



Compensation for wind drift during raptor migration improves with age through mortality selection

Fabrizio Sergio ^{1,3}✉, Jomar M. Barbosa^{2,3}, Alessandro Tanferna¹, Rafa Silva ^{1,3}, Julio Blas¹ and Fernando Hiraldo¹

Each year, billions of flying and swimming migrants negotiate the challenging displacement imposed by travelling through a flowing medium. However, little is known about how the ability to cope with drift improves through life and what mechanisms drive its development. We examined 3,140 days of migration by 90 GPS-tagged raptorial black kites (*Milvus migrans*) aged 1–27 years to show that the ability to compensate for lateral drift develops gradually through many more years than previously appreciated. Drift negotiation was under strong selective pressure, with inferior navigators subject to increased mortality. This progressively selected for adults able to compensate for current cross flows and for previously accumulated drift in a flexible, context-dependent and risk-dependent manner. Displacements accumulated en route carried over to shape the wintering distribution of the population. For many migrants, migratory journeys by younger individuals represent concentrated episodes of trait selection that shape adult populations and mediate their adaptation to climate change.

Each year, billions of flying and swimming migrants must negotiate cross flows in order to reach their destination^{1,2}. When facing unfavourable flows, migrants can be passively pushed off course because of their incapability to resist the displacement (maladaptive drift) or can enact orientation strategies evolved to oppose and even exploit cross flows^{3–5} (Fig. 1a, Supplementary Fig. 1 and Video 1). These primarily include: waiting for favourably oriented currents (wind selectivity), changing heading to compensate for lateral displacement (compensation) or drifting to various degrees, where a migrant accepts the displacement to gain an advantage (adaptive drift)^{3,6–9}. According to theoretical models of optimal migration, the profitability of each strategy may change according to the length of the remaining journey and the stability and predictability of cross-flow direction¹⁰. For example, migrants should constantly compensate for drift in a current that never changes direction but should drift freely when the direction alternates along the route in a balanced way^{4,11}. In unpredictably changing crossflows, migrants should either drift at the beginning of the journey and compensate later or overcompensate in the first portion and drift towards the end (Zermelo's optimal solution)⁸. Previous empirical studies have found conflicting results with a wide array of negotiation responses ranging from maladaptive drift to full compensation and overcompensation^{1,3,8–10,12,13}. However, one aspect of cross-flow negotiation that has received scarce attention is how drift management capabilities develop through life within and across individuals.

Current knowledge on this aspect is limited to a single satellite-tracking study which showed that one-year-old juveniles on their first migration are less capable than adults to compensate for cross flows¹⁴. Furthermore, the above study was based on a dichotomous comparison between recently born juveniles and unknown-age adults, probably because of the enormous challenge of sampling the in-between initial years of life. Thus, we still don't know whether the ability to negotiate cross flows is acquired gradually or abruptly through life (for example, through a single-step acquisition of route familiarity), whether it bears fitness or population

consequences and whether it is shaped by individual learning or by progressive removal of inferior navigators. Therefore, our understanding of when, how and why migrants develop their elusive capability to negotiate drift to navigate to their far away destinations is still rudimentary.

Here we fill this knowledge gap by examining the lifelong orientation strategies of a medium-sized, migratory raptor, the black kite (*Milvus migrans*). In particular, we tested whether and how wind-negotiation strategies improved with age and whether this was mediated by experiential learning or by a process of selective removal of inferior performers. On the basis of previous work on this population^{15,16}, we expected age-related improvements to be more radical and visible during the more challenging pre-breeding migration (Methods provide more detailed predictions). Throughout, we use the term 'individual improvement' for trait amelioration within an individual as it ages and 'improvement' as a more general term for trait amelioration generated by individual improvements and other cross-sectional mechanisms, such as the progressive removal of inferior performers.

Black kites (hereafter, 'kites') usually start breeding when 3–6 years old¹⁷, after spending their first one–two winters in Africa. Key vital rates, such as reproductive success and survival, are highest between age 7–11 and subsequently decline¹⁶. Populations of western Europe winter in western Africa after a narrow-front migration funnelled through the Strait of Gibraltar¹⁸ (Fig. 1b). Kites migrate only diurnally and can forage in the early morning and late afternoon (fly-and-forage migration¹¹) or during travelling interruptions at staging stopover sites. Migrating kites often travel within loose flocks of up to thousands of other kites, raptors and storks¹⁹. As in other soaring birds, migratory advancement is mainly achieved by exploiting the uplift generated by air convection, the birds gaining height by circling in buoyant air and then gliding to the next thermal²⁰. Migration concentrates most of the year-round mortality, particularly during the crossing of the inhospitable Sahara Desert²¹. The current analysis is based on GPS tracking data over 3,140 days of migration (1,520 pre-breeding and 1,620 post-breeding days)

¹Department of Conservation Biology, Estación Biológica de Doñana–CSIC, Seville, Spain. ²Department of Applied Biology, Universidad Miguel Hernández, Elche, Spain. ³These authors contributed equally: Fabrizio Sergio, Jomar M. Barbosa. ✉e-mail: fsergio@ebd.csic.es

