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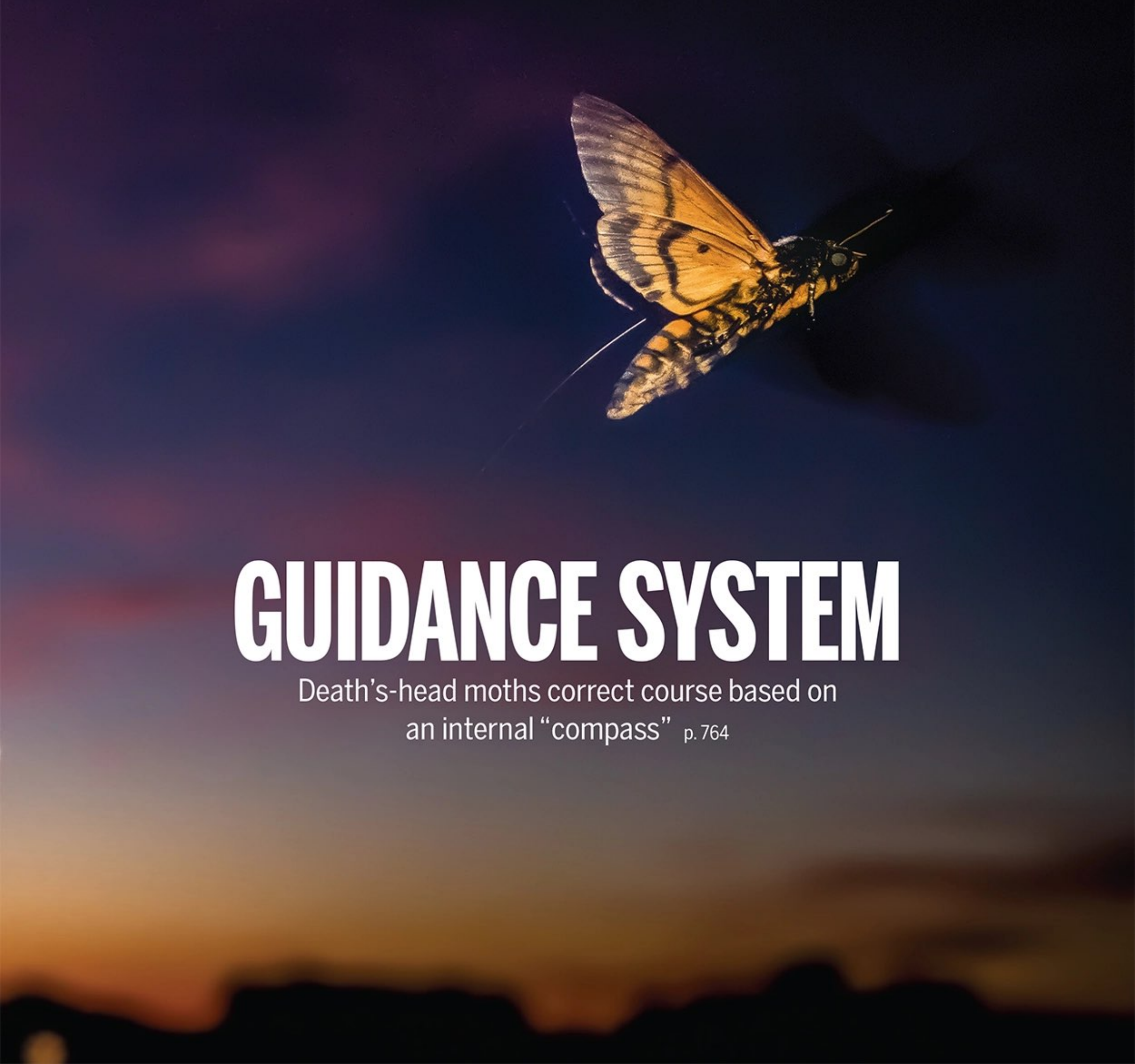

GUIDANCE SYSTEM

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INSECT MIGRATION

Individual tracking reveals long-distance flight-path control in a nocturnally migrating moth

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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 owing 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; during a given night, they also adjusted for head and crosswinds to precisely hold course. This behavior indicates that the moths use a sophisticated internal compass to maintain seasonally beneficial migratory trajectories independent of wind conditions, illuminating how insects traverse long distances to take advantage of seasonal resources.

