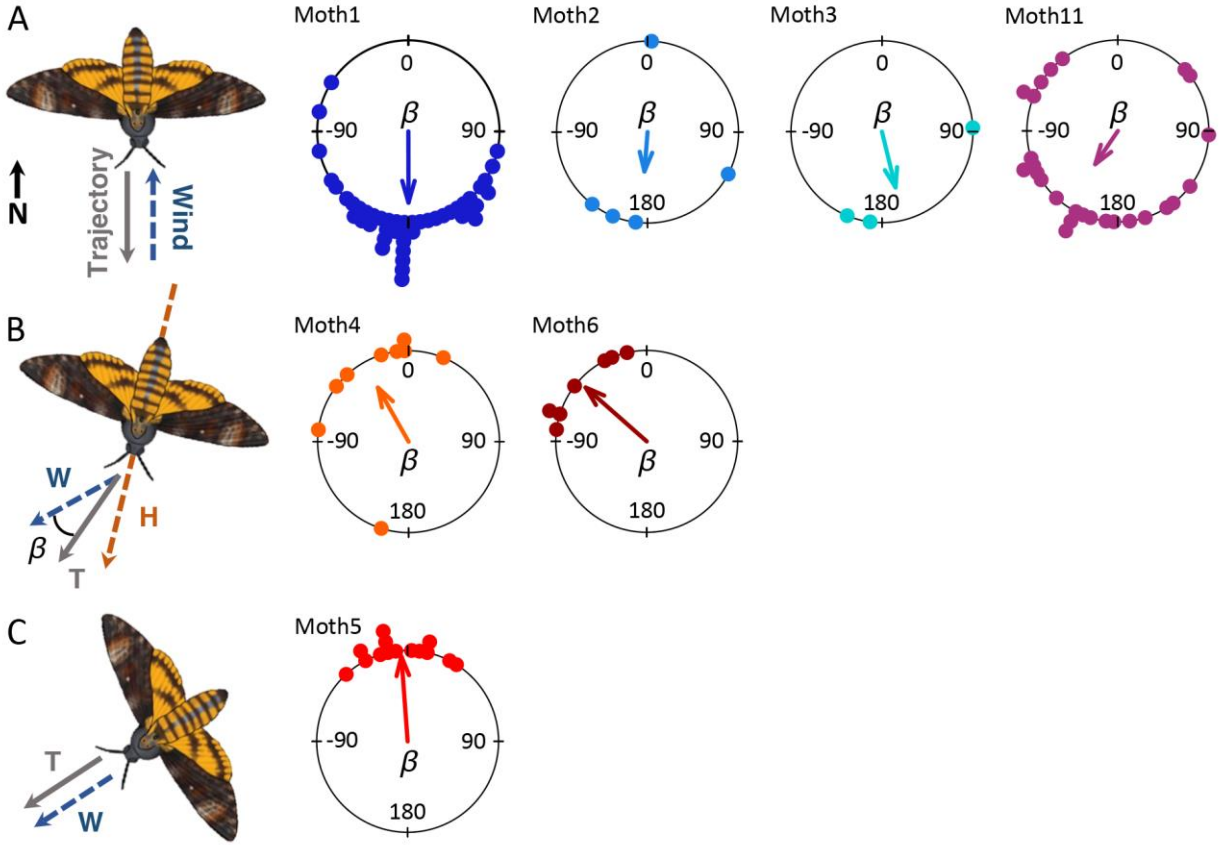
Fig. 4. Migrating hawkmoths modulate their airspeed in relation to wind assistance. Airspeed (m/s) of seven migrating *Acherontia atropos* individuals (A–G) in relation to wind assistance (m/s) en route. Wind assistance was calculated as the wind vector at the location of the moth in the direction of travel towards its next location, with positive values indicating tailwind and negative values indicating headwind. Moths generally increased their airspeed under headwind conditions (A–D) and reduced their airspeed in more favorable tailwind conditions (E–G). Ground speed per segment for each of the seven individuals (H). Colors represent different individuals and are consistent between figures. Regression lines from linear models (LMs) are presented for significant relationships. LMs were performed for individuals with more than five data points. Significance ($P < 0.05$) was based on likelihood-ratio tests. (A) Moth 1, $F = 651.91$, $P < 0.001$; (D) Moth 11, $F = 20.66$, $P < 0.001$; (E) Moth 4, $F = 0.065$, $P = 0.807$; (F) Moth 6, $F = 24.69$, $P = 0.008$; (G) Moth 5, $F = 0.465$, $P = 0.514$.
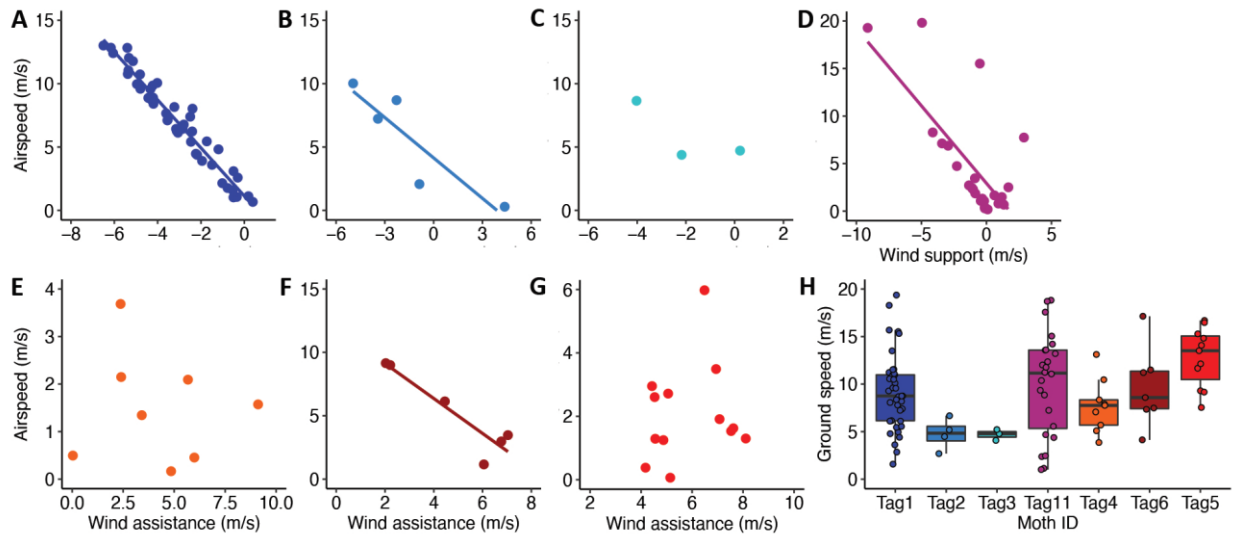
Supplementary Materials for