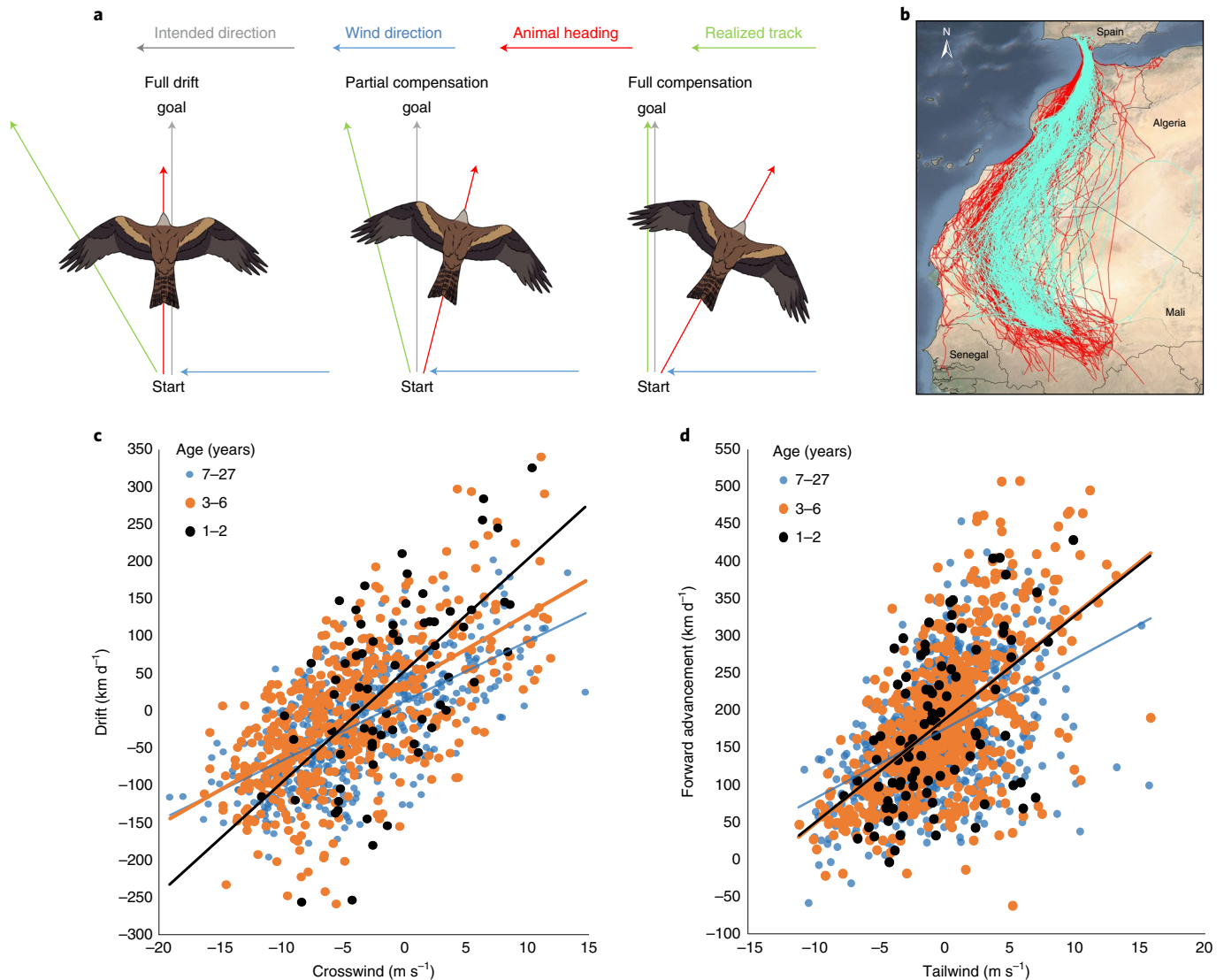


Fig. 1 | Strategies of drift negotiation by migrating black kites. **a**, Conceptual (non-vectorial) representation of crosswind negotiation strategies by migrating raptors; by orienting themselves progressively more towards a lateral crosswind, migrants can increasingly compensate for the drift imposed by the side flow. The outcome of such orientation strategies can range from full drift to partial compensation or full compensation (Supplementary Video 1). In Supplementary Fig. 1, we illustrate the same concept through the more classical 'triangle of velocities'. **b**, Travel routes of black kites migrating between Doñana National Park in Spain and the Sahel of Africa during their pre-breeding (red) and post-breeding (light blue) journeys. Tracks starting from further south were shortened for clarity of presentation. **c**, The capability to compensate for the effect of crosswinds improved with age (that is, the slope became progressively less steep) for kites travelling over the Sahara and Sahel during their pre-breeding migration ($N=1,508$ days of migration from 70 individuals). A steeper slope indicates that a given level of lateral flow imposes a larger drift (that is, a lower capability to compensate for cross flows). **d**, The effect of axial winds on the rate of advancement towards the breeding quarters declined with age, implying that younger individuals were more dependent on tailwind support and more constrained by headwinds than older ones ($N=1,520$ days of migration from 70 individuals). All tests were two-sided and can be found in Supplementary Table 2a.19 (**c**) and 2a.49 (**d**). Illustration credit: F. J. Hernández. Map credit: ESRI World Imagery.

by 90 individuals born in Doñana National Park (south-western Spain). This population is subject to long-term marking²², which allowed us to sample all ages of the life cycle (1–27 years old). Hereafter, for simplicity, we define 1–2-year-olds at their first migration as 'juveniles' and 3–6-year-olds as 'young adults'. For clarity of presentation, we placed most statistical tests in tables so as to avoid constant text interruption with long reports of statistical figures. To quickly find the relevant results within extensive tables, whenever necessary, we identified each model by a letter and each tested variable by a progressive row number. Thus, the notations 'Supplementary Table 1a.4', 'Supplementary Table 1a.5–6' or 'Supplementary Table 1a' refer to the variable of row 4 of model a;

to the variables of rows 5 and 6 of model a; or to the whole model a of Supplementary Table 1, respectively.

Results and Discussion

In the pre-breeding return migration (northern spring), departure decisions incorporated moderate wind selectivity; kites departed with declining barometric pressure (Supplementary Table 1a.1), probably forecasting changes in wind conditions and lower probabilities of dust storms²³, while younger individuals waited for winds to switch from the prevailing headwind to tailwind conditions (Supplementary Table 1a.5–6 and Supplementary Fig. 2), which may have contributed to their later departure¹⁶. Once travelling, drift

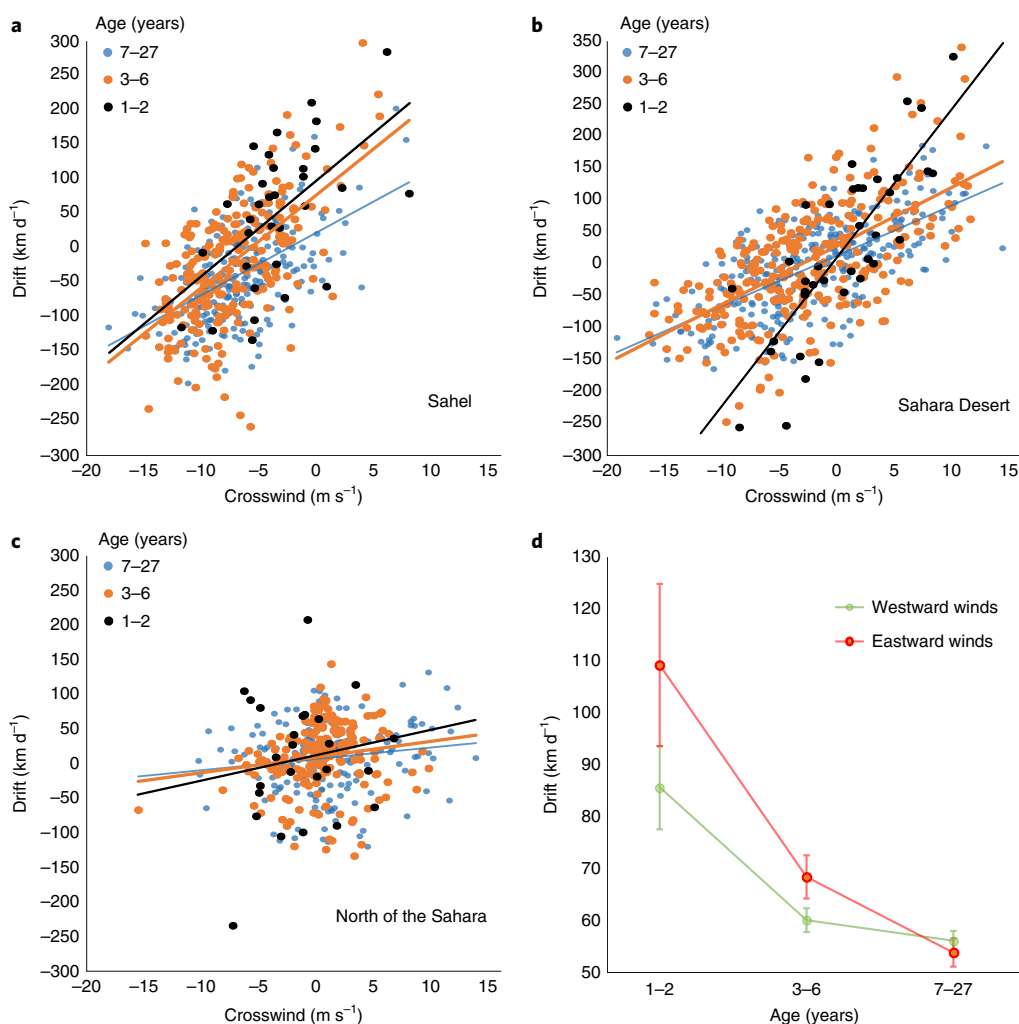


Fig. 2 | Age-dependent drift changed by geographic area and with wind direction in the pre-breeding migration. a–c, The drift levels imposed by crosswinds declined with age in the Sahel (**a**), were particularly high for juveniles migrating over the Sahara Desert (**b**) and became minimal in the final portion of the journey (**c**). **d**, Adults were ‘impermeable’ to wind direction, while juveniles and young adults suffered more drift from eastward than westward winds, which put them at greater risk of being dangerously blown into the inhospitable interior of the Sahel and Sahara Desert. Error bars represent 1 standard error of the mean (s.e.m.). Tests are based on a sample of 1,508 days of migration from 70 individuals. All tests were two-sided and can be found in Supplementary Table 2a.18 (**a,b,c**) and 2a.23 (**d**).

increased by 7.5 km d⁻¹ and forward advancement by 12.0 km d⁻¹ for every m s⁻¹ increase in crosswind and tailwind speed, respectively. Drift was affected by a complex array of interactions: for all kites, tailwinds (Supplementary Table 2a.5) and sudden changes in crosswind direction (Supplementary Table 2a.7) increased the displacement caused by crosswinds, while high ecosystem productivity attenuated drift, probably by promoting travelling interruptions for foraging (Supplementary Table 2a.8). More importantly, orientation strategies depended on age (Supplementary Table 2a.18–19 and Fig. 1c). First, the drift-impact of crosswinds depended on the interaction between age and geographic area; kites drifted progressively less with increasing age, a pattern that was most pronounced in the Sahara and Sahel but virtually absent further north, where drift was negligible for all individuals (Supplementary Table 2a.18–19 and Fig. 2). Juveniles in particular drifted extremely strongly in the Sahara, where they suffered average daily lateral displacements of 105 km and up to 327 km (Fig. 2b). Second, drift was modulated by the interaction between age and wind direction; juveniles and young adults drifted more with eastward than westward blowing winds, while adults were unaffected by wind direction (Supplementary Table 2a.23 and Fig. 2d). This would place younger kites more at risk

of being unsafely blown towards the Sahara interior. Third, the effect of past accumulated drift on current drift became more negative with age (Supplementary Table 2b.24 and Supplementary Fig. 3). This implied that adults were more capable than young individuals to exploit adaptive drift, resisting drift when this increased their already accumulated displacement and accepting it opportunistically when it lowered net displacement.