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 (macromoths), 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, because 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, owing 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 flight paths, 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 southward 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 that stems from its sinister skull-like thoracic markings, unusual habit of raiding beehives to steal honey, and startling acoustic capabilities (*16*, *17*). *A. 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 [2.65 ± 0.15 g (mean ± SE), n = 14] and capable of carrying tiny very high frequency (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 (every 5 to 15 min, when possible).

We recorded nocturnal migratory flights of 14 moths, with eight at high spatiotemporal frequency, as they migrated toward the Mediterranean (Fig. 1, B and C, and table S1). Moths initiated migration at a similar time after sunset (62 ± 4.9 min, range 42 to 81 min, n = 8) and were then followed for a minimum of 1 hour and up to 3.65 hours (2.5 ± 0.30 hours, 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 and tables S1 and S2), the longest distance over which any insect has been continuously tracked in the field. The overall migration direction was toward the south-southwest [Rayleigh test: 208.70° ± 0.42° (mean ± SD), mean vector length (r) = 0.917, $P \le 0.001$, n = 14; Fig. 1D]. This track direction is very similar to the preferred headings of a range of migratory insects (moths, butterflies, and hoverflies) that were 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 traveled with a mean ground speed of 9.4 ± 0.4 m/s (33.8 km/hour; n = 99 segments; Fig. 1E) and a maximum recorded ground speed of 19.4 m/s (69.7 km/hour). 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. Although there was variation in individual migration direction, all moths maintained straight tracks (straightness index: mean = 0.95, range = 0.80 to 0.99, n = 7; Fig. 1C and table S2) along their entire flight paths, which lasted 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, because 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 and table S1)].

To answer the question of how moths are 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 used three distinct behavioral strategies, which resulted in the flight paths of the moths grouping into three directional clusters (Fig. 1, C and D). These clusters appeared to be partly determined by the ambient wind conditions experienced along the flight path (Fig. 2) and partly by the topography of the landscape (Fig. 1C).

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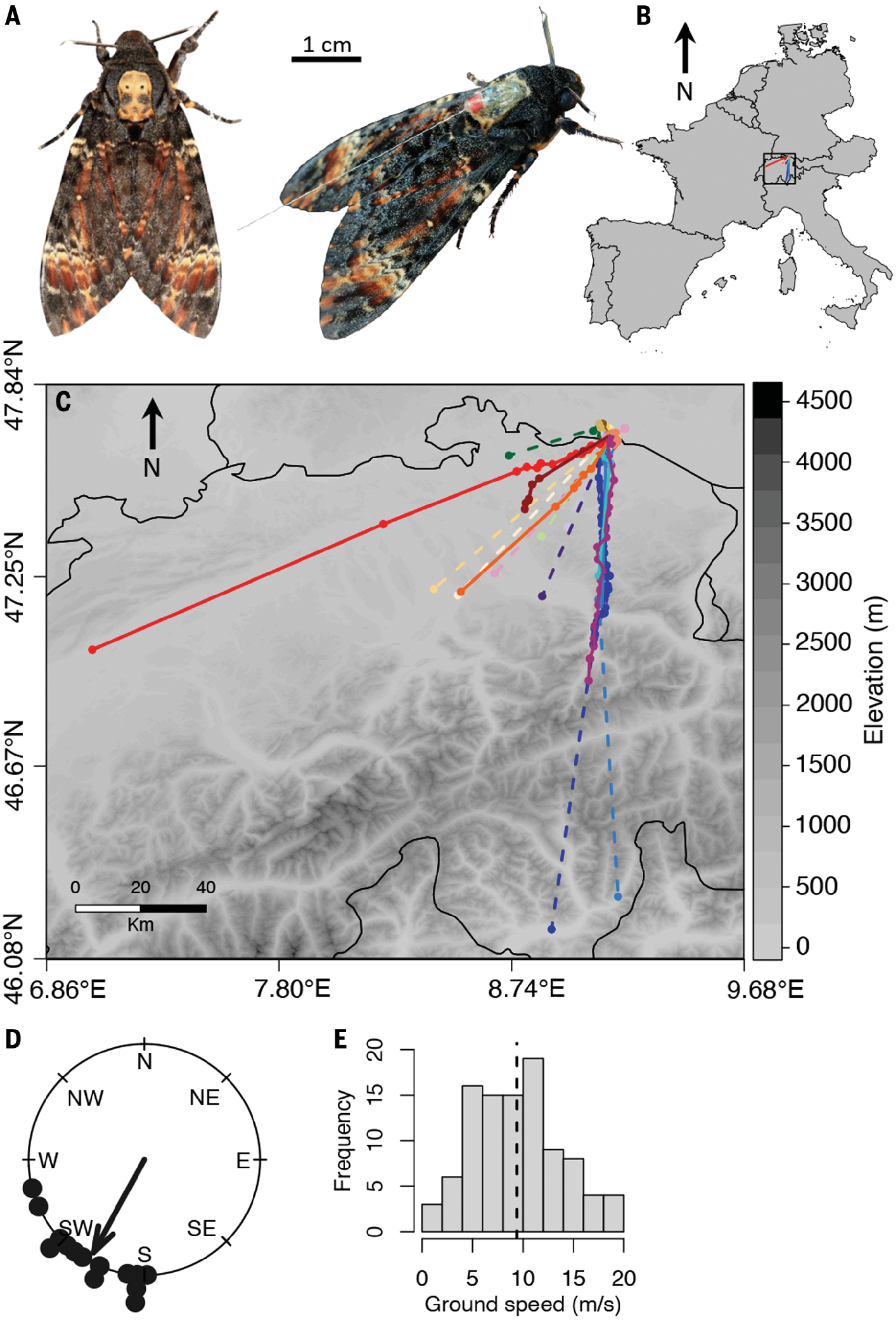