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Captions for Data S1 to S2

Other Supplementary Materials for this manuscript include the following:

Data S1 to S2
MDAR Checklist

Materials and Methods

Experimental animals

We trialed the tracking system using three wild adult *Acherontia atropos*, captured on migration at Col de Bretolet in the Swiss Alps (46.143°N, 6.796°E) in September 2018. Subsequent tracking in 2018 and 2019 was undertaken using moths reared from wild larvae collected from potato (*Solanum tuberosum*) fields in the vicinity of Ins, Switzerland (47.006°N, 7.106°E) during the month of July. Only large, fifth instar caterpillars were collected and transported to the laboratory, and all individuals pupated within a few days of collection. Larvae were kept individually in plastic containers (15.5 cm high x 11 cm diameter) covered with a tissue and fed potato leaves *ad libitum* until pupation. Rearing took place at room temperature under natural light conditions. Larvae were provided with potting soil in which to pupate and kept under similar conditions until eclosion. Adults were kept in the same containers and fed with 50% honey-water solution (*26*) until they were released for the tracking experiments and had no prior experience with the release location or local conditions.

Telemetry

Naïve moths were released in the afternoon/evening at Konstanz Airfield, Germany (47.681°N, 9.140°E). Moths were fitted with a VHF radio-transmitter (Sparrow Systems, 240 mg; V5 Nano-Sender, Telemetrie-Service Dessau, 270 mg; LB-2X, Holohil Systems Ltd., 280 mg, 400 mg) attached to the dorsal side of the thorax using adhesive (Evo-Stik Impact Adhesive). Transmitter weight was between 8% and 15% (based on a 270 mg tag) of the body weight of the moths (mean ± SE: 2.65 ± 0.15 g, range = 1.8–3.5 g, $n = 14$), which is lower than previous tracking studies on flying insects (where tags often weighed more than 30% of the animals' body weight (*15*, *27*–*31*)).