Advancement in the intended direction was similarly affected by the interplay of environmental forcings and their interactions. For example, it was propelled by tailwinds (Supplementary Table 2.31) and reduced by higher NDVI values (Supplementary Table 2.36), while the effect of tailwinds was maximum in the Sahara, intermediate in the Sahel and minimum further north (Supplementary Table 2b.42–43 and Supplementary Fig. 4). Again, the negotiation of wind support varied by age. First, the impact of wind support was stronger on juveniles and young adults, which were more dependent on tailwinds and more slowed by headwinds, especially in the Sahara and the Sahel (Supplementary Table 2b.49–50 and Fig. 1d). This implied that adults advanced more slowly for a given level of tailwind, possibly as a way to lower energy expenditure^{24,25}. Second, the advancement was modulated by a complex interaction between

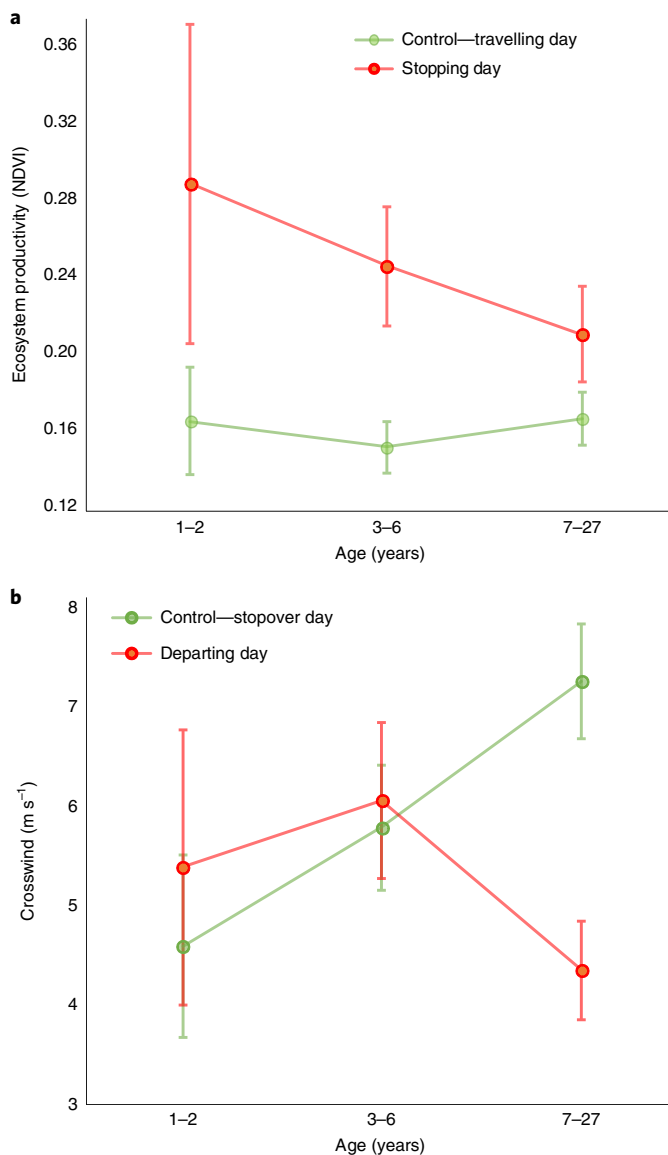


Fig. 3 | Migrating black kites strategically interrupted and restarted their journeys on the basis of wind conditions and local food availability, as estimated by ecosystem productivity (NDVI). a, b. Such strategic decisions changed with age. Younger kites selected stopover sites with higher food availability than adults ($N=281$ days from 47 individuals) (**a**), while adult kites were better capable to restart their journeys with more favourable crosswinds ($N=223$ days from 47 individuals) (**b**), which allowed them to better exploit stopovers as wind-negotiation tools that reset the favourability of their travelling condition. Error bars represent 1 s.e.m. All tests were two-sided and can be found in Supplementary Table 1b.13 (**a**) and 1c.18 (**b**).

age, tailwind and the lateral drift accumulated so far; juveniles and young adults had higher rates of advancement than adults when they were already drifting substantially (Supplementary Table 2b.51).

Temporary travelling interruptions of up to 15 days were integral to an overall strategy of wind negotiation but also depended on food availability. All kites interrupted their journey with more eastward and stronger crosswinds and headwinds (Supplementary Table 1b.8–10), but juveniles and young adults more frequently used stopover sites with higher ecosystem productivity (Supplementary Table 1b.13 and Fig. 3a), probably because their lower foraging proficiency made them more exigent. This would allow adults a

more flexible capability to stop as soon as wind conditions deteriorated. Adults were also more capable than younger kites to restart their journey with more favourable crosswinds (Supplementary Table 1c.18 and Fig. 3b), while all individuals retook their journeys with stronger tailwinds (Supplementary Table 1c.16). Thus, kites exploited stopovers as emergency pauses that reset their travelling conditions to more favourable values. For example, on average, crosswind interference declined by 33.6% and tailwind support increased by 79.1% between the beginning and end of a stopover, and adults were better capable to exploit such advantage.

What shaped the age improvements in wind negotiation? The drift response (slope of drift on crosswind) improved (became less negative) with age within an individual in the initial years of life (Fig. 4a) but not significantly so (Supplementary Table 3a). Instead, selective mortality removed from the population those individuals that drifted more (Supplementary Table 3c), especially at younger ages (Fig. 4c). For advancement, the slope response to tailwinds did not vary through time within the individual (Supplementary Table 3b and Fig. 4b), but kites with faster advancement rates suffered higher mortality (Supplementary Table 3d), especially at younger ages (Fig. 4d). Thus, orientation strategies were mainly subject to survival selection.

Apart from a lower ecosystem productivity, travelling conditions were substantially more favourable in the post-breeding migration (northern autumn), with an average improvement of 42% in crosswinds, 126% in tailwinds and 39% in uplift (Supplementary Table 4). Furthermore, younger individuals had more opportunity to travel together with more experienced adults than in spring¹⁶. This resulted in a generally easier, shorter journey with fewer stopovers^{15,16}. The only aging change in wind negotiation was the capability of older kites, also observed in the pre-breeding migration, to exploit current drift in order to compensate for past accumulated drift (Supplementary Table 5a.16 and Supplementary Fig. 5). This had potential cascading effects on wintering distribution because the lateral drift accumulated by an individual at the end of its journey affected its longitude of arrival (Supplementary Table 3.e), which in turn affected the mean longitude of its initial wintering area (Supplementary Table 3.f). Thus, the prevailing trade winds²³ promoted more westward arrival and wintering areas for juveniles (Supplementary Table 3.e and 3.f), which were less capable to correct their accumulated drift. The effect remained significant also when using the whole wintering period (likelihood ratio test = 10.1, $P < 0.018$, $\Delta\text{AICc} = 3.5$), but the signal was predictably weaker ($R^2 = 9.9$; rationale in Methods). These results suggest a mechanism by which selection, via its effect on drift negotiation, could modulate the age-dependent spread of wintering areas, thus shaping the connectivity of migrants to their non-breeding quarters²⁶. These carryover repercussions of drift could apply even more to species with more static and restricted wintering areas (that is, that stay all winter where they land). Finally, the drift and advancement slopes of the post-breeding migration did not change within an individual and had no repercussion on its subsequent survival.