Fig. 1. Individual tracking reveals consistently straight flight paths in migrating hawkmoths. (**A**) Death's-head hawkmoth (*A. atropos*) showing the characteristic skull-like marking (left) and fitted with a miniaturized VHF radio transmitter (weighing 240 mg) (right). (**B**) Map of Europe with the tracking region outlined [magnified view shown in (C)]; the release site was ~50 km north of the Swiss Alps. (**C**) Nighttime 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**) Frequency distribution of track segments in each of 10 ground-speed categories (each bar represents a range of 2 m/s) for the seven moths that were tracked continuously on migration (n = 99 segments). The dashed line indicates the mean of 9.4 m/s. [Photo credit: Christian Ziegler]

The first strategy was used under opposing wind directions and resulted in moths taking the most direct route to the wintering grounds by maintaining a constant southward track (Fig. 2, A and B). Under this strategy, the moths continuously adjusted their headings so that distributions of β had 95% confidence intervals (CIs) that overlapped 180° and had a mean β close to that value (Fig. 3A and table S2), resulting in more-or-less upwind flight (Fig. 4, A to D). Examination of ground speeds and wind speeds along the track (figs. S1 and S2) (*21*) indicated that moths that used this orientation strategy must have flown close to the ground (50 m or lower), that is, 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 of their trajectory (*4*, *22*)].

The second and third strategies were both used 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 that used these strategies flew about 300 m above the ground, considerably lower than the wind-speed maxima available (figs. S1 and S2) but high enough to receive some wind assistance (Fig. 4, E to 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. 2, C and 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% CIs do not overlap with 0°; Fig. 3B and table S2). The final orientation strategy, which was used by a single individual (moth 5), involved flying directly downwind (as indicated by the 95% CI of β overlapping 0°; Fig. 3C and table S2), resulting in a track toward the west-southwest (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*).