Tracking took place from 10 September to 4 October 2018 (seven moths released) and 17 September to 13 October 2019 (19 moths released). One to three moths were released simultaneously on each of eight nights. On the penultimate night of the study (11 October 2019), we released an additional 10 moths (table S1). Moths were released on clear nights with appropriate conditions for flying the airplane. Moths were located from the air using a Cessna 172 airplane (flown by MW) with two wing-mounted receiver antennas and followed as far as it was possible given the terrain (i.e., until they flew into the Alps), or until the plane was required to land. The airplane was used to search for the moths on subsequent days. Local searches were also undertaken from the ground by car. Signals from the radio-transmitters were detected up to 15 km from the plane. When the aircraft passed over the transmitter, the receiver signal from both antennas switched to a 'deep, strong 'whop'' sound, instead of a regular beeping. Demonstration of the accuracy of the tracking method is presented in McCracken et al. (*18*).

During airplane tracking, locations of the moths were recorded at regular intervals (5-15 mins where possible) using a handheld GPS. Tracking of multiple individuals led to longer time intervals between locations. One individual lost its tag, which was subsequently recovered, and another was located inside a honeybee (*Apis mellifera*) hive, the primary food source for the species (*17*, *26*). Seven individuals were tracked for a full night and a further seven were located during searches in the following days, following departure from the release site ($n = 14$, Fig. 1C, table S2). All tracking data are available from the MoveBank data repository (doi created upon acceptance) and as Data S2 (wind variables).

Calculation of wind variables

All analyses were conducted in R (*32*), unless otherwise specified. Wind vector data were provided by the Swiss Federal Office of Meteorology and Climatology MeteoSwiss (https://www.meteoswiss.ch), derived from the COSMO-1 model. Hourly data were extracted for the four tracking nights (10 and 13 September, and 4 October 2018, and 21 September 2019) from 00:00-23:00 hrs UTC, in grids of 1.1 km spatial resolution. Wind vectors (U-component: easting, V-component: northing) were extracted for 16 pressure layers corresponding roughly to altitudes from 50 m a.g.l. (above ground level) to 1500 m a.g.l. (see Data S1), the average altitude at which the plane was flying. Altitudinal intervals were 50 m, and 100 m intervals from 100 m to 1500 m a.g.l. Wind data were processed using the R package '*ncdf4*' (*33*). Each location along a migratory trajectory was associated with the wind information closest in space and time using the R package '*raster*' (*34*). It was inferred that the moths were flying below the plane, relatively low to the ground, based on signal strength and prior tracking knowledge.

Statistical analysis

We tested whether the 14 moths that exhibited migratory behavior (table S1, Fig. 1C,D) showed uniformity in their overall trajectories, using a Rayleigh test (*35*) in the R package '*circular*' (*36*). Direction of the trajectories was calculated as the bearing between the beginning and the end point of the track.

We conducted further analysis on the detailed migratory trajectories where we obtained at least three locations per individual ($n = 7$, table S1). Multiple individuals were often followed at a time, resulting in a greater number of locations for some animals (range 3–46 locations, table S2). Detailed migratory tracks were those where we were able to follow an individual moth over the course of a night and it exhibited migratory behavior, characterized by continuous, directed flight following departure from the release site. For each track, we calculated horizontal distance, segment speed (ground speed), and direction between consecutive locations (Data S1), using the R package '*move*' (*37*). Track distance was calculated as the distance covered by the whole tracking period, whereas Euclidean distance represents the straight-line distance between the first and last locations of a migratory track (table S1).

We investigated if moths maintained a straight flightpath throughout a night by calculating track straightness, the Euclidean distance divided by the total track distance (table S2, range 0–1, where 0 is tortuous and 1 is completely straight). Uniformity in the direction of movement for the seven detailed tracks was tested using Rayleigh tests (table S2) and further supported the hypothesis that moths held a consistent bearing ($r = 0.609$–0.989, $P < 0.001$ aside from moth 5). We didn't perform a Rayleigh test on the headings for moth 3, due to the relatively low number of data points.