Overall, the challenge of highly interactive, ever-changing atmospheric agents promoted a predictable development of context-dependent, instantaneous and delayed tactics, whose efficiency improved more slowly than previously appreciated through several initial years of life. The large displacements of younger individuals were probably caused by maladaptive drift, given that they entailed clear risks (for example, drifting towards the Sahara interior) and led to higher mortality. The adults that passed such a mortality filter were capable to compensate or partially compensate for their current and past drift, to resist risky displacements in a direction-sensitive manner and to reset the favourability of their travelling conditions through strategic exploitation of emergency stopovers. These compensatory and adaptive drift tactics implied that kites became progressively more capable to detect cross-flow strength and direction,

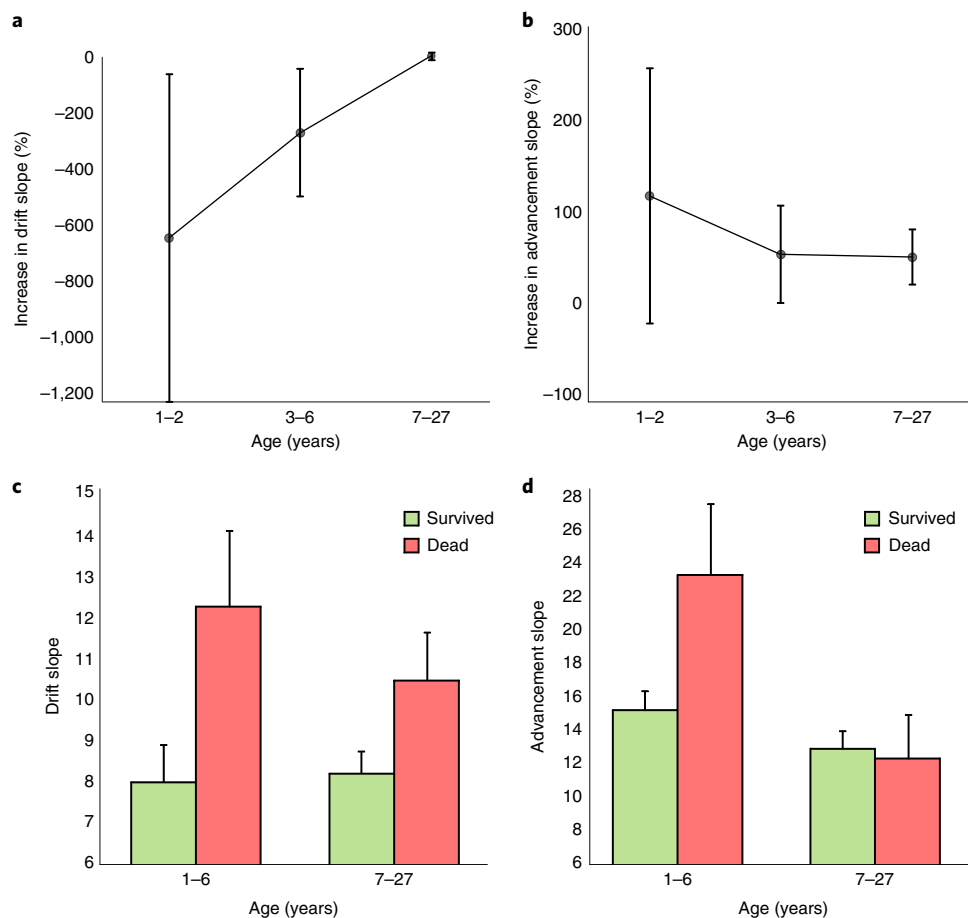


Fig. 4 | Individual improvements in wind-negotiation capabilities by migrating black kites and their mortality consequences. **a, b**, Within each individual migrant, the capability to compensate for drift improved at younger ages and stabilized at older ages (**a**), while the effect of tailwinds on advancement did not vary through life (**b**). **c, d**, Individuals more capable to compensate for drift (with lower drift slopes) (**c**) and less dependent on tailwind support (with lower advancement slopes) (**d**) survived better, especially at younger ages, implying that wind-negotiation strategies were subject to mortality selection. Error bars represent 1 s.e.m. Sample size was $N = 65$ and 57 (data from 33 kite individuals) for **a** and **b** and $N = 126$ and 123 (data from 64 kite individuals) for **c** and **d**. All tests were two-sided and can be found in Supplementary Table 3a.1 (**a**), 3a.3 (**b**), 3a.5 (**c**) and 3a.7 (**d**). Box plot versions of **c** and **d** are shown in Supplementary Figs. 6 and 7.

estimate their displacement and correct their orientation accordingly, implying the gradual integration of a map sense and/or key landmarks to attain true goal-oriented navigation^{1,10,14}. The slow, gradual development and mortality costs of acquiring such abilities by juveniles and young adults underpin their complexity and may contribute to the explanation of why long-lived migrants often defer the challenge of their first pre-breeding migration to the second or third year of life^{1,18}.

While a complementary role of individual learning cannot be fully excluded (Fig. 4a), for the first time we show that wind-negotiation and orientation strategies were under strong survival selection, an assumption commonly posed in migration biology^{3,4,27,28} but still in need of empirical support. Survival selection promoted individuals more capable of drift compensation, that suffered less from headwind conditions and that advanced slower for a given level of tailwind, which may have allowed them to save more energy and safeguard their condition upon arrival^{24,29–31}. This implied fitness advantages for cautious migrants that were more ‘in control’ of wind conditions rather than ‘blown by the wind’ and that probably traded rapid advancement for lower lateral displacements, risks and energy consumption. Such selection for slow and prudent advancement complemented the benefits of early departure that allowed adult kites to arrive earlier than younger ones, despite

travelling slower^{15,16}, leading to an overall strategy that simultaneously safeguarded the three pillars of optimal migration: time, energy and safety^{6,27}.

In conclusion, the challenges and opportunities by an ever-changing atmosphere generated a delicate balance between maladaptive decisions and proficient wind exploitation that gradually shifted with age to produce an eventually flexible strategy that varied with flow characteristics, the safety risks of potential displacements, the trophic profitability of traversed landscapes and the previous performance of the migrant along the journey. This necessarily multi-faceted and context-dependent flexibility within a single population may explain the variety of apparently conflicting results on flow negotiation mostly obtained by studying individuals of all ages over small portions of a route^{3,12}. Given that climate change will frequently alter flow regimes^{32,33}, impacts on migrants will be hard to forecast given the interactive nature of multiple atmospheric agents (Supplementary Tables 2 and 5) and will depend on the extent to which the current negotiation flexibility of a population can absorb such changes or be reshaped by natural selection quickly enough to accommodate them. In this sense, the higher variability of routes and responses by younger individuals may increase resilience by maintaining options that could become favoured in the future, as postulated by the ‘serial residency hypothesis’²⁶.

When present, climate impacts are likely to become suddenly apparent above certain thresholds of flow alteration, as they could initially hide behind the erosion of the younger portion of a population, more liable to environmental impacts. For migrating animals, tight selection for flow negotiation is likely to impose strong links between migratory strategies, fitness, demography and distribution. As a consequence, environmental and climate changes affecting migratory flyways are likely to impose disproportionate impacts on migrants, an aspect that we are just starting to uncover^{34–36}.

Methods

This study is complementary to a previous evaluation of age-related effects¹⁶. In the previous analysis, we focused on the performance of different-aged individuals averaged over an entire migratory journey, while here we focus on their daily wind-negotiation decisions. Because many of the methods are similar, here we present a shortened version and refer to ref. ¹⁶ for more detail.

GPS satellite marking. More than 4,000 black kites have been marked with metal and plastic rings as nestlings in Doñana National Park in past decades, so a large portion of the population is composed of individuals of known ages^{21,37}. This enabled us to deploy GPS satellite tags (model PTT-100 Solar Argos/GPS PTT, manufactured by Microwave Telemetry) on 90 kites of known age (1 to 27 years old) between March and June 2008–2012 (>1,300 h of selective trapping). The transmitters weighed 22 grams (<3% of the body mass) and had a declared lifespan of 3 years³⁸, but some were still functioning after five years. All PTTs had the same set-up, and received GPS locations eight times per day scattered throughout the day. Transmitters were attached as backpacks through a Teflon harness³⁹, which had no detectable impact on body condition, foraging performance, breeding output, survival, recruitment and longevity or on the capability to raise healthy offspring³⁸.

Annotated environmental variables. To investigate wind negotiation, we obtained data on wind conditions and a number of key environmental and atmospheric variables that could affect departure decisions, travelling tactics and refuelling opportunities, such as thermal convection, changes in barometric pressure and the potential availability of trophic resources. For each GPS location, environmental and atmospheric data were extracted for the grid value that was closest to the animal position in both space and time, so that the two could be realistically matched. All meteorological variables were derived from the Copernicus Climate Change Service (C3S) Climate Data Store⁴⁰ (accessed 9 January 2021).

Wind conditions were estimated through east–west U winds (positive values for eastward-directed winds) and north–south V winds (positive values for northward-directed winds), available on a hourly scale at a 0.25° resolution. U winds and V winds were combined into a single vector incorporating wind strength and direction. We have previously shown that kites migrate at a mean elevation of 1,655 m above sea level over the Atlas Mountains of Morocco and at 868 m over the lowland rest of the route¹⁶. Thus, we annotated wind data for a pressure level of 850 hPa (~1,500 m elevation) for all locations above the Atlas Mountains and for a pressure level of 925 hPa (~750 m elevation) for the rest of the route.