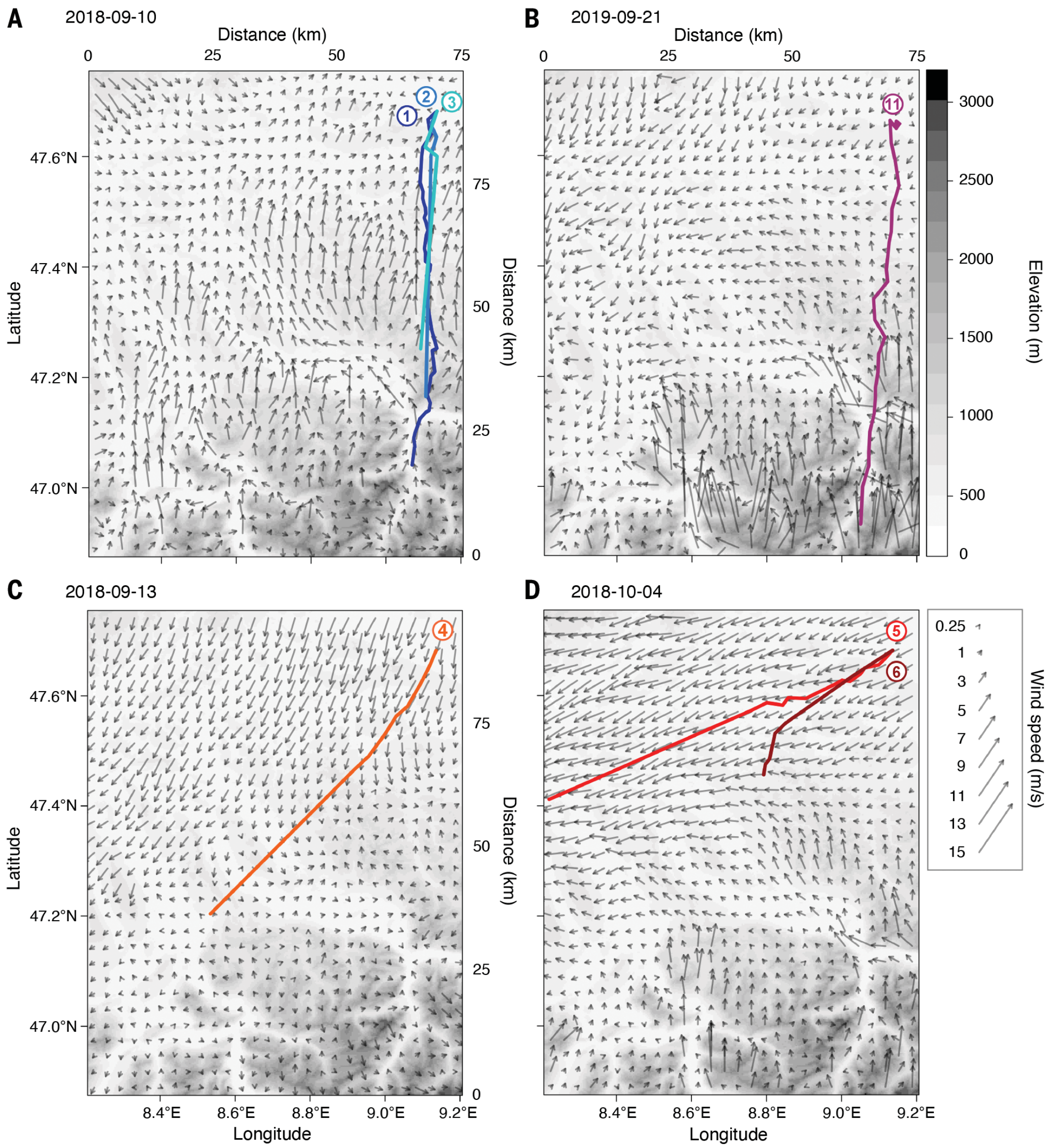

Fig. 2. Migrating hawkmoths continuously compensate for wind to maintain straight flight paths. (**A** to **D**) Tracks of migrating *A. atropos* in relation to wind direction and speed (length of the arrows). The moths exhibit different strategies under different wind conditions, traveling due south through the Alps when primarily encountering headwinds [(A) and (B)] but traveling toward 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 above ground level [(A) and (B)] and 300 m above ground level [(C) and (D)], the estimated altitudes at which the moths were flying in the corresponding cases.

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 Earth's magnetic field to navigate toward 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, because 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 southwest through the Alps and a wide valley running west-southwest 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.