To test if moths exploited favorable tailwinds on migration, or instead maintained a seasonally-beneficial trajectory, regardless of winds, we calculated the angle of deviation [β, the difference between the trajectory and the *downwind* direction (*19*)] at each segment along the migratory track, for each of the 16 altitudinal layers (Fig. 2). Although we do not know the precise altitude at which the moths were flying, we were able to predict their likely altitude, based on their ground speeds and the wind assistance along their trajectories (Fig. S1, S2). The mean ground speed recorded (9.4 m/s) is consistent with what we would expect to be the upper limit of self-powered flight in *A. atropos*. Hawkmoths are among the fastest flying insects and while there are no available estimates of the flight speed of *A. atropos*, the similar-sized *Manduca sexta* has been recorded flying at 5 m/s under laboratory conditions (*38*) and is predicted to be able fly up to 7–10 m/s, based on allometry (*39*). Wind assistance (m/s) was calculated as the wind vector at the location of the moth in the direction of travel towards its next location (Data S1). Positive wind assistance values represented tailwind and negative values headwind. Wind assistance was calculated for each of the 16 altitudinal layers. We used segment speed and wind assistance to calculate airspeed (segment speed relative to air) between consecutive locations along the trajectory, following Safi et al. (*40*).

Based on the available conditions and our predictions about the self-powered flight speeds of *A. atropos*, we determined that moths 1, 2, 3 and 11 were most likely flying low to the ground, in the lowest pressure layer (50 m a.g.l.). On the nights that these moths were migrating (10 September 2018 and 21 September 2019), winds were generally unfavorable in all layers (Figs. S1A, B, S2A, C, E, G), leading us to conclude that migration would most likely be within the flight boundary layer, where trajectory control could be maintained (*22*). On nights with favorable winds (13 September and 4 October 2018), moths were most likely flying in the layers with positive wind assistance, around 300 m a.g.l. (Figs. S1C, D, S2B, D, F), which allowed them to achieve consistently high ground speeds (Fig. 4H). We excluded ground speed and airspeed estimates less than 1 m/s and greater than 20 m/s ($n = 17$ of 113 and 18 of 113 locations, respectively) as these were considered to be implausible, based on what we predicted about the self-powered flight speeds of *A. atropos* and the wind assistance available.

Finally, we tested whether there was a positive relationship between wind assistance and airspeed, for each of the moths, using linear models (LMs), which were carried out in R. Significance of the predictor variable, wind assistance, was tested by comparing a model with and without the variable, using likelihood ratio tests (ANOVA). Model assumptions were checked by visual inspection of the residuals.

Fig. S1.

The degree of wind assistance during the four tracking nights in relation to altitude. Lines represent the 16 pressure levels that correspond to altitude (50–1500 m a.g.l.).
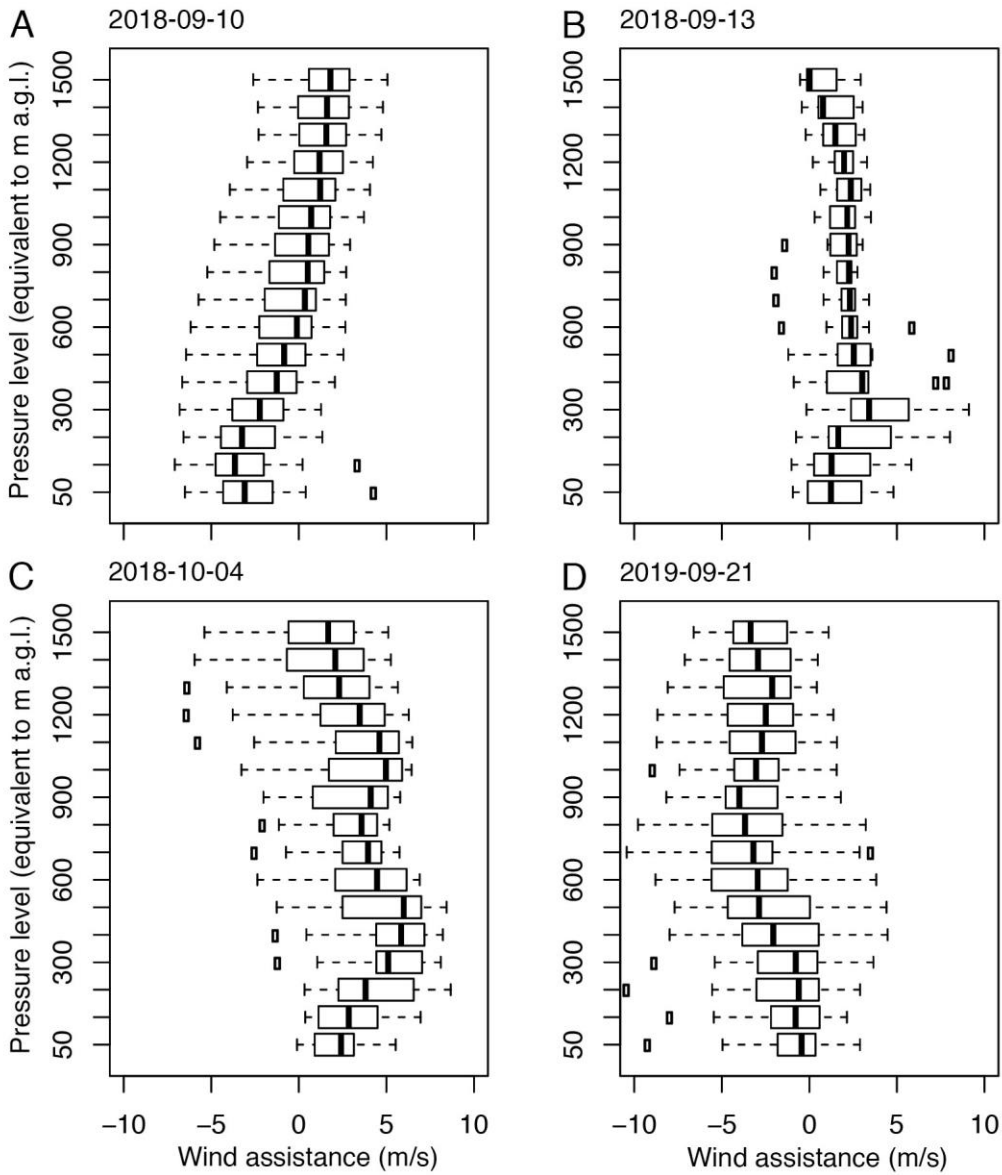
Fig. S2.