Migratory movements of soaring birds can be affected by three types of air motion: (1) vertical movements of air masses, usually convective uplift in thermals; (2) horizontal winds oriented along the axis of migration (axial winds, composed of tailwinds or headwinds); and (3) horizontal winds oriented transversally to the main axis of migration and potentially causing drift (crosswinds)^{14,41,42}. To estimate thermal uplift, we employed the convective velocity scaling coefficient w^* (hereafter, 'lift') previously used in other studies on soaring migrants^{42–44} and calculated as $w^* = (gzHT^{-1})^{1/3}$, where g is the gravitational acceleration, z the mean flight elevation, H the surface sensible heat flux and T the potential temperature in Kelvin.

Forward and lateral wind components were assessed by: (1) estimating the 'intended direction' of the birds at each location (see below) and (2) calculating the forward and perpendicular components of the wind vector along the intended direction, following refs. ^{14,41} (see below). Estimating the desired direction of a migrant is difficult, and various methods have been employed^{41,42,45}. Here we assume that in long-lived species, endogenous programmes and route familiarity over several journeys will lead to migrants having a sense of where they want to go throughout the journey. Thus, given the large number of tracked individuals, we used the mean direction of the population at any one location as the intended heading for all birds. Therefore, we: (1) divided the migration region into a grid of 444 × 444 km quadrants (~4°) and (2) calculated the mean heading of tracked birds in each quadrant. First-time migrants were included in these calculations despite their unfamiliarity with the route because their exclusion did not change the desired bearings (mean difference of 0.1°). All heading calculations were based on circular statistics⁴⁶ and implemented through the 'CircStats' package in R⁴⁷. In a few exceptional cases, using the mean quadrant headings was impossible because a quadrant contained a single individual or resulted in biologically unlikely desired directions (for example, kites crossing the Mediterranean out of the Strait

of Gibraltar, which was never accomplished by tagged kites). In these cases, we imposed the heading of the most direct terrestrial route to the most obvious next migratory goal. For example, for the individual that ended up in the Mediterranean coast of Algeria far to the east of any other individual in the northern migration (Fig. 1b), we imposed as desired heading the most direct terrestrial heading to the average crossing point of the Strait of Gibraltar along the Moroccan coast.

Data on barometric pressure were collected for three reasons: (1) changes in pressure can forecast alterations of wind and thermal conditions over the coming days^{23,44}, (2) birds are capable of detecting even small changes in pressure⁴⁸ and (3) previous studies have linked changes in pressure with departure tactics by migratory birds^{49–51}. Thus, we fitted changes in pressure to our models on departure decisions. Pressure gradients were estimated as the mean difference in sea level pressure between the target day and each of the previous four days.

Finally, we used the NDVI index of primary productivity⁵² (hereafter, food availability or ecosystem productivity) to estimate the favourability of feeding conditions along the route. We assume that in arid and semi-arid environments, such as those travelled by our species, high primary productivity is a good surrogate of food availability for herbivores and thus for insectivores and higher predators, as shown by several previous studies^{53–56}. NDVI values were annotated at a 250 m spatial resolution from <https://lpdaac.usgs.gov/products/myd13q1v006/>.

Statistical analysis. Throughout, we ran separate analyses for the pre-breeding (northward) and post-breeding (southward) migrations because these impose different environmental conditions and fitness consequences for this population^{15,16}. We used a series of multi-variate models to study how kites departed, travelled or halted their migration for a stopover in relation to cross flows and other potentially relevant variables that could interact with cross flows (wind-negotiation models; Supplementary Tables 1, 2, 5 and 6). In these models, the sample unit was a whole day of tracking data. To characterize the environmental conditions of a day, we averaged them over all the diurnal GPS locations available for that day but gave double weight to the GPS fixes recorded between 11:00 and 15:00 (following ref. ⁴¹) because these are the hours of maximum travelling speed and progression when we would expect wind effects to be strongest. For this reason, days that lacked GPS data in the centre of the day were removed from analysis.

To estimate the daily lateral drift (hereafter, drift) and forward advancement of an individual in the intended direction (hereafter, advancement), we calculated the forward and perpendicular components of the daily displacement of an individual along the intended direction (km d⁻¹) (refs. ^{14,41}), through the formulas: tailwind = $\omega \{ \cosine [\text{radians}(\alpha - d)] \}$ and crosswind = $\omega \{ \text{sine} [\text{radians}(\alpha - d)] \}$, where ω = wind speed, α = wind direction and d = intended direction. These daily components were calculated from midnight of one day to midnight of the following day. Because kites travelled exclusively by day, these estimates incorporated the whole daily displacements experienced by kites during successive steps of a journey separated by staging, stationary night periods. Thus, the analyses centred on how a migrating individual woke up each day and negotiated that day's conditions to progress towards its goal. As a convention, crosswinds and drift had positive values when oriented towards the right of a bird flying in its intended direction and negative towards its left. Axial winds and forward advancement were positive with favourable tailwinds and with progress along the intended direction and negative with opposing headwinds and in the case of return movements in the opposite of the desired direction.

We used linear mixed models (LMMs)⁵⁷ to test the effect of crosswinds on drift, following the method originally proposed by ref. ¹⁴ and commonly used in other drift studies^{41,58–60} (Supplementary Tables 2 and 5). By this method, a steeper slope of crosswinds on drift implies progressively higher levels of drift (larger lateral displacements imposed by stronger cross flows) with a slope of 1 corresponding to full drift, a flat slope of 0 corresponding to full compensation and in-between values corresponding to partial drift (also equivalent to partial compensation) (Fig. 1). To test whether drift was driven by more comprehensive strategies than a simple univariate response to crosswinds, we also fitted the following covariates, chosen on the basis of previous theoretical and empirical studies in migration biology:

1. Tailwinds, thermal uplift and food availability, employed as the other main determinants of flying conditions and foraging opportunities for a fly-and-forage soaring migrant.
2. Wind direction, because cross flows may entail asymmetric risks depending on their orientation (for example, more dangerous if they drifted kites towards the unsafe Sahara interior)^{41,59,61}.
3. Changes in wind direction (from positive to negative and vice versa from one day to the next) because these were hypothesized to challenge wind negotiation by complicating flight through wind turbulence and shear and by disorienting migrants, who had to reorient their heading to obtain the same compensatory effect of the previous day^{44,62,63}.
4. Broad geographical zone, because certain regions could affect wind negotiation more than others because of differential landmark availability, stronger flows or higher risks involved⁴¹. For example, the Sahara Desert represented a particularly dangerous area because of its high temperatures, strong winds and low food availability, while the upper part of the route in

northern Morocco–southern Spain had an almost constant availability of landmarks given its constant proximity to coastlines and mountains. Thus, we divided the journey region in three macro-sectors: the Sahara Desert and the regions to its north (Atlas Mountains of Morocco up to southern Spain) and to its south (Sahel of West Africa). This also allowed examination of the hypothesis that kites could drift more at the beginning of their journey and compensate at the end or vice versa³⁸.

- The drift accumulated so far along the journey (hereafter, accumulated drift), because an individual could adjust its current negotiation to its previous cumulative performance^{36,64}. Thus, for each individual on each day, we summed the drift of all its previous travelling days. Note that an individual that had previously drifted to the right and left of the desired direction in a balanced way would accumulate a zero net displacement despite drifting even strongly over certain portions of the route.
- The lateral displacement of a travelling individual compared with the mean route of the population (hereafter, lateral position), because kites could have a sense of where they are compared with their ideal (population mean) position and negotiate wind to approach such route. Thus, we calculated the horizontal displacement of each kite from the population mean route, estimated by averaging the longitude coordinates of all tracks along 0.1° latitudinal increments (calculated separately for the pre- and post-breeding migration)¹⁶.

We discarded from drift analysis all days in which kites operated return movements (travelled in the opposite of the desired direction) in response to strong headwinds because the intended goal direction for calculating lateral flows and displacements became equivocal. We also discarded travelling days too close to the ocean coastline, as done by previous authors¹⁴, because no kites ever drifted into the ocean and because migrants near coastlines are usually more buffered from drift¹. We reasoned that kites close to the ocean coastline but subject to westward crosswinds were not as 'free' to respond to drift as kites travelling more inland. Therefore, to minimize statistical noise and to avoid complicating the model with interactions that applied to a minority of cases, we discarded from analysis all days with westward crosswinds: (1) below 33.7° latitude N and within 70 km of the coastline or (2) between 33.7° and 35.6° latitude N and within 20 km of the coastline. The lower cut point of 20 km for the upper part of the route was chosen because larger values would have removed all travelling days because of local geography. The cut points were arbitrarily chosen to minimize statistical noise without removing whole zones of migration. Finally, we discarded all days in which kites crossed the ~20 km sea stretch of the Strait of Gibraltar because the small spatio-temporal scale of such crossings (<1 h) was incompatible with the daily scale of this assessment.