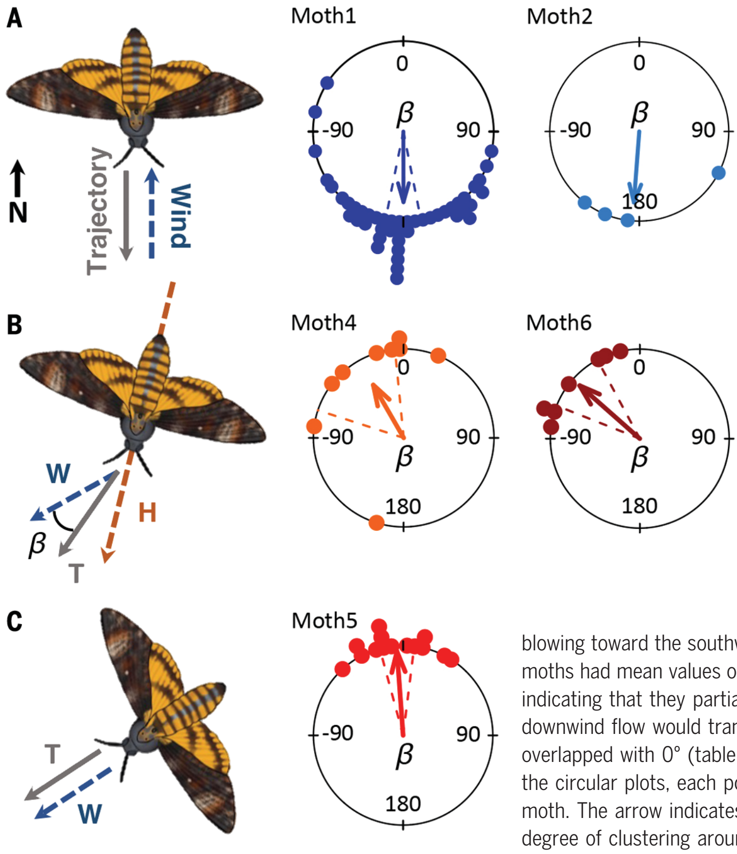

Fig. 3. Strategies of migrating hawkmoths in relation to winds. The flight behavior of migrating *A. atropos* in relation to winds encountered along the route was explored by analyzing distributions of the angle of deviation [β, the difference between the trajectory (T) and the wind direction (W)] for 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% CIs that overlapped 180° in all cases (table S1), indicating that they compensated for drift and maintained a southward track by selecting a flight heading (H) directly upwind. (**B** and **C**) Under favorable conditions (i.e., winds blowing toward the southwest), moths showed one of two strategies. As shown in (B), some moths had mean values of β around 45° and 95% CIs that did not overlap with 0° (table S1), indicating that they partially compensated for drift to migrate closer to south than the downwind flow would transport them. As shown in (C), moth 5 had a distribution of β that overlapped with 0° (table S1), indicating that 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 credit: H. J. Williams]