The degree of wind assistance along each track for each moth. Lines represent the 16 pressure levels that correspond to altitude (50–1500 m a.g.l.). Moths 1, 2, 3 and 11 (A, C, E, G) experienced headwinds along much of their track, whereas moths 4 and 6 (B, D) experienced consistent tailwinds for at least part of their track, and moth 5 (F) had tailwinds across the whole track, regardless of altitude. The dashed line represents no wind assistance.
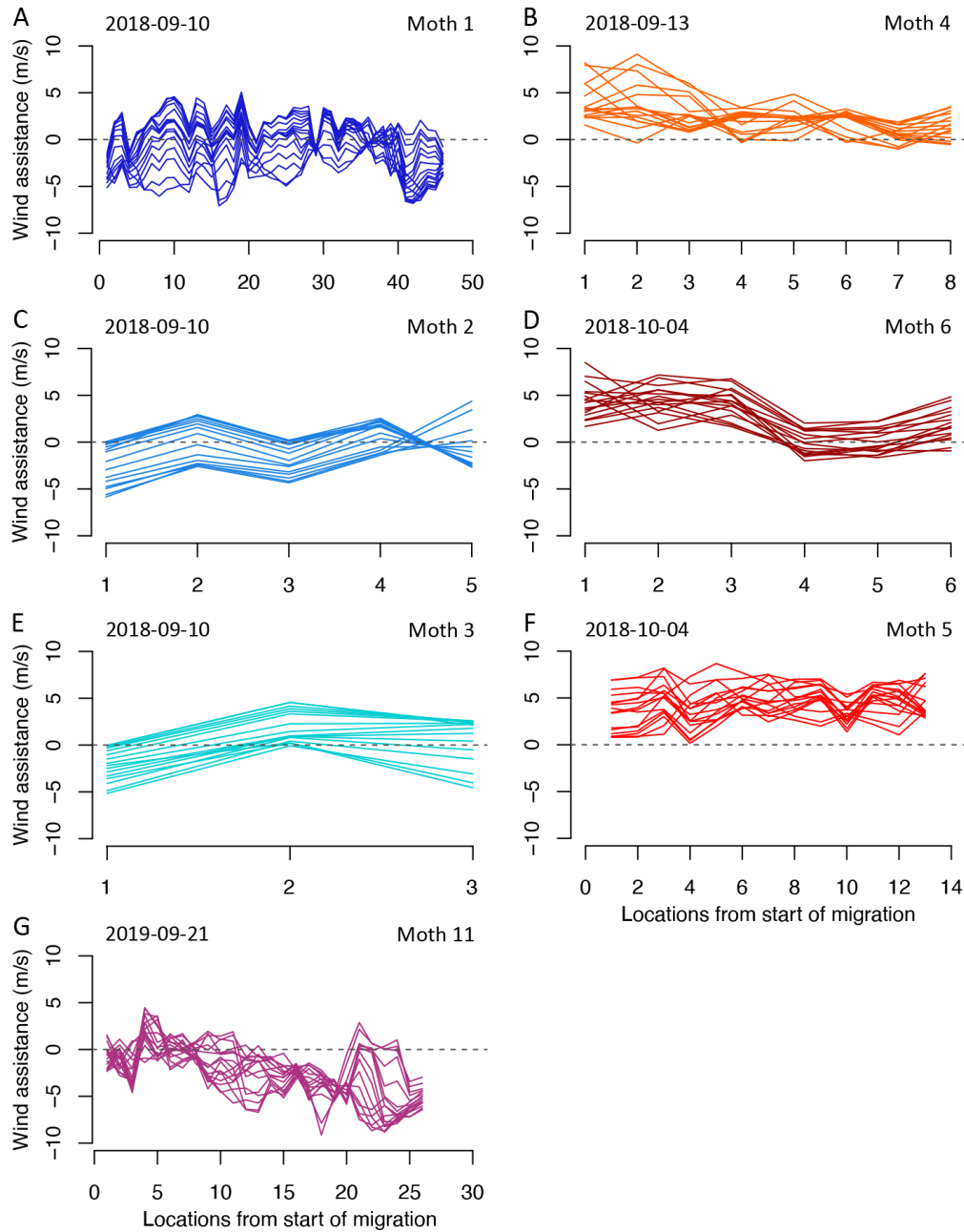
Table S1.