Similarly, we used LMMs to test the effect of axial winds (tailwinds and headwinds) on forward advancement^{44,41} (Supplementary Tables 2 and 5). In this analysis, the regression slope indicates the advancement rate for a given level of axial wind support and the intercept indicates the advancement achieved under windless conditions. Again, we fitted all the covariates above to test whether advancement also responded to geographic zone, past performance and broader environmental conditions. For both models on drift and advancement, the results were the same whether fitting the identity of an individual, the identity of a track (a migration journey, for example, the pre-breeding migration of an individual in 2012) or the year as random terms, individually or in combination. Therefore, for simplicity, we show the models with only track identity as a random term. To take into account temporal auto-correlation, we incorporated an autoregressive correlation structure into the models by fitting various R correlation functions (for example, 'corAR1', 'corSpher', 'corLin', 'corRatio', 'corGaus', 'corExp') to the maximal model and retaining the one with the lowest AICc, following ref. ⁵⁷.

To investigate whether wind selectivity during departure contributed to the overall strategy of wind negotiation, we used a generalized mixed linear model (logistic GLMM with binomial errors and a logit link function⁵⁷) to compare the conditions of the first travelling day of migration with the conditions of a day randomly chosen among the eight days preceding departure (Supplementary Tables 1 and 6). The eight-day cut point was chosen because this was the average difference in departure date between a year and the next within the same individual. Thus, we hypothesized that each individual could select favourable conditions for departure within an approximate eight-day time window. To examine the decision rules for interrupting the journey for a stopover stage and re-taking it afterwards, we used a logistic GLMM to compare the conditions of the day in which a kite started a stopover (or re-departed for migration from a stopover) with the conditions of the previous two days defined as control—travelling days (or control—stopover days).

To test whether wind-negotiation strategies changed with age through individual improvements or selective mortality, we: (1) calculated the slope of crosswind on drift or of axial wind on advancement for every migration episode of an individual, as an estimate of its negotiation response to the wind flow encountered en route (for example, its compensatory capability under different cross flow conditions); (2) computed the percentage change in slope between one year and the next for that individual, calculated as: $(X_{t+1} - X_t)/X_t$, where X is the slope and t the year; (3) tested whether such changes in slope varied with age by means of a LMM (consistent with within individual improvements) with individual

identity as a random term; and (4) examined whether the slope of a migration episode affected the survival of an individual over the following six months (that is, before the next migration episode, consistent with mortality selection) by means of a logistic GLMM with random effects for individual identity and age class (Supplementary Table 3). The period of six months was chosen in order to incorporate mortality imparted during migration itself or by potential carryover effects, while excluding the following migration episode. Mortality events versus continued survival were assessed by GPS data and ring readings, demonstrating a moving-alive individual, and by detecting deaths and differentiating them from tag failure through a method of inspection of tag diagnostic data allowing 100% correction in death identification^{21,65}. In step 1 of the procedure above, we discarded slopes calculated on excessively low sample sizes (<7 travelling days) or based on excessively favourable, non-challenging winds throughout the journey (that is, always <5 m s⁻¹) because these could generate flat slope artefacts.

To examine whether the lateral displacements accumulated in the post-breeding migration could carry over to shape the longitude of a migrant's wintering area, we built two LMMs (with individual identity as a random effect) that tested: (1) whether the drift accumulated en route and age affected the longitude of arrival and (2) whether such longitude of arrival and age affected the mean longitude of the wintering distribution of an individual (mean longitude of all GPS fixes) (Supplementary Table 3). Because in this population some individuals operate a second migration further southeast about two months after arrival, we calculated the mean wintering longitude over the initial two months after arrival. The effect of arrival longitude on wintering longitude remained significant also when using the whole wintering period, but the signal was predictably weaker (Results).

Because we expected kites to respond in an age-structured way to the whole atmosphere in an integrated manner rather than to a single factor at a time, we fitted to the wind-negotiation models: (1) the two-way interactions among crosswind or axial winds and the other explanatory variables; (2) the two-way interactions between age and each of the other explanatory variables and (3) the three-way interactions between age, crosswind (or axial wind) and each of the other explanatory variables. Black kites pass through sequential life stages based on the attainment of breeding status and the start of senescence, corresponding to variations in breeding performance and survival^{17,21,22,37}. For this reason, we fitted age both as a continuous variable and a factorial variable with the following levels: (a) age 1–2 years (youngest individuals; they almost never breed and mostly remain in Africa during the breeding months); (b) age 3–6 years (young adults attempting to establish a territory or during their initial, usually unsuccessful breeding attempts); (c) age 7–11 years (prime age of maximum breeding and survival rates); and (d) age 12–27 years (senescent stage with lower breeding and survival rates). Note that the composition of the youngest class was modified between seasons to separate first-time migrants from the rest and maintain coherence; in the post-breeding migration, this class included only fledglings in their first southward journey. However, because approximately two thirds of the individuals delayed their first return to Europe beyond their first year of age, for the northern spring we pooled ages 1–2 years, as they both included individuals on their first return migration. When testing age effects, we were interested to see whether age was best modelled as a linear predictor, as a quadratic effect or as a factor. To determine which form of the variable gave the best fit, we: (1) fitted each of the three alternatives to the maximal model and used the one which gave the best AICc-value and (2) once a final model was reached, compared again the AICc of the final model built with the alternative forms of the age effect. When multiple forms were equally plausible, we retained age as a linear predictor to simplify model outputs, given the large number of interactions in the models. For visual clarity, in the graphs, we depict age variation by dividing it into sequential, categorical life stages, but we pooled the prime and senescent stage because these were always extremely similar and caused unnecessary visual clogging of some already complex figures.

All continuous variables were standardized before being fitted to mixed models. However, descriptive estimates of drift and advancement slopes and intercepts given in the text were calculated with unstandardized values to conform with previous studies^{14,41}. Mixed models were built through a backward stepwise procedure following ref. ⁵⁷; all explanatory variables were fitted to a maximal model, extracted one at a time, and the associated change in model deviance was assessed by a likelihood ratio test; at each step, we also calculated the AICc of each model and considered as the final competitive model the one with the lowest AICc containing only significant terms. Variables with $0.05 < P < 0.1$ in the likelihood ratio test were considered as marginally significant. Throughout, we assessed collinearity through variance inflation factor (VIF) values, which were always <1.5 (ref. ⁵⁷). Model assumptions were checked by looking at QQ (quantile-quantile) plots, histograms of residuals and plots of standardized and normalized residuals against fitted values and against explanatory variables or by incorporating variance structures VarIdent or VarFixed^{57,66}. All R^2 values were calculated according to ref. ⁶⁷. All models were implemented in R.3.6.2 (ref. ⁴⁷), all tests were two-tailed, statistical significance was set at $\alpha < 0.05$ and all means are given ± 1 s.e.m. All figures display raw aggregated data. The study was conducted in accordance with the national and European laws concerning the use of animals for scientific purposes (protocols EBD-11/09 and EBD-11/25 approved

by the Animal Care and Bio-Ethics Sub-Committee of the Consejo Superior de Investigaciones Científicas - CSIC).

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Data are available from DIGITAL.CSIC at <https://doi.org/10.20350/digitalCSIC/14652>.