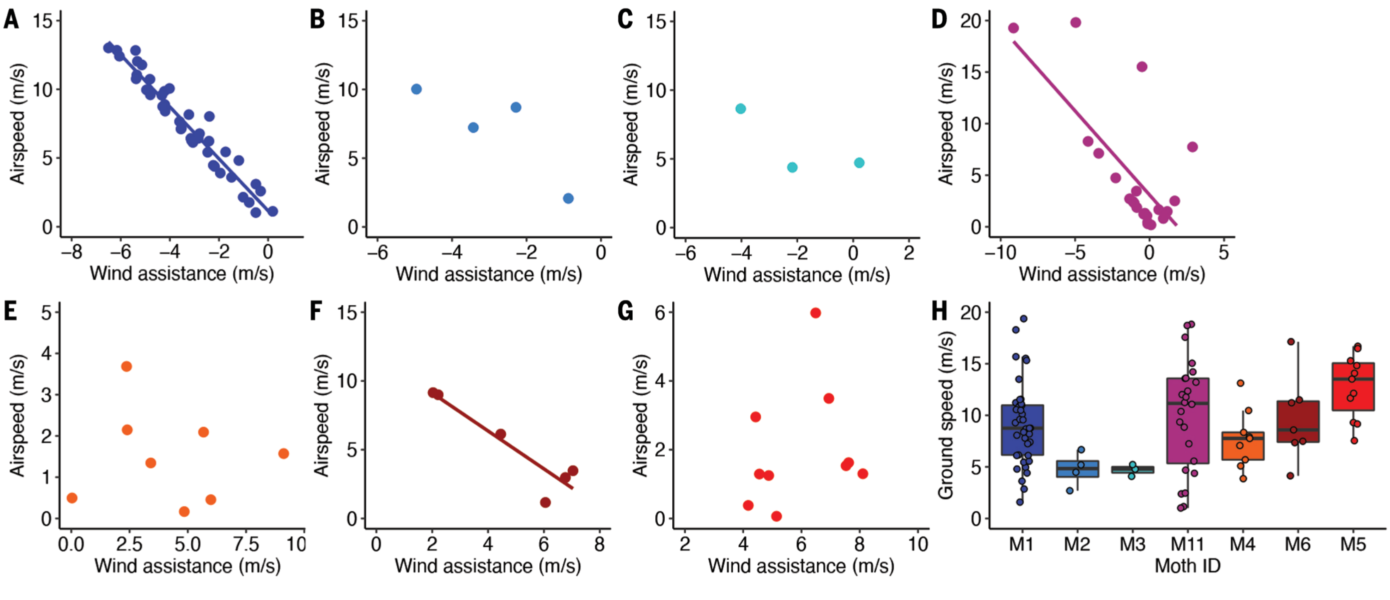

Fig. 4. Migrating hawkmoths modulate their airspeed in relation to wind assistance. (**A** to **G**) Airspeed (m/s) of seven migrating *A. atropos* individuals [(A) to (G)] in relation to wind assistance (m/s) en route. Wind assistance was calculated as the wind vector at the location of the moth in the direction of travel toward its next location, with positive values indicating tailwind and negative values indicating headwind. Moths generally increased their airspeed under headwind conditions [(A) to (D)] and reduced their airspeed in more favorable tailwind conditions [(E) to (G)]. (**H**) Ground speed per segment for each of the seven individuals. Boxes represent the 25th and 75th percentiles [interquartile range (IQR)], and whiskers indicate data within ±1.5 times the IQR. The central bars represent median values. 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, $F = 24.69$, $P = 0.008$; and (G) moth 5, $F = 0.465$, $P = 0.514$.

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ACKNOWLEDGMENTS

Special thanks to C. Ziegler for assistance in the field and providing images; the Swiss Ornithological Institute for providing access to the field site at Col de Bretolet; M. Thoma for discussion regarding the migration of *A. atropos*; D. Dreyer and R. Massy for discussion of circular statistics; I. Couzin for useful discussion of the project; and D. Dechmann, K. Safi, and two anonymous reviewers for constructive comments on the manuscript. **Funding:** This project has received funding from the European Union's Horizon 2020 research and innovation program under Marie Skłodowska-Curie grant agreement no. 795568 to M.H.M.M. and the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) under Germany's Excellence Strategy – EXC 2117 – 422037984 to M.W. Rothamsted Research receives grant-aided support from the Biotechnology and Biological Sciences Research Council of the UK. **Author contributions:** Conceptualization: M.H.M.M., M.W.; Data collection: M.H.M.M., H.-M.B.-S., M.W.; Data analysis: M.H.M.M., M.S.; Writing – original draft: M.H.M.M., J.W.C., M.W., H.J.W.; Writing – review and editing: M.H.M.M., H.J.W., H.-M.B.-S., D.R.R., M.S., J.W.C., M.W. **Competing interests:** The authors declare no competing interests. **Data and materials availability:** The datasets generated and analyzed during the current study are available in the Movebank Data Repository (*26*). Custom code for extraction of wind variables is available in data S1.

SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abn1663
Materials and Methods
Figs. S1 and S2
Tables S1 and S2
References (*27–41*)
Data S1
MDAR Reproducibility Checklist

Submitted 22 November 2021; accepted 14 July 2022
10.1126/science.abn1663

Science

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Science, 377 (6607), • DOI: 10.1126/science.abn1663

Staying on course

We still know little about how many migrating species navigate across vast distances. This is especially true for invertebrates, which are challenging to monitor. However, new technologies leading to extremely light, animal-mounted tags are opening up new research avenues in this area. Menz *et al*. used such tags to track the flight of death's-head hawkmoths that migrate between Europe and sub-Saharan Africa. They found that the moths were able to correct to their specific course even in the face of disruptive winds and high mountains. This work suggests that the moths are not merely passively moving in the right direction, but instead actively navigating based on an internal map or compass. —SNV