Summary of tracking results for *Acherontia atropos*. Track distance is the distance covered by the whole tracking period, whereas Euclidean distance represents the distance covered between the first and last location. Days located represents the number of calendar days where we detected an individual in the study area. Moths are designated as having clearly migrated ('Migration'), or undertaken local movements ('Local'), depending upon whether they remained within 5 km of the release site or moved beyond this distance, respectively. 'Directly-tracked' indicates the moth was followed by plane during its migratory flight, whereas 'Indirectly-tracked' indicates the moth's trajectory was inferred after relocation of a tagged moth on a subsequent day.

Moth ID	Stage collected	Date released	Movement type	No. locations	Days Located	Track distance (km)	Euclidean distance (km)	Track direction (°)
Moth 1	Adult	2018-09-10	Migration (directly-tracked)	48	2	173.98	169.00	186.17
Moth 2	Adult	2018-09-10	Migration (directly-tracked)	7	2	161.81	157.20	179.05
Moth 3	Adult	2018-09-10	Migration (directly-tracked)	4	1	49.47	47.91	183.94
Moth 4	Larva	2018-09-13	Migration (directly-tracked)	10	1	70.50	69.88	220.74
Moth 5	Larva	2018-10-04	Migration (directly-tracked)	15	1	176.10	174.03	246.01
Moth 6	Larva	2018-10-04	Migration (directly-tracked)	8	1	37.75	36.04	225.96
Moth 7	Larva	2018-10-04	Migration (indirectly-tracked)	2	1	40.17	40.17	211.36
Moth 8	Larva	2019-09-17	Migration (indirectly-tracked)	13	6	73.91	58.47	216.86
Moth 9	Larva	2019-09-17	Local	22	7	21.57	2.46	156.94
Moth 10	Larva	2019-09-18	Migration (indirectly-tracked)	8	2	39.01	31.24	257.77
Moth 11	Larva	2019-09-18	Migration (directly-tracked)	43	4	104.53	83.68	184.40
Moth 12	Larva	2019-09-19	Local	14	4	7.08	1.57	342.20
Moth 13	Larva	2019-09-19	Local	18	5	84.54	71.41	220.61
Moth 14	Larva	2019-09-20	Local	14	3	13.74	0.77	312.83
Moth 15	Larva	2019-09-20	Local	11	2	8.72	1.09	18.96