Received: 30 September 2021; Accepted: 20 April 2022;

Published online: 09 June 2022

References

- Newton, I. *The Migration Ecology of Birds* (Academic Press, 2008).
- Dingle, H. *Migration: The Biology of Life on the Move* (Oxford Univ. Press, 1996).
- Chapman, J. W. et al. Animal orientation strategies for movement in flows. *Curr. Biol.* **21**, R861–R870 (2011).
- Alerstam, T. Wind as a selective agent in bird migration. *Ornis Scand.* **10**, 76–93 (1979).
- Berthold, P. *Bird Migration: A General Survey* (Oxford Univ. Press, 2001).
- Alerstam, T. & Lindstrom, A. in *Bird Migration: Physiology and Ecophysiology* (ed. Gwinner, E.) 331–351 (Springer, 1990).
- Chapman, J. W. et al. Wind selection and drift compensation optimize migratory pathways in a high-flying moth. *Curr. Biol.* **18**, 514–518 (2008).
- Hays, G. C. et al. Route optimisation and solving Zermelo's navigation problem during long distance migration in cross flows. *Ecol. Lett.* **17**, 137–143 (2014).
- Chapman, J. W. et al. Adaptive strategies in nocturnally migrating insects and songbirds: contrasting responses to wind. *J. Anim. Ecol.* **85**, 115–124 (2016).
- Alerstam, T. Optimal bird migration revisited. *J. Ornithol.* **152**, 5–23 (2011).
- Alerstam, T. & Hedenström, A. The development of bird migration theory. *J. Avian Biol.* **29**, 343–369 (1998).
- Shamoun, J., Felix, B. & Wouter, L. Atmospheric conditions create freeways, detours and tailbacks for migrating birds. *J. Comp. Physiol. A* **203**, 509–529 (2017).
- Liechti, F. Birds: Blowin' by the wind? *J. Ornithol.* **147**, 202–211 (2006).
- Thorup, K., Alerstam, T., Hake, M. & Kjellén, N. Bird orientation: compensation for wind drift in migrating raptors is age dependent. *Proc. R. Soc. B* **270**, 8–11 (2003).
- Sergio, F. et al. Migration by breeders and floaters of a long-lived raptor: implications for recruitment and territory quality. *Anim. Behav.* **131**, 59–72 (2017).
- Sergio, F. et al. Individual improvements and selective mortality shape lifelong migratory performance. *Nature* **515**, 410–413 (2014).
- Sergio, F., Blas, J. & Hiraldo, F. Predictors of floater status in a long-lived bird: a cross-sectional and longitudinal test of hypotheses. *J. Anim. Ecol.* **78**, 109–118 (2009).
- Bildstein, K. L. *Migrating Raptors of the World: Their Ecology and Conservation* (Cornell Univ. Press, 2006).
- Zalles, J. I. & Bildstein, K. L. *Raptor Watch: A Global Directory of Raptor Migration Sites* (Birdlife International, 2000).
- Kerlinger, P. *Flight Strategies of Migrating Hawks* (University of Chicago Press, 1989).
- Sergio, F. et al. When and where mortality occurs throughout the annual cycle changes with age in a migratory bird: individual vs population implications. *Sci. Rep.* **9**, 17352 (2019).
- Sergio, F. et al. Raptor nest decorations are a reliable threat against conspecifics. *Science* **331**, 327–330 (2011).
- Parker, D. & Diop-Kane, M. *Meteorology of Tropical West Africa: The Forecaster's Handbook* (2017).
- Liechti, F., Hedenström, A. & Alerstam, T. Effects of sidewinds on optimal flight speed of birds. *J. Theor. Biol.* **170**, 219–225 (1994).
- Liechti, F. & Bruderer, B. The relevance of wind for optimal migration theory. *J. Avian Biol.* **29**, 561–568 (1998).
- Cresswell, W. Migratory connectivity of Palaearctic–African migratory birds and their responses to environmental change: the serial residency hypothesis. *Ibis* **156**, 493–510 (2014).
- Alerstam, T., Hedenström, A. & Åkesson, S. Long-distance migration: evolution and determinants. *Oikos* **103**, 247–260 (2003).
- Bowlin, M. S. et al. Grand challenges in migration biology. *Integr. Comp. Biol.* **50**, 261–279 (2010).
- Mitchell, G. W., Woodworth, B. K., Taylor, P. D. & Norris, D. R. Automated telemetry reveals age specific differences in flight duration and speed are driven by wind conditions in a migratory songbird. *Mov. Ecol.* <https://doi.org/10.1186/s40462-015-0046-5> (2015).
- Rotics, S. et al. The challenges of the first migration: movement and behaviour of juvenile vs. adult white storks with insights regarding juvenile mortality. *J. Anim. Ecol.* **85**, 938–947 (2016).
- Horvitz, N. et al. The gliding speed of migrating birds: slow and safe or fast and risky? *Ecol. Lett.* **17**, 670–679 (2014).
- Reichler, T. *Changes in the Atmospheric Circulation as Indicator of Climate Change* (Elsevier, 2009).
- Kling, M. M. & Ackerly, D. D. Global wind patterns and the vulnerability of wind-dispersed species to climate change. *Nat. Clim. Change* **10**, 868–875 (2020).
- Drake, A., Rock, C. A., Quinlan, S. P., Martin, M. & Green, D. J. Wind speed during migration influences the survival, timing of breeding, and productivity of a neotropical migrant, Setophaga petechia. *PLoS ONE* **9**, e97152 (2014).
- Newton, I. Can conditions experienced during migration limit the population levels of birds? *J. Ornithol.* **147**, 146–166 (2006).
- Loonstra, A. H. J., Verhoeven, M. A., Senner, N. R., Both, C. & Piersma, T. Adverse wind conditions during northward Sahara crossings increase the in-flight mortality of black-tailed godwits. *Ecol. Lett.* **22**, 2060–2066 (2019).
- Blas, J., Sergio, F. & Hiraldo, F. Age-related improvement in reproductive performance in a long-lived raptor: a cross-sectional and longitudinal study. *Ecography* **32**, 647–657 (2009).
- Sergio, F. et al. No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring. *J. Appl. Ecol.* **52**, 1665–1675 (2015).
- Kenward, R. *A Manual for Wildlife Radio Tagging* (Academic Press, 2001).
- Hersbach, H., et al. ERA5 hourly data on pressure levels from 1979 to present. Copernicus Climate Change Service Climate Data Store <https://doi.org/10.24381/cds.bd0915c6> (2018).
- Klaassen, R. H. G., Hake, M., Strandberg, R. & Alerstam, T. Geographical and temporal flexibility in the response to crosswinds by migrating raptors. *Proc. R. Soc. B* **278**, 1339–1346 (2011).
- Bohrer, G. et al. Estimating updraft velocity components over large spatial scales: contrasting migration strategies of golden eagles and turkey vultures. *Ecol. Lett.* **15**, 96–103 (2012).
- Shannon, H. D., Young, G. S., Yates, M. A., Fuller, M. R. & Seegar, W. S. Measurements of thermal updraft intensity over complex terrain using American white pelicans and a simple boundary-layer forecast model. *Bound. Layer Meteorol.* **104**, 167–199 (2002).
- Stull, R. B. *An Introduction to Boundary Layer Meteorology* (Springer, 1988).
- Safi, K. et al. Flying with the wind: scale dependency of speed and direction measurements in modelling wind support in avian flight. *Mov. Ecol.* **1**, 1–13 (2013).
- Batschelet, E. *Circular Statistics in Biology* (Academic Press, 1981).
- R Core Team. *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, 2019).
- O'Neill, P. Magnetoreception and baroreception in birds. *Dev. Growth Differ.* **55**, 188–197 (2013).
- Bingman, V.P. and Moore, P. in *Aeroecology* (eds. Chilson, P. B. et al.) 119–143 (Springer International Publishing, 2017).
- Liechti, F. and McGuire, L. P. in *Aeroecology* (eds. Chilson, P. B. et al.) 179–198 (Springer International Publishing, 2017).
- Richardson, W. J. Wind and orientation of migrating birds: a review. *EXS* **60**, 226–249 (1991).
- Pettorelli, N. et al. Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends Ecol. Evol.* **20**, 503–510 (2005).
- Dodge, S. et al. Environmental drivers of variability in the movement ecology of turkey vultures (*Cathartes aura*) in North and South America. *Philos. Trans. R. Soc. B* **369**, 20130195 (2014).
- Schaub, M., Kania, W. & Köppen, U. Variation of primary production during winter induces synchrony in survival rates in migratory white storks *Ciconia ciconia*. *J. Anim. Ecol.* **74**, 656–666 (2005).
- Despland, E., Rosenberg, J. & Simpson, S. J. Landscape structure and locust swarming: a satellite's eye view. *Ecography* **27**, 381–391 (2004).
- Trierweiler, C. et al. A Palaearctic migratory raptor species tracks shifting prey availability within its wintering range in the Sahel. *J. Anim. Ecol.* **82**, 107–120 (2013).
- Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. *Mixed Effects Models and Extensions in Ecology with R* (Springer, 2009).
- Sapir, N., Horvitz, N., Dechmann, D. K. N., Fahr, J. & Wikelski, M. Commuting fruit bats beneficially modulate their flight in relation to wind. *Proc. R. Soc. B* **281**, 20140018 (2014).
- Becciu, P., Panuccio, M., Catoni, C., Dell'omo, G. & Sapir, N. Contrasting aspects of tailwinds and asymmetrical response to crosswinds in soaring migrants. *Behav. Ecol. Sociobiol.* **72**, 28 (2018).
- Klaassen, R. H. G. et al. Loop migration in adult marsh harriers *Circus aeruginosus*, as revealed by satellite telemetry. *J. Avian Biol.* **41**, 200–207 (2010).
- Strandberg, R., Klaassen, R. H. G., Hake, M. & Alerstam, T. How hazardous is the Sahara Desert crossing for migratory birds? Indications from satellite tracking of raptors. *Biol. Lett.* **6**, 297–300 (2010).

62. Pennycuik, D. J. *Modelling the Flying Bird* (Academic Press, 2008).
63. Shepard, E. L. C., Ross, A. N. & Portugal, S. J. Moving in a moving medium: new perspectives on flight. *Phil. Trans. R. Soc. B* **371**, 20150382 (2016).
64. Van Doren, B. M., Horton, K. G., Stepanian, P. M., Mizrahi, D. S. & Farnsworth, A. Wind drift explains the reoriented morning flights of songbirds. *Behav. Ecol.* **27**, 1122–1131 (2016).
65. Sergio, F., Tanferna, A., Blas, J., Blanco, G. & Hiraldo, F. Reliable methods for identifying animal deaths in GPS- and satellite-tracking data: review, testing, and calibration. *J. Appl. Ecol.* **56**, 562–572 (2019).
66. Crawley, M. J. *The R Book* (Wiley, 2013).
67. Nakagawa, S. & Schielzeth, H. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133–142 (2013).

Acknowledgements

We thank F.J. Chicano, F.G. Vilches, J.M. Giral and M. Anjos for help in the field, I. Afán and D. Aragónés of LAST-EBD for support with GIS analyses, the personnel of the Reserva Biológica de Doñana–ICTS for logistical help and accommodation, E. Palazuelos for preparing Supplementary Video 1 and F.J. Hernández for the kite drawing in Fig. 1. Part of the study was funded by Natural Research Ltd. and research projects CGL2008-01781 (F.S.), CGL2011-28103 (F.S.), CGL2012-32544 (J.B.) and PGC2018-095860-B-I00 (F.S.) of the Spanish Ministry of Science and Innovation/Economy and Competitiveness and FEDER funds; 511/2012 (J.B.) of the Spanish Ministry of Agriculture, Food and the Environment (Autonomous Organism of National Parks); JA-58 (F.S.) of the Consejería de Medio Ambiente de la Junta de Andalucía and by the Excellence Projects RNM 1790 (F.S.), RNM 3822 (F.S.), RNM 7307 (F.S.) and

P18-FR-4239 (F.S.) of the Junta de Andalucía. J.M.B. was supported by Generalitat Valenciana (CIDEGENT/2020/030).

Author contributions

F.S., A.T., J.B. and F.H. conducted fieldwork. F.S., A.T. and J.M.B. prepared the database, extracted and processed the environmental data from internet sources and analysed the data. F.S., J.B. and F.H. obtained funding. F.S., J.M.B., A.T., R.S., J.B. and F.H. took part in the conceptual planning of the study and in the preparation of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41559-022-01776-1>.

Correspondence and requests for materials should be addressed to Fabrizio Sergio.

Peer review information *Nature Ecology & Evolution* thanks Jason Chapman, Will Cresswell and two other, anonymous, reviewers for their contribution to the peer review of this work.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© The Author(s), under exclusive licence to Springer Nature Limited 2022

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our [Editorial Policies](#) and the [Editorial Policy Checklist](#).

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a Confirmed

- The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
- A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- The statistical test(s) used AND whether they are one- or two-sided
Only common tests should be described solely by name; describe more complex techniques in the Methods section.
- A description of all covariates tested
- A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
Give P values as exact values whenever suitable.
- For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

Data collection

Data analysis

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

The datasets generated and analysed during the current study are available from the corresponding author on reasonable request. They will be placed in a public repository as soon as the authors have finished publishing and exploiting them.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

Life sciences Behavioural & social sciences Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Statistical analysis of the tracking data of Black kites to study their wind negotiation strategies during migration, with particular emphasis on drift negotiation
Research sample	Black kite population of Doñana National Park. This is a unique population where all ages of a very long-lived bird can be sampled, allowing unique insight into how life history traits can vary with age from recently born individuals to 27 years old ones
Sampling strategy	The sample is based on 90 individuals, one of the largest available samples for tracking data, which allowed us to adequately sample all age classes in the population
Data collection	The birds were trapped and radio-tagged, after which the data were acquired by remote sensing (GPS locations collected and transferred to the researcher through the Argos-CLS satellite system)
Timing and spatial scale	Tags were deployed between 2008-2012 and data received between 2008-2014. The spatial scale incorporates a latitudinal range of about 2500 km, from southwestern Spain to the Sahel region of Mauritania-Mali (portrayed in the map of Fig. 1)
Data exclusions	Data from days with too few GPS locations to accurately portray the heading of a bird during a specific day (bearing from midnight of a day to the midnight of a following day) were excluded from analysis. For analyses of lateral drift, we deleted days with return movements (i.e. backward movements towards the opposite of the intended direction), as establishing an intended direction to estimate drift was impossible in these cases. We discarded travelling days too close to the ocean coastline, as done by previous authors, because no kites ever drifted into the ocean and because migrants near coastlines are usually more buffered from drift. We reasoned that kites close to the ocean coastline but subject to westward crosswinds were not as "free" to respond to drift as kites travelling more inland. Therefore, to minimize statistical noise and to avoid complicating the model with interactions that applied to a minority of cases, we discarded from analysis all days with westward crosswinds: (1) below 33.7 degrees latitude and within 70 km of the coastline; or (2) between 33.7 - 35.6 degrees latitude and within 20 km of the coastline. The lower cutpoint of 20 km for the upper part of the route was chosen because larger values would have removed all travelling days because of local geography. The cutpoints were arbitrarily chosen to minimize statistical noise without removing whole zones of migration. Finally, we discarded all days in which kites crossed the circa 20 km sea-stretch of the Strait of Gibraltar, because the small spatio-temporal scale of such crossings (< 1 hour) was incompatible with the daily-scale of this assessment.
Reproducibility	n/a. The paper is not based on an experiment.
Randomization	n/a. The paper is not based on an experiment.
Blinding	n/a. The paper is not based on an experiment.
Did the study involve field work?	<input checked="" type="checkbox"/> Yes <input type="checkbox"/> No

Field work, collection and transport

Field conditions	Fieldwork was implemented in Doñana National Park (south-western Spain), during the period March-June, exclusively under calm days with mild temperatures (10-20 degrees C) and no rain.
Location	Doñana National Park (36°56'51"N 6°21'31"W). Elevation = 1-33 m a.s.l
Access & import/export	All fieldwork complied with the regulations issued in the permits emitted by Doñana National Park, which include instructions on prohibited fieldwork activities, as also discussed in ad hoc reunions with the Park Authority. All fieldwork activities followed the bioethical procedures established by the relevant bio-ethical permits and legislature.
Disturbance	Each bird was quickly measured and radio-tagged upon GPS-marking. Comparison of the vital rates of the marked birds with those of control individuals of comparable age showed no effect of satellite-tagging on body condition, foraging performance, breeding output, survival, recruitment and longevity, or on the capability to raise healthy offspring. See details in: Sergio, F. et al. No effect of satellite tagging on survival, recruitment, longevity, productivity and social dominance of a raptor, and the provisioning and condition of its offspring. <i>J. Appl. Ecol.</i> 52, 1665–1675 (2015).

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

Methods

- | n/a | Involved in the study |
|-------------------------------------|---|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Antibodies |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Eukaryotic cell lines |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Palaeontology and archaeology |
| <input type="checkbox"/> | <input checked="" type="checkbox"/> Animals and other organisms |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Human research participants |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Clinical data |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Dual use research of concern |

- | n/a | Involved in the study |
|-------------------------------------|---|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> ChIP-seq |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Flow cytometry |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> MRI-based neuroimaging |

Animals and other organisms

Policy information about [studies involving animals](#); [ARRIVE guidelines](#) recommended for reporting animal research

Laboratory animals

n/a

Wild animals

We trapped 90 individual Black kites (*Milvus migrans*) of age 1-27 years old, by cannon-netting. Individuals were tagged in situ and released in the wild.

Field-collected samples

The study did not involve laboratory samples collected in the field.

Ethics oversight

The study was conducted in strict accordance with the national and European laws concerning the use of animals for scientific purposes (protocols EBD-11/09 and EBD-11/25 approved by the Animal Care and Bio-Ethics Sub-Committee of the CSIC)

Note that full information on the approval of the study protocol must also be provided in the manuscript.