Moth 16	Larva	2019-09-21	Migration (indirectly-tracked)	13	4	40.92	33.41	202.29
Moth 17	Larva	2019-10-11	Local	2	2	3.21	3.21	339.76
Moth 18	Larva	2019-10-11	Local	3	3	2.40	1.79	110.53
Moth 19	Larva	2019-10-11	Local	2	2	1.51	1.51	193.51
Moth 20	Larva	2019-10-11	Migration (indirectly-tracked)	2	2	74.83	74.83	226.01
Moth 21	Larva	2019-10-11	Local	2	2	1.66	1.66	36.02
Moth 22	Larva	2019-10-11	Local	3	3	6.84	4.30	186.11
Moth 23	Larva	2019-10-11	Migration (indirectly-tracked)	2	2	58.38	58.38	200.74
Moth 24	Larva	2019-10-11	Local	2	2	4.37	4.37	331.99
Moth 25	Larva	2019-10-11	Local	3	2	6.28	3.89	315.82
Moth 26	Larva	2019-10-11	Migration (indirectly-tracked)	3	3	21.54	20.77	185.46

Table S2.

Details of *Acherontia atropos* that were continuously tracked on migration. Hours tracked and tracking distance is the time and distance an individual was followed during a migration event. Rayleigh tests were used to investigate uniformity of direction in the segments for each moth (when $n \geq 3$), where r is the clustering of the segment directions around the mean (from 0 to 1) and p represents its significance value. n is the number of segments along the migratory track. Track straightness is calculated as the Euclidean distance divided by the total track distance (see table S1 for details; range 0-1, where 0 is tortuous and 1 is completely straight). The angle of deviation (β, the difference between the trajectory and the wind direction) was calculated for each moth. *Rho* indicates the distribution of β about the mean β per individual, where *rho* is the length of the vector in Fig. 3.

Moth ID	Date tracked	Hours tracked	Tracking distance (km)	Straightness	*r*	*p*	*n*	*β*	Lower 95% CI of *β*	Upper 95% CI of *β*	*rho*
Moth 1	2018-09-10	2.62	76.33	0.97	0.924	<0.001	46	+179.9	-168.5	+168.7	0.780
Moth 2	2018-09-10	2.85	60.11	0.97	0.609	0.159	5	-175.4	-	-	0.435
Moth 3	2018-09-10	2.75	49.47	0.97		-	3	+166.3	-	-	0.630
Moth 4	2018-09-13	2.75	70.50	0.99	0.989	<0.001	9	-29.5	-71.9	-5.6	0.684
Moth 5	2018-10-04	3.65	77.25	0.99	0.937	<0.001	14	-4.2	-15.1	+7.1	0.937
Moth 6	2018-10-04	1.07	37.75	0.95	0.944	<0.001	7	-48.6	-28.3	-68.4	0.896
Moth 11	2019-09-21	3.00	89.61	0.80	0.809	<0.001	26	-145.7	-110.2	+179.2	0.443

Data S1. R Code for extraction and calculation of wind variables.

Data S2. Annotation of the variables included in the separate supplementary data file.
timestamp: time (UTC) for the GPS location, location.long: longitude (WGS84), location.lat:
latitude (WGS84), turnAngle: the turning angle between the segments, grSpeed: ground speed of
the segment (m/s), stepLength: horizontal distance (m) between locations, timeLag: time (s)
between locations, HoursFromRelease: time (hr) since the animal was released,
trackDurationHours: time (hrs) that a moth was continuously tracked on migration, segmentDir:
direction of the segment (°), net2dist: net squared displacement, totTrackingLength: total length
of the track (m), euclDist: Euclidean (straight line) distance of the track (m) from the start to the
end point, straightness: straightness index of the track calculated as the Euclidean distance
divided by the total track length (range 0-1, where 0 is tortuous and 1 is completely straight),
overallTrackDir: direction of the track (°) from the start to the end point, driftAngle: the
difference in the segment direction and the overall track direction (°), tag.local.identifier: tag
number (MoveBank field), U_z01 to U_z16: zonal (easting) component of the wind for each of
the 16 pressure levels, V_z01 to V_z16: meridional (northing) component of the wind for each of
the 16 pressure levels, Wspeed_z01 to Wspeed_z16: wind speed (m/s) for each of the 16
pressure levels, Wdir_z01 to Wdir_z16: wind direction (°) for each of the 16 pressure levels,
devAngle_z01 to devAngle_z16: angle of deviation (°) at each of the 16 pressure levels,
windAssist_z01 to windAssist_z16: wind assistance, calculated as the wind vector at the location
of the moth in the direction of travel towards its next location, for each of the 16 pressure levels.